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ARTICLE

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Cougars, wolves, and humans drive a dynamic landscape of fear for elk

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Abstract

To manage predation risk, prey navigate a dynamic landscape of fear, or spatiotemporal variation in risk perception, reflecting predator distributions, traits, and activity cycles. Prey may seek to reduce risk across this landscape using habitat at times and in places when predators are less active. In multipredator landscapes, avoiding one predator could increase vulnerability to another, making the landscape of fear difficult to predict and navigate. Additionally, humans may shape interactions between predators and prey, and induce new sources of risk. Humans can function as a shield, providing a refuge for prey from human-averse carnivores, and as a predator, causing mortality through hunting and vehicle collisions and eliciting a fear response that can exceed that of carnivores. We used telemetry data collected between 2017 and 2021 from 63 Global Positioning System-collared elk (*Cervus canadensis*), 42 cougars (*Puma concolor*), and 16 wolves (*Canis lupus*) to examine how elk habitat selection changed in relation to carnivores and humans in northeastern Washington, USA. Using step selection functions, we evaluated elk habitat use in relation to cougars, wolves, and humans, diel period (daytime vs. nighttime), season (summer calving season vs. fall hunting season), and habitat structure (open vs. closed habitat). The diel cycle was critical to understanding elk movement, allowing elk to reduce encounters with predators where and when they would be the largest threat. Elk strongly avoided cougars at night but had a near-neutral response to cougars during the day, whereas elk avoided wolves at all times of day. Elk generally used more open habitats where cougars and wolves were most active, rather than altering the use of habitat structure depending on the predator species. Elk avoided humans during the day and ~80% of adult female mortality was human caused, suggesting that humans functioned as a "super predator" in this system. Simultaneously, elk leveraged the human shield against wolves but not cougars at night, and no elk were confirmed to have been killed by wolves. Our results add to the mounting evidence that humans profoundly affect predator–prey interactions, highlighting the importance of studying these dynamics in anthropogenic areas.

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KEYWORDS
Canis lupus, carnivore, *Cervus canadensis*, human shield, human super predator, landscape of fear, predator–prey interactions, *Puma concolor*, step selection function, ungulate

INTRODUCTION

To survive and reproduce, prey must mitigate risk across a landscape of fear, reflecting dynamic interplay among predator habitat use, predator activity cycles, and habitat structure (Laundré et al., 2001). To navigate this perceptual landscape, prey can shift vigilance levels and movement patterns to forage in places and times of lower risk (Lima & Bednekoff, 1999; Lima & Dill, 1990). However, prey are often subject to multiple predators that can have contrasting patterns of activity and habitat use (Montgomery et al., 2019), making the landscape of fear complex. In these multipredator systems, prey may be unable to fully respond to chronically high levels of background risk with behavioral trade-offs (i.e., the risk allocation hypothesis; Lima & Bednekoff, 1999). Humans can profoundly influence predators, prey, and the interactions among them (Guiden et al., 2019). Yet, because large carnivores are often studied within protected areas where human impacts are limited, the influence of humans on interactions between carnivores and their prey remains largely unknown (Kuijper et al., 2016).

Predator–prey interactions, and thus the landscape of fear, are strongly shaped by contextual factors including landscape features, predator traits, prey characteristics, and temporal cycles (Palmer et al., 2022; Wirsing et al., 2021). For instance, prey are expected to move into more open landscapes when subject to higher risk from stalking predators, and to take refuge in areas of higher cover to mitigate risk from coursing predators (Preisser et al., 2007). In a multipredator system, however, such responses may avoid one threat while increasing risk from another. Prey might attempt to balance multiple threats by avoiding areas predators use or by reducing their movement during times when predators are most active (Lima & Bednekoff, 1999; Lima & Dill, 1990). For example, elk (*Cervus canadensis*) in Yellowstone National Park avoided cougars (*Puma concolor*)—primarily ambush predators that hunt nocturnally—at night, and wolves (*Canis lupus*)—primarily coursing predators that hunt crepuscularly where human influence is minimal—at dawn and at dusk, creating windows of opportunity to use these otherwise high-quality but risky foraging areas (Kohl et al., 2018, 2019).

Humans have the potential to shape a temporally dynamic landscape of fear (Palmer et al., 2022) because our behavior is strongly diurnal and open landscapes can increase risk from hunters equipped with firearms (Gaynor et al., 2022). However, studies have documented conflicting responses of ungulates to humans. For example, elk, moose (*Alces alces*), and mountain goats (*Oreamnos americanus*) may use the "human shield" of anthropogenic areas to avoid human-averse carnivores (Berger, 2007; Hebblewhite et al., 2005; Sarmento & Berger, 2017), but other studies have documented stronger fear responses to humans relative to sympatric predators (Crosmary et al., 2012; Lone et al., 2014). Given that humans can cause substantial direct mortality via vehicle collisions and hunting, predators and prey alike may view humans as a "super predator" to be strongly avoided (Darimont et al., 2015; Prugh et al., 2023).

