

RESEARCH ARTICLE

Drought and growing season phenology over 35 years modulates species interactions among domestic and wild herbivores

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Abstract

1. Domestic animals represent the largest mammalian biomass on Earth, creating an urgent need to understand their effects on native species. Environmental change may further alter these interactions, particularly for large herbivores that are highly sensitive to climate-driven resource availability.
2. Interactions among assemblages of large herbivores include interference and exploitation competition, but the grazing optimization hypothesis paradigm suggests that interactions are often facilitative because defoliation from grazing stimulates compensatory regrowth of high-quality forage that benefits other species. We used 35 years of contemporaneous telemetry data on elk and domestic cattle to quantify spatial interactions within the context of climate-change-induced drought conditions.
3. We fit step-selection functions to assess the immediate response of elk to spatiotemporal cattle distribution and tested whether drought and phenological advancement of the growing season-mediated interactions. We also modelled elk selection for pastures that were ungrazed, currently grazed or previously grazed by cattle to assess competition and facilitation.
4. Our results refute the grazing optimization hypothesis and suggest elk are not attracted to areas previously grazed by cattle. Instead, elk avoided cattle throughout the entire growing season and at multiple scales. Elk were 2.9 times more likely to make movements to locations without cattle versus locations with 1 cow-calf pair/hectare, 23% less likely to use a pasture with cattle present, and 27% less likely to use one grazed by cattle earlier in the season, compared to an ungrazed pasture. After controlling for current season grazing status, elk were 30% less likely to use a pasture if it was grazed the previous year. Resource availability, influenced by growing season phenology and drought, mediated the magnitude of avoidance of cattle by elk. In the periods of most severe drought, elk

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reduced their avoidance of cattle ostensibly to seek out the remaining palatable forage regardless of cattle presence.

5. Increased overlap between domestic and wild ungulates should be anticipated as climate change continues to increase the intensity and frequency of drought, which may result in decreased weight gain or fitness consequences to both species, increased potential for disease transmission, and more encounters between predators and domestic livestock.

KEYWORDS

cattle, climate change, competition, elk, facilitation, grazing optimization hypothesis, step-selection function, ungulate

1 | INTRODUCTION

Domestic herbivores represent the largest biomass of mammals on Earth (Bar-On et al., 2018) and occur over a quarter of the planet's land where they co-occur with native species (Schieltz & Rubenstein, 2016). Understanding the nature of interactions between native and domestic species is critical given the fundamental role large herbivores play in terrestrial ecosystems via top-down control of vegetation, nutrient redistribution, and through trophic interactions that suppress smaller animals through competition and provision larger ones via predation (Pringle et al., 2023). In addition to their keystone role in ecosystems, large herbivores, particularly ungulates, are often abundant both in terms of species richness and biomass. The coexistence of many sympatric ungulate species reflects co-evolutionary processes between plants and herbivores as well as among herbivore species. Resource partitioning occurs through competition that drives divergence in foraging strategies, often structured along a grazing–browsing continuum (Gordon, 2003; Hofmann & Stewart, 1972). Yet interactions among ungulates are sometimes characterized by mutualistic relationships via facilitation in addition to competition (Bell, 1971; Sinclair & Norton-Griffiths, 1982). Facilitation occurs in ungulate guilds when larger-bodied species that favour forage quantity over quality reduce the standing biomass of lower-quality vegetation. According to the grazing optimization hypothesis (McNaughton, 1979), defoliation from grazing stimulates the growth of higher-quality vegetation that smaller-bodied ungulates are physiologically optimized to consume (Arsenault & Owen-Smith, 2002). Facilitative effects can occur within the same growing season or can have lagged effects that span across years (Arsenault & Owen-Smith, 2002; Frank & McNaughton, 1993). However, the generality of facilitative effects arising from defoliation through herbivory remains untested within a variety of environments and species assemblages.

When new herbivore species are introduced into existing ungulate communities, either through natural colonization or the introduction of domestic animals to wildlands, the addition of another consumer can alter species interactions. Just as interactions among native ungulate assemblages can range from positive to negative, so too can interactions between native and domestic herbivores.

Although numerous studies promote the notion that forage conditioning (i.e. improvements in forage quality following grazing) by domestic herbivores is ubiquitous (Alt et al., 1992; Anderson & Scherzinger, 1975; Frisina, 1992; Vavra & Sheehy, 1996), rigorous assessments are lacking, and even the best evidence is nuanced (Schieltz & Rubenstein, 2016). For example, domestic and native ungulates can synergistically deplete resources, even under strict management of domestic grazers, particularly in arid systems with lower productivity (Averett et al., 2019). Invasive plants are often introduced with domestic herbivores, and evidence is mixed as to whether native or domestic ungulates are more likely to consume and spread them (Bartuszevige & Endress, 2008). The potential for large impacts on native species, as well as the livelihoods of those depending on domestic livestock production, is particularly salient on public lands managed for multiple uses.

Among the most widespread and ecologically significant interactions among wild and domestic herbivore species in North America is the potential for competition and/or facilitation between elk (*Cervus canadensis*) and cattle (*Bos taurus*) which co-occur in rangelands and forests across millions of acres of public and private lands. Although these species are well studied, many questions remain about the generality, context, strength, and nature of their interactions (Kohl et al., 2023; Wisdom & Thomas, 1996). Despite these uncertainties, livestock grazing remains a central component of rangeland management across the western United States, and in some contexts, it is assumed to have neutral or even beneficial effects on vegetation structure or forage conditions for wild herbivores. However, elk and cattle exhibit moderate to high dietary overlap (49%–88%) which varies by season, ecotype, climate, grazing intensity, and presence and density of native ungulate species, with diets most likely to converge in late summer following the onset of vegetation senescence (Faber, 2017; Findholt et al., 2004; Kingery et al., 1996; Torstenson et al., 2006). While dietary overlap is often used to infer competition, behavioural responses such as spatial or temporal avoidance may provide more immediate and sensitive indicators of interspecific competition or facilitation. Additionally, interference competition (direct, antagonistic interactions) could cause separation between the species instead of or in addition to avoidance from exploitation competition.

However, behavioural metrics to elucidate such effects have been underutilized due to the logistical challenges of monitoring free-ranging animals at fine spatial and temporal scales. Nonetheless, several studies using telemetry have demonstrated that cattle displace elk with evidence that competition is highest during late summer (Coe et al., 2001; Stewart et al., 2002). Cattle use of riparian areas increases throughout the growing season as vegetation senesces (Rowland et al., 2025), offering evidence that spatial compression of palatable forage may intensify competition during late summer. Yet importantly, previous research conducted during relatively short time scales limits our ability to forecast how interactions could be affected by a changing climate.

In western North America, one of the most prominent symptoms of climate change is increasing summer drought (Polley et al., 2013). Precipitation during spring and summer is an important predictor of both dietary digestible energy and biomass of plant species selected by elk in the Intermountain West (Wisdom et al. *in prep*). Over the past two decades, the impacts of drought have also manifested in a 2-week reduction in the highly-nutritious greenup period of vegetative growth and a 3-week increase in the low-quality, senescent phase in semi-arid landscapes of the western United States (Aikens et al., 2020; Brown et al., 2022). Despite the ability of native ungulates to buffer against environmental variation within climatic norms (Gaillard et al., 2000), historically anomalous reductions in the growing season reduce body fat accumulation, and thereby fitness, in elk (Brown et al., 2025). In addition, drought can be particularly influential in altering dynamics between native and domestic ungulates due to insufficient time for native species to evolve and adapt to these interactions. Conversely, drought may enhance the relative importance of facilitation if livestock grazing improves forage quality through compensatory plant growth. Evaluating these behaviours across multiple decades is critical for understanding how climate extremes, particularly drought, mediate the nature of species interactions. However, to measure climate-related variation in species interactions requires extraordinary datasets that offer both sufficiently fine resolutions to infer interactions at small spatiotemporal scales, but also lengthy time series over which there has been substantial variation in climate.

We used 35 years of telemetry data from free-ranging elk ($N > 400$) and seasonally present cattle ($N > 400$) to understand the nature of their interactions in relation to drought, phenology, and grazing status. We first used step-selection functions to ask whether elk movements were influenced by the spatiotemporal density of cattle during each successive elk telemetry location. This model was used to make inference on the immediate and direct spatial response of elk to cattle, for which we have two alternative hypotheses depending on the type of competition operating. If interference competition drives elk–cattle interactions, we hypothesized that elk would avoid cattle even during periods when resources were least limiting (early season and low drought conditions). But with exploitation competition, elk response to cattle should vary with resource availability, which could be influenced by both annual elk abundance as well as spatiotemporal cattle density, and we hypothesized that

elk should be indifferent to cattle when resources were least limiting. As forage becomes moderately limiting (late summer or during mild drought), however, elk should avoid cattle (particularly when elk abundance is high), since resource overlap increases but alternative foraging options remain available. Under either form of competition, however, in periods of extreme resource scarcity (late summer combined with severe drought), avoidance may break down. In this case, elk and cattle would be forced to converge on the few remaining patches of nutritious forage, not because competition disappears, but because both species have no choice but to share the same restricted resource base (Ager et al., 2004; Johnson et al., 1996). In addition, because the step-selection function could not easily evaluate facilitative effects whereby elk could be attracted to areas previously grazed by cattle, we fit an additional model of elk space use at a coarser scale to assess whether elk altered their use of cattle grazing units as a function of within-season grazing status (ungrazed, currently grazed, or previously grazed) while also assessing the effect of previous-season grazing status. In accordance with the grazing optimization hypothesis (McNaughton, 1979), we hypothesized elk would disproportionately select for pastures previously grazed by cattle.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted in the Starkey Experimental Forest and Range, a research area in the Blue Mountains of northeastern Oregon (Figure 1). Starkey is bounded by a 2.4-m fence, enclosing 101 km² across several study areas that completely prevents the passage of elk (Rowland, 1997), which have varied in abundance between approximately 175 and 700 individuals over the course of our study (Loonam et al., 2025). The other native ungulates—mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*)—are partially restricted by the perimeter fence, while predators including cougars, black bears, bobcats, and coyotes regularly cross the perimeter fence (Ruprecht et al., 2021). Several major creek systems create riparian areas and topographical features ranging from 1122 to 1500 m. Annual precipitation averages 58.6 cm, mostly in the form of winter snow. The study area receives mean monthly rainfall of 4.8, 1.7, and 2.0 cm in June, July and August, respectively. Precipitation has decreased in the past 35 years which has contributed to increased drought severity (Figure 1a).

The landscape is characteristic of the Intermountain West with a mosaic of dry forest (including Ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*)) and moist forest (characterized by Douglas fir (*Abies* and *Pseudotsuga* spp.), spruce (*Picea* spp.) and western larch (*Larix occidentalis*)), both of which are interspersed with dry grasslands dominated by native bunchgrasses and invasive annual grasses (Rowland, 1997). Dominant perennial bunchgrasses in the study area include *Poa secunda*, *Pseudoroegneria spicata*, *Festuca*