To examine how prey navigate risks from predators in the context of humans, we collared and monitored elk, cougars, and wolves in northeastern Washington, USA between 2017 and 2021, identified causes of elk mortality, and developed step selection functions of elk movement. We used these data to test three interrelated hypotheses: that elk would navigate the landscape of fear by responding to predators dependent on their hunting traits (H_1) and temporal variation in risk (H_2), and that humans could affect these interactions (H_3). More specifically we expected that elk would shift toward open habitats in areas with higher cougar use, while avoiding open habitats in areas occupied by wolves, reflecting predator hunting mode (H_{1a}). It was alternatively possible that elk would respond to predators irrespective of hunting mode (H_{1b}) considering that predator hunting mode did not affect the probability of elk transitioning between encamped and exploratory movement (Bassing, 2022), and wolves generally selected for forested terrain in this system (Bassing et al., 2023). We also hypothesized that elk would respond to a daily dynamic landscape of fear (H_{2a}) to account for diel shifts in risk. Because cougars are primarily nocturnal hunters (Ruth & Murphy, 2010) and wolves tend to be more nocturnal than crepuscular in areas with humans (Theuerkauf, 2009), we predicted that elk would avoid these carnivores most strongly at night. We also expected that elk would avoid cougars and wolves more strongly in the summer when neonatal elk are most vulnerable to predators (Griffin et al., 2011; H_{2b} seasonally dynamic landscape of fear), and that elk with a calf would avoid predators more strongly than elk without a calf. If humans posed a major threat to elk, evidenced by humans representing the dominant cause of mortality, we predicted that elk would avoid human-affected areas, especially during the fall hunting season and during the day when human hunters are most active (H_{3a} human super predator hypothesis). Alternatively, if cougar and wolf predation represent the dominant cause of mortality, we predicted that elk would prefer areas of higher human impact in an attempt to reduce predation risk from human-averse predators, especially in the summer when calves are most vulnerable (H_{3b} human shield hypothesis). Additionally, we expected that elk with calves would choose areas with higher human impacts than elk without calves. Leveraging a rare dataset concurrently tracking both prey and their predators (c.f., Isbell et al., 2018) across a gradient of human impacts and activities, we investigate the spatiotemporal factors shaping a dynamic landscape of fear that elk navigate to examine how humans affect predator–prey interactions (Isbell & Young, 1993).

METHODS

Study area

This research occurred in a region spanning Stevens and Pend Oreille Counties of northeastern Washington, USA defined by the range of elk that were radiocollared for our study (latitude: c. 47.90° to 48.72° N; longitude: c. 118.30° to 117.20° W; ~5200 km^2; Figure 1). Physiographic and climatic details are detailed in Appendix S1: Section S1. Cougars occur at high density relative to other regions; Beausoleil et al. (2021) recently estimated ~2 cougars/100 km^2 (SD = 0.2) directly north of our study system. Four wolf packs occupied the study area for the duration of the project, and wolves occurred at a much lower density than cougars (~0.19 wolves/100 km^2 [SD = 0.03]) based on the minimum count of wolves in the region from 2016 to 2021 (Washington Department of Fish and Wildlife et al., 2022). Black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), mule deer (*Odocoileus hemionus*), moose, and white-tailed deer (*O. virginianus*) are also native to the area. During the study period, archery hunting of male and female elk was permitted for ~2 weeks in September and adult male elk were hunted with rifles from October through December, with exact dates varying by year (https://www.eregulations.com/washington/hunting/elk-general-seasons). Antlerless harvest was also permitted on the Spokane Indian Reservation, in the southwest of the study area, in November. Occasional permits (mean = 40, SD = 11, range 23–51 per year) were also issued outside of the hunting season for crop depredations across the study area (generally 1 July–31 March; A. Prince, personal communication).

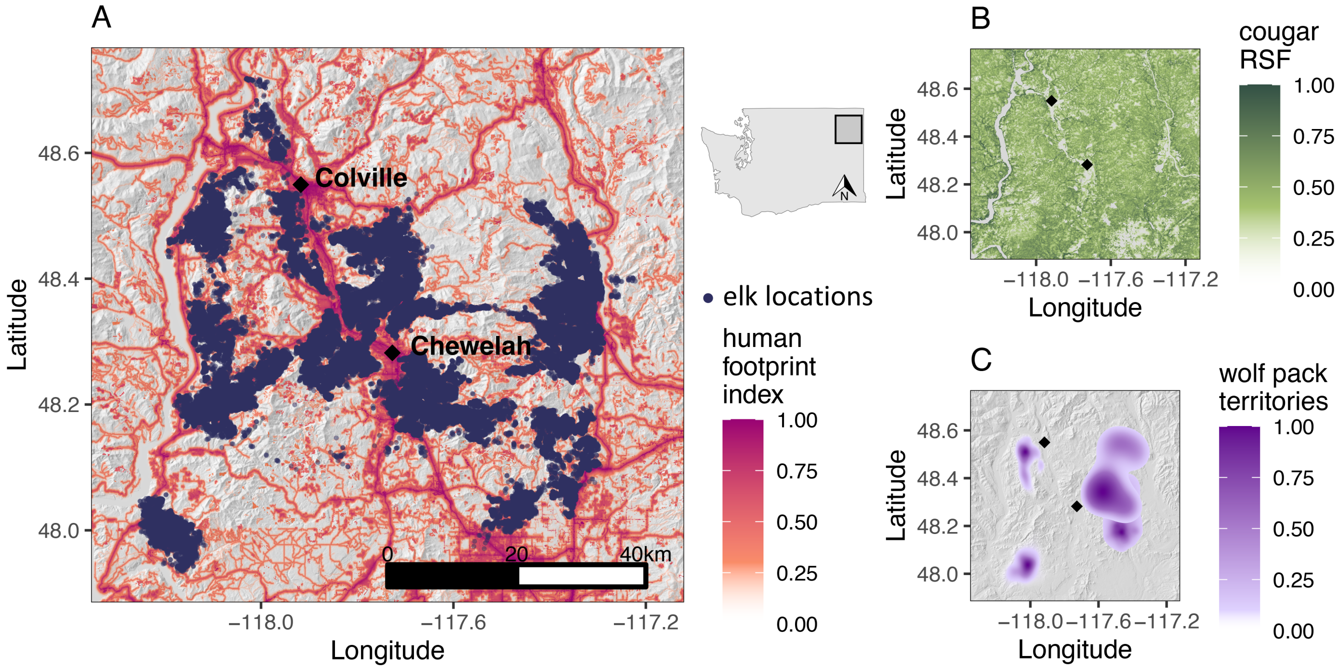

FIGURE 1 Locations of Global Positioning System-collared elk ($n = 63$) overlaid over the human footprint index across the study area in northeastern Washington, USA from 2017 to 2021 (A). Predicted relative likelihood of cougar use (B) was based on resource selection functions (Manly et al., 2007) adapted from Bassing (2022), whereas wolf pack territories (C) were modeled with localized density distributions (Kittle et al., 2016).

Animal capture and handling

To evaluate elk movement and causes of mortality we captured, collared, and monitored adult female and neonatal elk for 53 months (January 2017 to June 2021; Appendix S1: Section S2). Adult elk were fit with Global Positioning System (GPS) radiocollars (Model Survey, Vectronic Aerospace, Berlin, Germany) that recorded a fix every 4 h and that were equipped with mortality sensors that sent emails and SMS notifications after 9 h of inactivity. Neonatal elk 0–10 days old were fit with expandable GPS collars (Model Survey, Vectronic Aerospace, Berlin, Germany) that transmitted one fix daily or very high frequency (VHF) tracking collars (Models M2230B and M4210, Advance Telemetry Systems, Isanti, Michigan, USA). Calf collars signaled mortality after 8 h of inactivity, and calves were monitored remotely (if GPS collared) or with radiotelemetry (if VHF collared) daily from capture to the end of summer (31 August), twice per week through the fall (September–December), and weekly from January onward, until reaching 1 year of age. Following a mortality notification, we conducted a field investigation as rapidly as possible to determine the cause of death. We confirmed predation with hemorrhaged bite wounds and identified the predator based on the mortality scene and salivary DNA collected from lethal bites (Ganz et al., 2022).

We captured cougars using trained dogs and baited cage traps (Kertson et al., 2011) and fit them with GPS collars (Model Vertex Lite, Vectronic Aerospace). Wolves were captured with padded leg-hold traps and by aerial darting (Frame & Meier, 2007), and fit with GPS collars (Models Vertex Lite and GPS Plus, Vectronic Aerospace, and Model TGW, Telonics Inc., Mesa, Arizona, USA). Cougar collars were programmed to record a fix every 4 hours and wolf collars were programmed to collect locations every 4–12 h. Elk and cougar capture and handling followed protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol no. 4226-01). Wolves were captured as part of existing management and conservation activities (Washington Department of Fish and Wildlife et al., 2022) by the Washington Department of Fish and Wildlife and the Spokane Tribe of Indians in accordance with their agency-approved capture and handling protocols (Washington Department of Fish and Wildlife, 2019) and the guidelines of the American Society of Mammologists (Sikes et al., 2016).