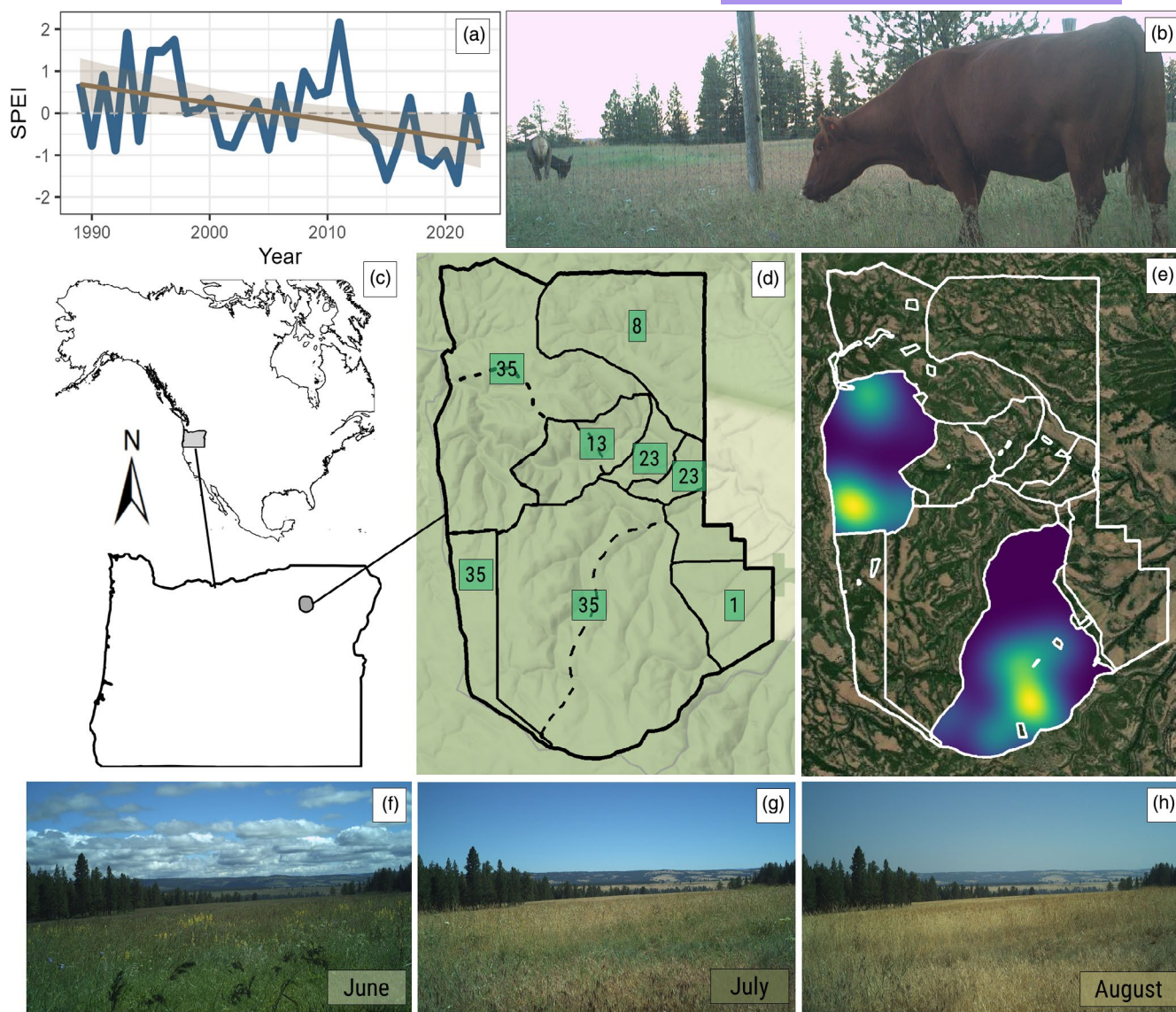


FIGURE 1 (a) Standardized Precipitation Drought Index in the study area during the course of the study, (b) photo of elk and cattle grazing in different pastures, (c) Starkey's position within Oregon and North America, (d) grazing units within Starkey with dotted lines indicating fences constructed during the course of the study and number of years of elk and cattle data analysed in each grazing unit, (e) example of cattle utilization distributions in which cattle are grazing in two different grazing units, (f–h) photographs of a grassland site in the study area taken in June, July and August respectively, used as an aid to visualize phenological advancement of growing season conditions.

idahoensis, *Koeleria macrantha* and *Danthonia unispicata* (Averett & Endress, 2022). Laboratory and field studies show mixed evidence for compensatory responses to defoliation in these species, with outcomes depending on timing, frequency, intensity, competition, and environmental conditions (especially moisture). Some studies report increased nutritive value in *P. spicata* and *F. idahoensis* following defoliation (Ganskopp et al., 2004; Pitt, 1986), while others found no change (Westenskow-Wall et al., 1994). Evidence for increased biomass is limited: *F. idahoensis* was unaffected below ~30% defoliation but declined at higher intensities (Jacobs & Sheley, 1997), and *P. secunda* exhibited reduced biomass after cattle grazing (Kimball & Schiffman, 2003). While survival of *P. secunda* generally declines post-clipping, *P. spicata* survival can increase under some defoliation scenarios (Denton et al., 2021).

2.1.1 | Grazing system

Starkey has a rich history of cattle grazing that preceded the establishment of the research area (Figure 1b). During our study, both the US Forest Service and Oregon State University administered grazing allotments within the study area, each composed of multiple fenced grazing units (Figure 1d). Whereas the US Forest Service allotment is leased to private individuals in Starkey's Main and NE Study Areas, the Oregon State University allotment in the Meadow Creek Study Area is used for research purposes (e.g. Rowland et al. (2025)). Grazing prescriptions for both allotments follow a deferred rotation design. This means that the sequence of cattle movement through grazing units was reversed each year and therefore are robust to pasture × season

effects. Grazing units ranged from 201 to 3580 ha. A fixed number of cattle moved between grazing units of different sizes meant that there was high variation in cattle densities, though in general they are representative of surrounding landscapes (Rowland et al., 2025). The number of days cattle were allotted to each grazing unit differed in rough proportion to their size. The number of cow–calf pairs prescribed to grazing units varied between 399 and 500 in the Main Study Area, was fixed at 50 pairs in the NE Study Area, and averaged 62 pairs in the Meadow Creek Study Area. Grazing occurred between 16 June and 15 October each year or until the maximum allowable forage utilization (45%–55%) was met. Move dates between pastures were defined when >50% of telemetered cattle were herded and moved into the subsequent grazing unit and were used to characterize grazing status into ungrazed, currently grazed, and previously grazed categories.