Model framework

We used step selection functions (Fortin et al., 2005) to examine how elk navigated the landscape of fear. We created separate population-level models for elk in the summer (June–August) and in the primary hunting season in the fall, hereafter "fall" (September–December). We excluded locations associated with migration and removed individual elk with fewer than 200 fixes ($n = 3$) from all datasets (all others had >700 fixes; Appendix S2). To determine whether selection reflected maternal behavior to mitigate calf predation risk, we also created and compared summer step selection functions for cow elk known to have a calf (collared calves that survived through summer) to those known not to have a calf (either the cow was not pregnant at capture the prior winter, or the calf died before reaching 10 days old). For the step selection functions, we generated 20 random steps per taken step with the turning angle drawn from a von Mises distribution and step length drawn from a gamma distribution (Thurfjell et al., 2014) using the *amt* package in R (Signer et al., 2019). Random steps were compared with steps taken with conditional logistic regression in R package *amt* (Signer et al., 2019). All analyses were conducted in program R version 4.1.3 (R Core Team, 2022).

Covariates

Seasonal models contained the following covariates: cougar and wolf use indices, elevation, slope, percent open habitat, and the human footprint. We took different approaches to describe cougar and wolf use to account for differences in their density and distribution. The area is fully occupied by cougars (Beausoleil et al., 2021; Ganz, 2022), so we used resource selection functions (RSFs; Manly et al., 2007) as an index of cougar risk to elk (Bassing, 2022; Appendix S1: Section S3). Cougar RSF values ranged from 0 to 1 and incorporated data from 42 cougars (Bassing, 2022). Because we collared wolves from all wolf packs in the study area and movement from individual wolves within a pack tends to reliably describe pack-level use (Benson & Patterson, 2015), we effectively had a census of wolf packs. Additionally, track and camera surveys indicated that transient wolves outside of known wolf pack territories were rare (Washington Department of Fish and Wildlife et al., 2022). Therefore, to describe wolf pack presence while accounting for areas outside of pack territories, we created localized density distributions (LDDs; Kittle et al., 2016) for summer and fall to use as an index of wolf risk to elk (Appendix S1: Section S4). Wolf LDDs were scaled from 0 to 1 to align them with the cougar index, and they incorporated data from 16 wolves.

We sourced elevation and slope layers from the Shuttle Radar Topography Mission (SRTM) Digital Elevation

Model (DEM; Farr & Kobrick, 2000). We created a continuous covariate describing the proportion of open terrain within a 250 m moving window at 30 m resolution, selecting a 250 m buffer to reflect the median step length taken by elk (summer: median = 243 m, fall: median = 255 m). We defined open terrain as areas classified as agriculture, mesic grass, xeric grass, and xeric shrub in annual layers produced by the Cascadia Partner form (TerrAdapt:Cascadia; https://www.cascadiapartnerforum.org/terradapt). Open habitat should disadvantage the stalking hunting style of cougars, while favoring the coursing hunting style of wolves (Kohl et al., 2018, 2019). To describe human presence and associated landscape impacts, we used the TerrAdapt:Cascadia annual human footprint index, which represented the degree to which a landscape was used and altered by humans. Values ranged from 0 (unimpacted areas) to 1 (urban areas). Intermediate values described timber harvest (~0.3–0.5), agricultural and rural development (~0.5–0.7), and residential areas (~0.8–0.9). If elk avoided humans, it would suggest that elk perceived humans as predators (H_{3a}), whereas preference for human-impacted areas could indicate that elk were exploiting the human shield as a refuge (H_{3b}).

Our models included interactions: open × cougar, open × wolf, open × time of day, cougar × time of day, wolf × time of day, and human footprint × time of day. We did not expect elk responses to elevation and slope to depend on the time of day, so no such interactions were considered. We included the interactions between carnivores (cougars and wolves, separately) and open habitat to test for an effect of predator hunting mode (H_{1a}), expecting that elk would avoid open areas more strongly with higher wolf use and prefer open areas with higher cougar use. We classified the end of each step as day (between sunrise and sunset) or night (after sunset and before sunrise) using the R package *suncalc* (Thieurmel & Elmarhraoui, 2019). Interactions with time of day allowed us to test if the response to covariates depended on day versus night (H_{2a}), as we expected that elk would avoid cougars and wolves more strongly at night while responding to human impacts more strongly in the day. Due to a lack of overlap between areas of high human footprint and high predator use, we could not include an interaction between humans and predators (Appendix S1: Figure S1).

All covariates were mapped at 30 m resolution. Elevation and slope were standardized such that the mean = 0 and standard deviation = 1, whereas cougar, wolf, human footprint, and percent open habitat layers ranged from 0 to 1. We checked Pearson's correlations between the covariates to ensure that none were characterized by $|r| > 0.7$, and we evaluated the performance of the models with leave-one-individual-out cross-validation (Boyce et al., 2002).

RESULTS

We collared 63 adult female elk and 30 neonatal calves (16 female, 14 male). Deaths were investigated within 1–16 days (median = 2 days, SD = 5). Fourteen adult female elk died over the 53 months of the study (staggered entry Kaplan–Meier annual survival estimate of females 1–10 years old = 0.93, SE = 0.02; annual survival of females ≥10 years old = 0.88, SE = 0.06; Ganz, 2022). Adult female elk primarily (79%; 11/14) died from human causes (six legally harvested, three vehicle collisions, and two harvest wounding losses). Two adult female elk died from an unknown disease, and one adult female elk died of an unknown cause. Fifteen of 30 elk calves were confirmed to survive to 1 year old (annual survival = 0.63, SE = 0.09; Ganz, 2022); 11 died and four had unknown outcomes due to dropped collars. Bear ($n = 2$) and cougar ($n = 3$) predation accounted for nearly half the confirmed calf mortalities. One calf died from entanglement in a fence, and five calves died of unknown causes. Of the five unknown causes of death, we suspected black bears were potentially responsible for three of the unclassified mortalities and coyotes may have caused one unclassified mortality. There were no confirmed cases of wolves killing collared elk during the study.

Step selection functions

Sixty elk informed the summer and fall adult female elk step selection functions (summer: 77,988 used locations, range 347–2127 per female; fall: 98,357 used locations, range 318–2833 per female; Appendix S2: Table S1). Step selection functions performed well, evidenced by Spearman's correlation coefficients between the relative probability of use and the frequency of observed locations of 0.96 for the summer and 0.99 for the fall model (Boyce et al., 2002). We compared data from 15 elk with calves surviving the summer (7566 used locations, range 431–534 per female) with those of 12 elk without calves (6013 used locations, range 414–531 per female).

Elk responded to nearly all considered covariates with pronounced effects by time of day (Table 1, Figure 2). Elk chose more open areas at night (most strongly in the summer) but avoided them during the day (most strongly in the fall). Averaged selection scores, $w(x)$, based on used locations across the range of wolf and cougar indices, revealed that these patterns held regardless of predator activity even though coefficient estimates indicated that elk avoided open areas more strongly with higher wolf use in the summer (Appendix S2: Figure S3).

TABLE 1 Model output for step selection functions of elk (*Cervus canadensis*) movement in the summer (June–August) and the hunting season (September–December) for Global Positioning System-collared elk in northeastern, Washington, USA from 2017 to 2020.

	Summer				Hunting season			
Covariate	$\hat{\beta}$	**SE**	***z*-score**	***p***	$\hat{\beta}$	**SE**	***z*-score**	***p***
Open-day	−2.86	0.06	−50.5	<0.0001	−3.37	0.06	−60.6	<0.0001
Open-night	3.78	0.06	64.2	<0.0001	4.15	0.06	75.0	<0.0001
Cougar-day	0.15	0.04	3.7	0.0002	−0.29	0.04	−6.7	<0.0001
Cougar-night	−2.76	0.06	-42.9	<0.0001	−3.20	0.06	−57.1	<0.0001
Wolf-day	−3.66	0.35	−10.3	<0.0001	−2.55	0.39	−6.5	<0.0001
Wolf-night	1.59	0.58	2.7	0.006	−7.15	0.55	−13.1	<0.0001
Open × cougar	2.02	0.11	18.3	<0.0001	1.70	0.09	18.1	<0.0001
Open × wolf	−3.37	0.67	−5.0	<0.0001	1.52	0.50	3.1	0.002
Human-day	−0.56	0.04	−15.5	<0.0001	−1.67	0.04	−39.8	<0.0001
Human-night	1.29	0.05	23.6	<0.0001	2.04	0.05	39.2	<0.0001
Elevation	0.39	0.01	33.7	<0.0001	0.57	0.01	52.4	<0.0001
Slope	−0.07	0.01	−14.2	<0.0001	0.00	0.00	1.1	0.29

Note: The effect of night is additive to the daytime effect for a particular covariate because time of day was modeled as an interactive effect. Thus, adding the coefficient estimates for day and night together for a covariate represents the response of elk to that predictor at night.