2.2 | Elk and cattle telemetry data

A subset of the elk population ($x^- = 36$ females per year) was monitored via telemetry collars since 1989. Between 1989 and 2006, relocations were acquired via an automated system that triangulated animal locations using a network of LORAN-C towers. Because the automated system would cycle through each active collar in sequence attempting to attain a successful triangulation, the fix rate depended on the number of collars deployed which was variable by year but averaged 80 min (range: 5 min in 1989 to 135 min in 1999). From 2003 to 2006, the Starkey project transitioned to GPS telemetry collars and since 2006 has relied exclusively on GPS. While fix rates from GPS collars have been collected at finer scales for specific study objectives both within and among years, we subset data to hourly fixes for all data collected using GPS collars. We monitored a total of 1263 elk-years (all female) between 1989 and 2023.

Cattle have similarly been monitored via telemetry since 1989 with an average of 45 collared per year. We monitored a total of 1584 cattle-years between 1989 and 2023. For both species, we restricted our analysis to the months of June through August, given that cattle first arrive to the study area in June, and in September, elk movements are influenced by hunting that occurs in the study area (Smith et al., 2022; Spitz et al., 2019).

Data for this study were collected in accordance with an animal care and use protocol approved by the Institutional Animal Care and Use Committee (#IACUC 92-F-0004).

2.3 | Integrated step selection analysis

Step selection analysis involves comparing actual movements (or steps) between telemetry locations collected at regular intervals to randomly drawn steps that the animal could have plausibly taken but did not (Fortin et al., 2005). While step selection functions are typically fit using conditional or case–control logistic regression, where

each used step is considered a 'case' and available steps are the control locations forming the choice set, we used the asymptotically equivalent Poisson approach to more easily include random effects (Muff et al., 2020; Appendix S1).

We included the natural log of step lengths and cosine of turning angles as predictors in the model, which results in an integrated step selection analysis (Avgar et al., 2016). We used the R package *amt* (Signer et al., 2019) to generate random steps, separately for each individual, using a gamma distribution for step lengths and a von Mises distribution for the turn angles. Because step lengths and turning angles are sensitive to fix interval, we included an interaction between fix interval and log(step length) and cosine(turning angle) so that the movement parameters would be reflective of the fix interval (Hofmann et al., 2024). We paired each used step with 20 random steps.

2.3.1 | Covariates

Because our primary interest for the step selection analysis was to describe elk movements in response to cattle, we first subset all location data to the days elk and cattle were both present in Starkey and then created spatiotemporal maps of cattle density. We did so by estimating utilization distributions (hereafter, UD) using kernel density estimators (Worton, 1989) to telemetered cattle. To best explain elk movements to the immediate presence and density of cattle, we fit separate utilization distributions using the pooled telemetry locations of all cattle during the period in which each elk step was being made. For example, for an elk step beginning at 1300 h with an hourly fix rate, we used all the recorded cattle locations between ≥ 1300 and ≤ 1400 h to fit the cattle UD for that step. We fit UD using the reference bandwidth in the R package *amt*. We followed the guidance of Gitzen et al. (2006) and tested various bandwidth methods before analysing data and found that the reference bandwidth, when overlaid with actual cattle telemetry locations, appeared to best represent cattle herds. Because UD often estimated some amount of probability density that extended beyond the grazing units in which cattle were confined, we clipped UD at the pasture boundary and renormalized them to sum to 1 (Figure 1e). To convert this cattle presence layer to cattle density, we multiplied each pixel by the number of cattle in the grazing unit, which was typically known with near certainty. The result was >140,000 raster layers of spatially explicit cattle density surfaces between 1989 and 2023, each one representing the expected number of cow–calf pairs in each 30 × 30 m pixel during the time interval of each elk step.

We were particularly interested in understanding how phenological advancement of the growing season, indexed by month (Figure 1f–h), and drought modified the effect of cattle on elk selection via a mechanism of decreasing forage availability (Figure 2). We therefore tested models with both month and drought severity as modifiers of the effect of cattle density, represented by interaction terms between month, drought severity

FIGURE 2 Photographs collected via remote cameras within Starkey Experimental Forest and Range for visual demonstration of interactions involving forage utilization of elk and cattle and phenological advancement of vegetation driven by season. Photos within each column are from the same camera at different times during the growing season.



and cattle density. Because month and drought severity are not spatially variable (at the scale of our study area), they were only included as interaction terms without their main effects included. We chose the standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al. 2010) for our measure of drought. SPEI uses temperature and precipitation data to describe water balance and has high explanatory power for elk demography in our study area (Loonam et al., 2025). We used SPEI values that, for each month in our analysis, measured the water balance since the previous November, that is the time at which precipitation would begin to influence current season forage conditions. A SPEI value of 0 represents mean conditions during the calibration period (1950–2010) and values above 0 (high water balance and low drought) or below 0 (low water balance and high drought) indicate the number of standard deviations from the long-term average. We also evaluated a model that included an interaction between annual elk abundance (Loonam et al., 2025) and cattle density to assess whether the response of elk toward cattle was influenced by intraspecific competition.