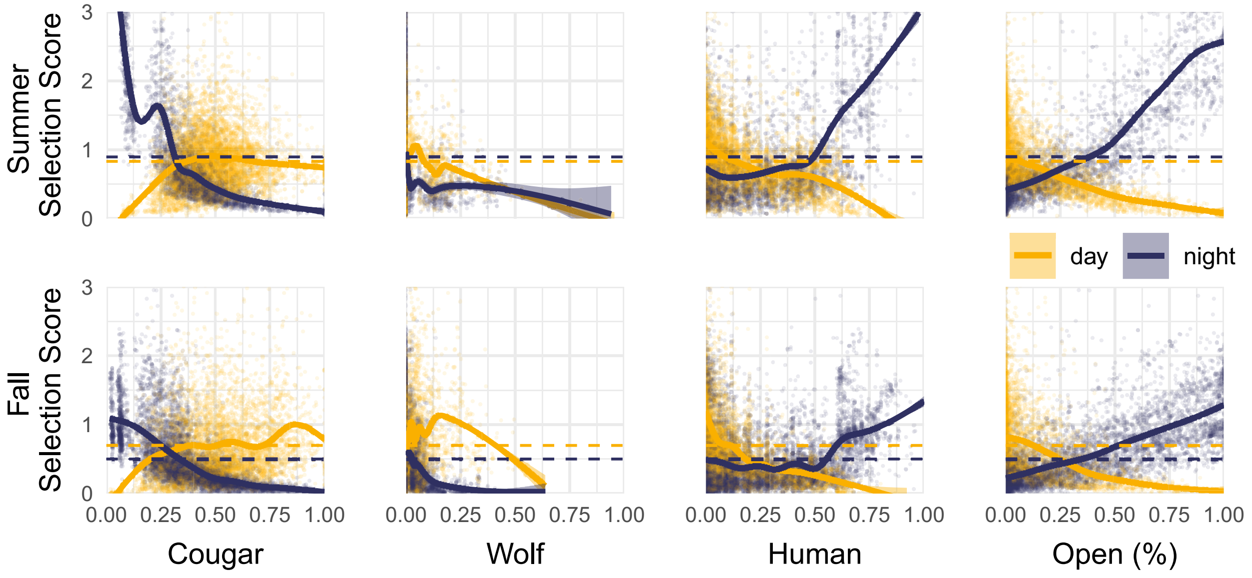

FIGURE 2 Average-effect plots illustrate elk response to cougars, wolves, the human footprint index, and percent open habitat for the summer (top row) and hunting season (bottom row) in the day (yellow) and night (blue). Average-effect plots show the selection score, $w(x)$, of used locations averaged over the range of a considered variable (solid trend lines, with shading indicating 95% confidence intervals), thus accounting for potential covariation between predictors (Avgar et al., 2017). Individual $w(x)$ scores as predicted by the models are shown as points, while horizontal dashed lines indicate the average $w(x)$ score for day and night. Elk did not use areas exceeding a wolf index of 0.95 in the summer, nor 0.64 in the hunting season.

Elk avoided cougars at night in both seasons, most strongly in the fall, whereas elk had a weaker response to cougars in the day (avoidance in the fall and a slight preference in the summer). Elk avoided wolves during the day, but that avoidance attenuated at night in the summer while strengthening in the fall. In both seasons, elk avoided areas with a relatively high human footprint during the day but moved toward higher human footprint areas at night. Accordingly, elk were more likely to use areas with higher human footprint at night within wolf pack territories, especially in the summer, whereas cougar activity did not appear to influence elk use of human-impacted areas (Figure 3; Appendix S2: Figure S2). Females with calves avoided cougars and wolves and moved toward areas with a greater human footprint than elk without a calf (Table 2; Appendix S2: Figure S1). Seasonal models revealed that elk, in general, did not use areas with a wolf index exceeding 0.95 in the summer and 0.64 in the fall, whereas the highest wolf index used by elk with calves was only 0.15 compared with 0.41 for elk without calves.