We additionally controlled for variables found explanatory in other studies of elk resource selection in our study area (Ruprecht et al., 2023; Spitz et al., 2018) (Table 1; Appendix S2). All continuous covariates were standardized to have mean 0 and SD 1, and all pairwise combinations of covariates had correlation values of $r < |0.7|$. We included a random slope for the effect of cattle density for each elk-year because we expected the elk response to cattle could be variable across individuals for a number of unmeasurable factors such as nutritional condition, calf presence, group association or variable exposure to cattle based on home range location. However, we limited the random slope to the cattle density variable because it was the focus of our inference and assumed all other covariates as fixed effects would control for population-level selection.

2.3.2 | Model selection

Although our primary objective was to characterize elk response to cattle in relation to drought, we assessed a limited set of alternative models that tested whether cattle density, time of day, month, annual elk abundance and drought improved explanatory ability over a 'null' model that included only habitat and movement parameters (Table 1). Our global model included habitat and movement covariates and a three-way interaction between cattle density, month and drought. We evaluated the relative support for each model using AIC.

2.4 | Assessing facilitation and competition at the level of the grazing unit

We tested the hypothesis that cattle facilitate elk within the grazing season via a mechanism of forage conditioning. We did so by assessing whether elk selection of cattle grazing units varied based on grazing status, which over the course of a season transitions from 'ungrazed' (before cattle arrive) to 'currently grazed' (when cattle are present) to the final state of 'previously grazed' (once cattle have left the pasture for the season). If cattle conditioned grasses such that cattle grazing stimulated vegetative regrowth that benefits elk, we hypothesized elk would increase their selection of pastures once cattle had arrived (currently grazed) or after they left (previously grazed) relative to the ungrazed status. In contrast, elk avoiding previously grazed units would be indicative of exploitation competition reducing selection. Elk avoiding currently grazed pastures could result from both interference and exploitation competition.

Elk could also benefit from lagged effects of cattle grazing, wherein units grazed the previous season may result in increased growth during the next year. Although nearly all grazing units in the study area were

TABLE 1 Descriptions of step selection models to evaluate spatial overlap between elk and domestic cattle.

Model	Covariates	Hypothesis
Null (Habitat + movement only)	Cosine(aspect), canopy cover, log(distance to road), log(distance to water), ruggedness, PVT, log(step length), cos(turning angle), log(step length) × fix interval, cos(turning angle) × fix interval	Elk movements are influenced only by habitat and not cattle density
Cattle density	Habitat + movement + cattle density	Elk movements are influenced by habitat and cattle density
Cattle density, diel	Habitat + movement + cattle density × time of day	Elk movements are influenced by habitat and cattle density, and the effect of cattle density varies by time of day
Cattle density, month	Habitat + movement + cattle density × month	Elk movements are influenced by habitat and cattle density, and the effect of cattle density varies by month
Cattle density, annual elk abundance	Habitat + movement + cattle density × annual elk abundance	Elk movements are influenced by habitat and cattle density, and the effect of cattle density varies with annual elk abundance
Cattle density, drought	Habitat + movement + cattle density × drought	Elk movements are influenced by habitat and cattle density, and the effect of cattle density varies by annual drought conditions
Cattle density, drought, and time period interaction	Habitat + movement + cattle density × drought + cattle density × time period (day and/or month) + cattle density × drought × time period	Elk movements are influenced by habitat, cattle density, drought, and time period, and the interaction of cattle density, time period, and drought

Note: PVT=potential vegetation type, a factor variable with a reference category set to 'grassland' and additional categories for dry forest, wet forest and other.

grazed each year, there were a total of 32 grazing unit-years that were not grazed. This allowed us to test the hypothesis that elk would be facilitated by the lagged (i.e. previous year) effect of cattle grazing. We reasoned that a lagged-season facilitative effect would be evidenced by a positive coefficient for the previous season grazing variable, that is elk would disproportionately select for grazing units grazed the previous year (relative to those not grazed the previous year). Similarly, avoidance of these grazing units can be interpreted as a lagged effect of exploitation competition from previous years.

We modelled the number of elk telemetry locations per grazing unit using a generalized linear mixed model with a Negative Binomial distribution and random intercepts for year and grazing unit ID. We also included offsets for the log-transformed proportion of the total study area occupied by each grazing unit and the log-transformed total number of possible telemetry locations, which is equivalent to a parametric version of a selection ratio (Appendix S3). We used this model with 2 covariates: a factor variable for within-season grazing status (with reference category set to 'ungrazed'), and a binary variable for previous-season grazing status (coded 0=ungrazed and 1=grazed).

3 | RESULTS

3.1 | Step selection analyses

The 'null' model containing only habitat and movement parameters ranked ≥89 AIC units higher than models that included cattle density, all of which suggested that elk avoid cattle (Appendix S4).

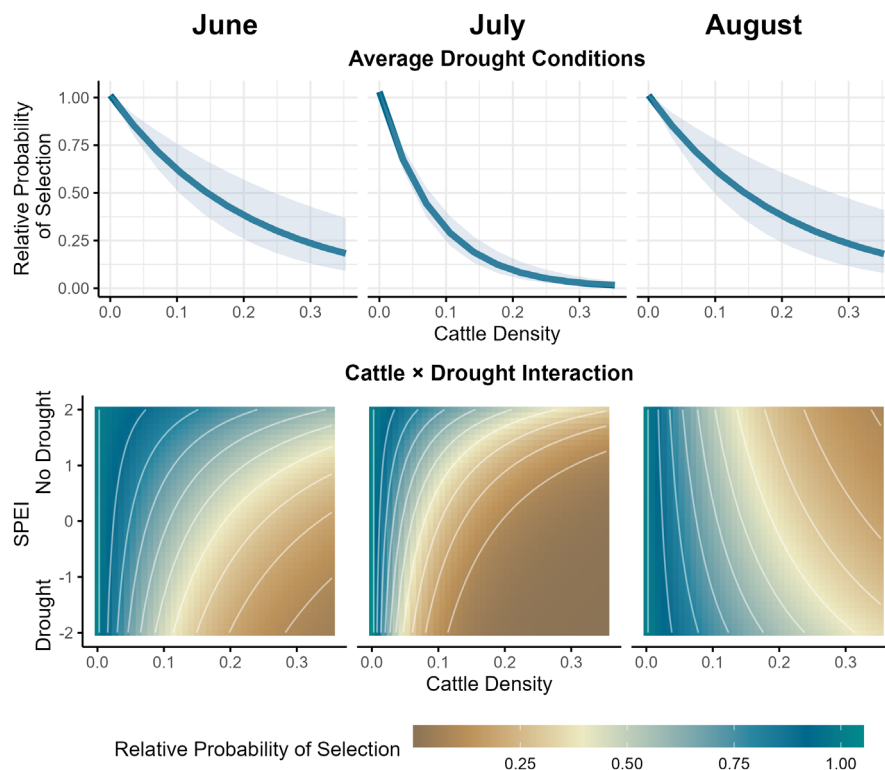
The cattle × time of day model performed second poorest and had a non-significant coefficient for time of day ($p=0.81$). Therefore, in all further models, we pooled telemetry locations across all times of day. Annual elk abundance did not influence the response of elk towards cattle ($p=0.77$). The top model, which was 39 AIC units lower than the next best model, included habitat and movement covariates plus cattle density, its interactions with month and SPEI, and the three-way interaction (cattle density × month × SPEI). This result indicates that elk movements were influenced by cattle density, and that the elk response to cattle varied both seasonally and with drought severity. Moreover, the magnitude of effect of drought on cattle avoidance differed among months.

The top model suggested that in average drought conditions, elk selected areas with lower densities of cattle in all months, though this effect was strongest in July, the reference category ($\beta=-0.42$, $p<0.001$) with the effect less negative in June ($\beta=0.25$, $p<0.001$) and August ($\beta=0.25$, $p<0.001$) (Table 2). Post hoc contrasts demonstrate that under average drought conditions, the effect of cattle in June ($\beta=-0.17$, $p<0.001$) and August also clearly indicated avoidance of cattle ($\beta=-0.17$, $p<0.001$). The effect of cattle density × SPEI, which measures conditions in the reference category of July, was positive ($\beta=0.15$, $p<0.001$) indicating that higher drought (lower SPEI) increased the magnitude of elk avoidance of cattle. The same pattern of greater drought causing greater elk avoidance of cattle was also observed in June ($\beta=-0.09$, $p=0.002$; Figure 3), although weaker than in July. Notably, in August the synergistic effects of cattle density, month and SPEI resulted in a pattern opposite of the other months: greater drought (lower SPEI) reduced elk avoidance of cattle.

TABLE 2 Parameter estimates, standard errors and *p*-values from the top step selection model.

Parameter	Estimate	Standard error	<i>p</i>
Intercept	-18.09	0.40	<0.001
Cosine(aspect)	0.036	0.002	<0.001
Canopy cover	0.090	0.014	<0.001
Log(distance to road)	0.117	0.002	<0.001
Log(distance to water)	0.012	0.002	<0.001
Vector ruggedness measure	0.043	0.002	<0.001
Cosine(turn angle)	-0.037	0.001	<0.001
Log(step length)	-0.0006	0.001	0.605
Cosine(turn angle): Fix interval	0.0003	0.001	0.818
Log(step length): Fix interval	0.015	0.001	<0.001
Potential vegetation type (wet forest)	0.241	0.005	<0.001
Potential vegetation type (dry forest)	0.227	0.005	<0.001
Potential vegetation type (other)	0.411	0.022	<0.001
Cattle density	-0.423	0.046	<0.001
Cattle density: June	0.251	0.053	<0.001
Cattle density: August	0.251	0.054	<0.001
Cattle density: SPEI	0.153	0.036	<0.001
Cattle density: SPEI: June	-0.093	0.039	0.017
Cattle density: SPEI: August	-0.187	0.046	<0.001

FIGURE 3 Predictions from step selection functions describing the relative probability of selection by elk in response to cattle density (expected number of cow-calf pairs per 30 × 30 m pixel), where cattle density was measured by utilization distributions. Top: Marginal plots demonstrating elk avoidance of cattle by month at average drought conditions. Bottom: Contour plots show how drought conditions mediate the avoidance of cattle by elk; drought intensifies avoidance in early summer, but dampens avoidance in August when resources are depleted and elk and cattle exhibit increased overlap.



3.2 | Selection at the level of the grazing unit

At the scale of the grazing unit, our negative binomial models of selection indicated that elk used ungrazed units at higher rates than grazed units, both within and across seasons (Figure 4). Compared to

the reference category of ungrazed units, elk use of currently grazed units was approximately 23% lower ($\beta = -0.26$; $\exp(-0.26) = 0.77$; $p = 0.006$; Table 3) and use of grazing units that had been grazed earlier in the season but were not currently grazed was 27% lower ($\beta = -0.32$; $\exp(-0.32) = 0.73$; $p = 0.002$; Table 3). Independent of

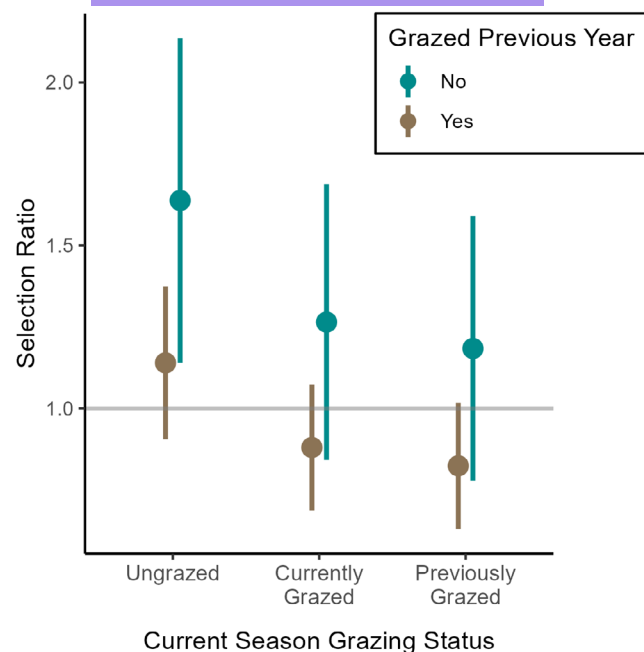


FIGURE 4 Selection Ratios of elk as measured from negative binomial regression models quantifying the effect of current and previous-season grazing status. Values above 1 indicate selection whereas values below 1 indicate avoidance.