DISCUSSION

Perceived predation risk, manifesting as a dynamic landscape of fear, can have important implications for prey habitat use, reproduction, and survival (Palmer et al., 2022). Yet, the effects of humans on predator–prey dynamics are difficult to predict given the myriad of novel factors and interactions in human-impacted areas (Guiden et al., 2019). In northeastern Washington, we found that elk adjusted habitat selection to reduce risk from both cougars and wolves, at times of day during which they actively hunt (H_{2a}), and with some differences in the magnitude of effect by season (H_{2b}). In doing so, elk avoided humans (H_{3a}) in the day but perhaps leveraged a human shield (H_{3b}) against wolves, but not cougars, at night. Elk responses to wolves ran counter to our predictions for this coursing predator (H_{1b}), potentially owing to the pervasive role of humans in this system. Our study revealed the importance of accounting for diel variation in animal movement and highlights critical differences in the impacts of cougars, wolves, and humans on their shared ungulate prey.

Elk responded to cougars in ways that were generally consistent with predictions for a nocturnal, stalking predator (Preisser et al., 2007; Ruth & Murphy, 2010). Namely, elk strongly avoided areas with higher cougar use at night and exhibited a weaker response to cougars during the day, as was similarly observed by Kohl et al. (2018). In areas with higher cougar use, elk were more likely to use

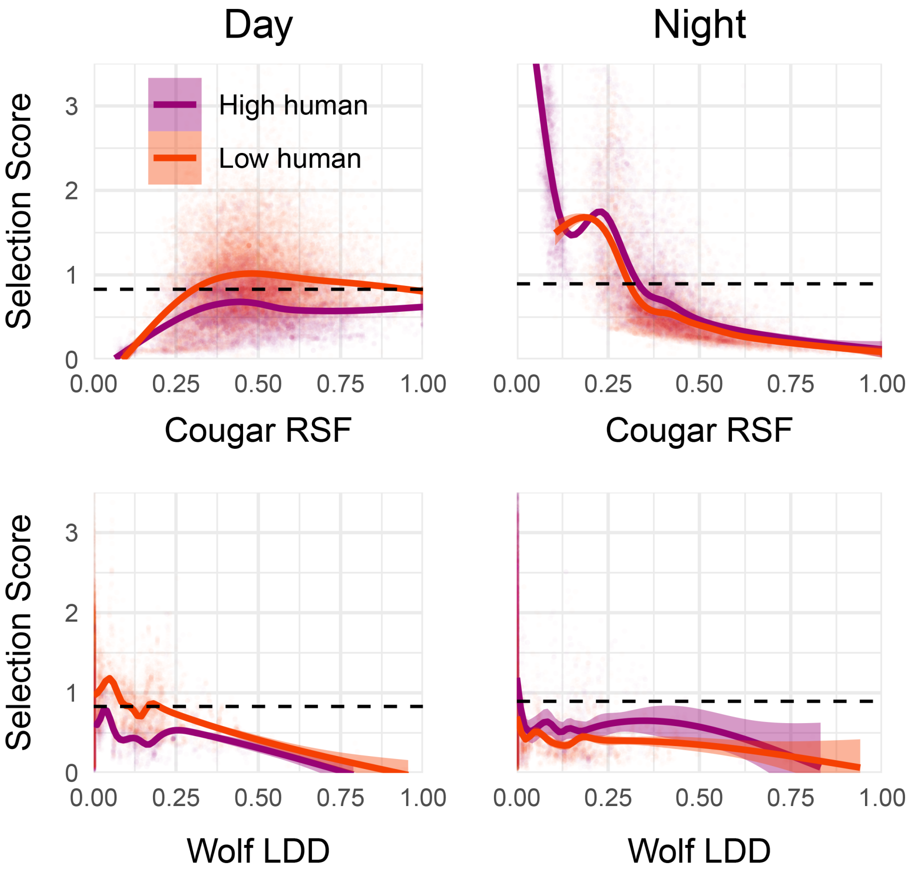

FIGURE 3 Average-effect plots show elk selection scores, *w*(*x*), at used locations relative to cougars (top row) and wolves (bottom row) in the day (first column) and at night (second column) across the range of predator index values in the summer. High versus low human areas were differentiated based on the mean human footprint index considering used and available locations (0.23 in the summer). Dashed lines identify the mean value of the selection score, *w*(*x*), at used locations. Trends for the fall were similar and are displayed in Appendix S2: Figure S2. LDD, localized density distributions; RSF, resource selection functions.

TABLE 2 Covariate estimates for step selection functions separately modeled for Global Positioning System-collared elk with calves ($n = 15$) and elk without calves ($n = 12$) in the summer (June–August) 2018–2020 in northeastern, WA, USA.