TABLE 3 Parameter estimates from negative binomial models for grazing unit-level selection based on current and previous season grazing status.

Parameter	Estimate	Standard error	p
Intercept	0.493	0.155	0.001
Current season grazing status (currently grazed)	-0.259	0.095	0.006
Current season grazing status (previously grazed)	-0.325	0.104	0.002
Previous year grazing status (grazed)	-0.363	0.146	0.013

current season status, elk use of grazing units that were grazed the previous year was 30% lower than those that were not grazed the previous year ($\beta = -0.36$; $\exp(-0.36) = 0.70$; $p = 0.013$; Table 3), even after controlling for year and grazing unit ID.

4 | DISCUSSION

Our results show that seasonally grazing domestic ungulates can strongly influence the behaviour and space use of native wildlife. Elk in our study consistently made movements to areas with lower cattle densities, where we quantified cattle distribution at fine spatiotemporal scales using telemetry data contemporaneous with each elk movement. Beyond these fine-scale movements, elk also avoided entire pastures with cattle present as well as those grazed earlier in

the same or previous season. This is significant given that cattle and elk co-occur across millions of acres of public and private land in western North America, where management decisions depend on a clear understanding of their spatial and competitive interactions rather than assumptions of mutualistic or neutral relationships. Our findings contradict the grazing optimization hypothesis, which predicts that smaller-bodied grazers should be attracted to sites previously grazed by larger herbivores due to stimulated forage regrowth. Despite common assumptions that this dynamic applies to elk and cattle, we found no evidence for it in our system, and its generality warrants critical evaluation in other wild-domestic herbivore systems.

Quantifying the effect size of covariates in step selection analyses is often challenging and prone to misinterpretation. For context, the relative selection strength (Augar et al., 2017) estimates how many times more likely an elk is to make a movement ending at a particular cattle density over another, while holding other variables constant. For example, in a typical July, an elk choosing between a location with 1 cow-calf pair/hectare versus a location with 0 cattle would be 2.9 times more likely to select the location without cattle. Compared to a location with 5 cow-calf pairs/hectare, elk would be 212 times more likely to select a location with no cattle. Additionally, because all continuous covariates in our models were standardized, differences in the magnitude of selection coefficients reflect their relative importance. The strongest effect observed among continuous covariates was elk avoidance of cattle during July ($\beta = -0.42$), which was considerably greater in magnitude than their selection for areas farther from roads ($\beta = 0.12$). While we were initially concerned that cattle density could be acting as a proxy for human activity due to human presence or anthropogenic features associated with grazing activity, the fact that elk avoided cattle during both day (when human presence is highest) and night, and that time of day was not a significant modifier of cattle avoidance reduced this concern.

Understanding how climate shapes competition between native and domestic species is increasingly important given that climate change is expected to reduce baseline forage through drought while amplifying year-to-year variability due to altered precipitation (Brown et al., 2022). Using a 35-year telemetry dataset, we found that elk responses to cattle were mediated by both phenological advancement of the growing season and drought. Under average drought conditions, elk avoided cattle throughout the growing season but most strongly in July. During severe droughts, elk avoidance of cattle intensified in June and July, likely because they could still find adequate forage in areas without cattle. By August, however, advancing phenology causes significant contraction of available nutritious forage (Brown et al., 2022) that is isolated in riparian areas and moist forest types heavily used by cattle (Rowland et al., 2025). In contrast to the pattern observed in June and July, elk reduced their avoidance of cattle in August, particularly during severe droughts. Elk indifference towards cattle during these periods of highest resource scarcity suggests that competition breaks down because both species are forced to converge on the last remaining patches of quality forage. These results align with forage allocation models from the study area, which predicted spatial and dietary segregation

early in the growing season followed by convergence after the onset of drought and vegetation senescence (Ager et al., 2004; Johnson et al., 1996). Similarly, Clark et al. (2017) found that during times of resource scarcity, elk focused movements toward finding the highest quality forage while cattle remained in place as an energy-conservation strategy, consistent with our finding that elk reduced their avoidance of cattle during late summer and/or periods of drought.

Although our methods cannot pinpoint the mechanism responsible for elk avoidance of cattle, our results suggest that interference competition and exploitation competition are both involved. Elk avoided cattle even during the times of highest resource availability (early summer in wet years), indicating interference competition or reasons other than competition for forage. As resources became depleted during midsummer and with drought, elk avoidance of cattle intensified, consistent with an effort to reduce exploitation competition. Regardless of the form of competition operating, our results demonstrate an overarching behaviour for elk to maintain spatial segregation from cattle when possible. If climate change continues to increase the frequency and magnitude of drought as expected (Figure 1a), wildlife and land managers as well as livestock producers should anticipate more overlap between elk and cattle. Increased overlap could have far-reaching consequences including fitness costs to elk and other native herbivores, economic losses for livestock producers (Torstenson et al., 2002), increased risk of disease transmission among both species (Proffitt et al., 2011), and potential increases in depredations of domestic livestock if predators seeking native prey encounter domestic animals more frequently.

Despite previous work suggesting that elk track the spatiotemporal distribution of cattle due to a facilitative effect via stimulation of vegetative regrowth (Vavra & Sheehy, 1996), we found no evidence of this. After controlling for year and grazing unit effects, elk selection of a given grazing unit was highest before cattle arrived for the season and lower during the times cattle were grazing and after they had grazed that season. Had within-season facilitation been prominent, the strongest selection for grazing units should have occurred after cattle had left, which was not the case. Elk avoiding grazing units with cattle present more likely indicates interference competition, unless exploitation competition occurred due to rapid depletion of forage by cattle. Similarly, among the subset of grazing unit-years in which there were years without grazing to use as a baseline, we found no evidence of lagged (previous season) effects of facilitation. In fact, elk strongly preferred grazing units that were not grazed the prior year, even after controlling for year, grazing unit and current grazing status. The finding that exploitation competition operates across years was an unexpected result and suggests that resting a grazing unit from cattle grazing for a single year may not be adequate to reset foraging conditions for elk, at least in drought-prone systems such as our study area.

To contextualize the effects of forage removal in this system, cattle stocking rates in our study averaged 5.6 cow–calf pairs per km² during the 121 day grazing season compared to 3.9 adult elk per km² annually (Loonam et al., 2025). Weights of mature cows and calves in our study

area average 518 and 190 kg respectively (Walburger, 2002) versus 230 kg for adult elk (Ager et al., 2004). Rough estimates indicate cattle biomass (~3965 kg/km²) outweighed adult elk biomass (~897 kg/km²) by a factor of 4 (ignoring the influence of calf elk). Using the Society for Range Management standard of 11.8 kg of dry forage consumed daily per 450 kg animal unit, cattle in our study area removed ~104 kg of dry forage per km² per day, a value that would be even higher on a wet-weight basis. For context, Stewart et al. (2009) estimated mean above-ground herbaceous biomass at 600–1650 kg per km² per day in one section of the study area, although these estimates have considerable uncertainty. Given the high dietary overlap between elk and cattle, it is unsurprising that elk avoided cattle to reduce exploitation competition. For facilitation to occur, cattle would need to stimulate compensatory regrowth with a nutritional value exceeding that of the ~104 kg/km²/day removed by cattle. Yet in a controlled experiment in our study area, Damiran et al. (2019) found that although elk consumed vegetation with less neutral detergent fibre after cattle grazing, there were no gains in crude protein, digestibility, or metabolizable energy, indicating that facilitation through forage regrowth is weak or nonexistent in this system.

The extent to which the non-native status of domestic cattle disrupts co-evolutionary processes among native herbivores and plants is unclear. In a previous experiment in our study area, elk in cattle-grazed paddocks had reduced bite counts and shifted diets from primarily graminoids to greater use of forbs and shrubs compared to ungrazed control paddocks (Damiran et al., 2019; Findholt et al., 2004). This suggests behavioural plasticity in elk foraging consistent with a shift along the grazing–browsing continuum in response to competition with other herbivores. Although total nutrient intake did not differ between grazed and ungrazed treatments (Damiran et al., 2019), potential fitness consequences (e.g. fat reserves or pregnancy rates) warrant further study.

While total herbivore biomass has been proposed as a stronger determinant of facilitation versus competition than species identity (Hobbs, 1996; Veblen et al., 2016), we found no evidence that elk abundance mediated elk responses to cattle. Future work should evaluate whether cattle exhibit spatial avoidance of elk, and whether native ungulates negatively affect (Hobbs et al., 1996a) or facilitate cattle (Hobbs et al., 1996b), which may vary according to water availability (Odadi et al., 2011). Herbivory from small mammals, such as rodents and lagomorphs (Augustine & Springer, 2013; Ranglack et al., 2015), can also be substantial and should be considered alongside the effects from large herbivores.

Although cattle grazing in our study area is representative of many grazing systems in the region (Rowland et al., 2025), responses may differ at lower cattle stocking rates or in systems with forage species that more consistently compensate for defoliation. Further, the local climatic and environmental conditions characteristic of our study area are not likely to generalize to all systems, particularly those with abundant summer rainfall and longer growing seasons. Future research should investigate spatial interactions among other assemblages of native and domestic herbivores in various ecosystem contexts given that climate-driven shifts in forage availability,

growing season phenology, and water distribution are likely to destabilize existing patterns of coexistence.

5 | CONCLUSION

Our results demonstrate that in semi-arid landscapes characteristic of much of western North America, cattle grazed at intensities similar to this study act as competitors, not facilitators, to elk, as evidenced by consistent elk avoidance of cattle. Spatial segregation appears to be a key mechanism elk use to alleviate competition, but this buffer weakens under drought when both species converge on the few remaining patches of high-quality forage. As climate change intensifies the severity and frequency of drought, such overlap is likely to increase, bringing ecological and economic consequences including fitness costs to native herbivores, reduced cattle weight gain, greater risk of disease transmission and elevated livestock depredation if predators encounter domestic animals more frequently.

AUTHOR CONTRIBUTIONS

Joel Ruprecht, Tavis D. Forrester, Casey L. Brown, Lara F. Mengak, Michael J. Wisdom, Darren A. Clark and Taal Levi conceived the ideas and designed the methodology. Joel Ruprecht analysed the data and led the writing. Joel Ruprecht, Tavis D. Forrester, Casey L. Brown, Lara F. Mengak, Michael J. Wisdom, Darren A. Clark and Taal Levi contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.m37pvmhdq> (Ruprecht et al., 2026).

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SUPPORTING INFORMATION

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

Appendix S1. Poisson formulation of step selection functions.

Appendix S2. Description of landscape and habitat covariates in step selection functions.

Appendix S3. Equivalence between selection ratios and negative binomial model.

Appendix S4. Model selection results from a set of candidate models assessing the influence of cattle density on elk movements.

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