	Calf				No calf			
Covariate	$\widehat{\beta}$	**SE**	***z*-score**	***p***	$\widehat{\beta}$	**SE**	***z*-score**	***p***
Open-day	−2.94	0.18	−16.1	<0.0001	−4.22	0.22	−18.8	<0.0001
Open-night	3.16	0.18	17.5	<0.0001	5.05	0.24	21.0	<0.0001
Cougar-day	−0.54	0.14	−3.9	0.0001	0.37	0.14	2.6	0.009
Cougar-night	−2.79	0.22	−12.8	<0.0001	−3.13	0.22	−14.0	<0.0001
Wolf-day	−9.72	4.37	−2.2	0.026	−7.58	0.99	−7.6	<0.0001
Wolf-night	4.19	6.15	0.7	0.50	6.20	1.59	3.9	0.0001
Open × cougar	3.24	0.40	8.2	<0.0001	3.11	0.38	8.2	<0.0001
Open × wolf	−25.51	15.09	−1.7	0.09	1.32	2.35	0.6	0.58
Human-day	0.45	0.11	4.1	<0.0001	0.11	0.13	0.9	0.37
Human-night	0.57	0.17	3.4	0.0008	0.61	0.20	3.1	0.002
Elevation	0.44	0.03	14.0	<0.0001	0.42	0.04	10.1	<0.0001
Slope	−0.15	0.02	−9.7	<0.0001	−0.10	0.02	−5.4	<0.0001

Note: The interactive effect of night is additive to the daytime effect for that covariate. Thus, adding the coefficient estimates for day and night together for a covariate represents the response of elk at night.

open habitat (H_{1a}), and elk generally used more open habitat at night (Table 1). We predicted that elk would avoid cougars more strongly when neonates were most vulnerable, but we found instead that elk avoided cougars more strongly in the hunting season than in the summer, possibly reflecting human activities (although elk with calves did avoid cougars more so than elk without calves). In this system, humans hunted both elk and cougars in the fall (September–December), so mutual avoidance of humans may have increased overlap between these species, suggesting that cougars are perceived by elk as the lesser of two evils. It is therefore possible that hunting could increase elk encounter rates with cougars (Van Scoyoc et al., 2023).

Wolves drove the strongest response of the considered predictors, and in contrast with cougars, elk avoided wolves throughout the diel period. However, elk avoided wolves most strongly during the day in the summer but at night in the fall (Figure 2), suggesting differences in risk perception by season. Elk also used locations with all but the highest values of wolf index in the summer (maximum = 0.95), whereas we did not observe elk using locations with a wolf index above 0.64 in the fall, indicating that elk likely moved outside of core wolf pack territories in the fall. These patterns may be explained by wolf biology, human influences, or both. Wolf pups in Washington are typically born in mid to late April (Washington Department of Fish and Wildlife; unpublished data), such that a pack is typically anchored to a den site when elk calf parturition begins ~1 month later. In the summer, elk may be able to use areas within wolf pack territories with relative safety by avoiding den and rendezvous sites. Conversely, wolves range more widely in the fall (Mech & Boitani, 2007), potentially making encounter risk more unpredictable for elk and necessitating broader avoidance of wolf pack territories to reduce risk. When directly comparing habitat selection for elk with calves to elk without calves, elk with calves avoided wolves in the summer to an especially strong degree (Table 2; Appendix S2: Figure S1). Thus, even if pup-rearing sites make wolf distribution more predictable, female elk appeared to further modify habitat selection depending on vulnerability to reduce the risk of wolf encounters. Additionally, elk preferred areas with a relatively high human footprint index within wolf pack territories at night, suggesting that elk leveraged a human shield at night to reduce wolf risk (Figure 3). This effect was stronger in the summer than in the fall, perhaps reducing the risk of wolf predation for vulnerable calves via a human shield.

In many ways, elk responses to wolves in this system differed from what has been observed in protected areas, potentially reflecting habitat structure, predator density and human influences. Specifically, elk avoided wolves more strongly than cougars and did not consistently avoid open habitats subject to increasing wolf predation (H_{1b}). Stalking predators (cougars) are expected to leave more predictable risk cues than wider-ranging coursing predators (wolves), eliciting stronger antipredator defenses from prey (Preisser et al., 2007). Although antipredator defenses can take many forms, including those that cannot be captured by quantifying habitat selection such as vigilance and herding behavior (Wirsing et al., 2021), it is nevertheless surprising that elk appeared to avoid wolves more strongly than cougars. Predator density may counterintuitively explain the relative response of elk to cougars and wolves. According to the risk allocation hypothesis (Lima & Bednekoff, 1999), prey should make behavioral trade-offs to reduce predation risk where risk is high relative to a variable background, but not under chronically high predation risk. Given that cougars likely occur at densities 10-fold greater than wolves in this system and were more uniformly distributed (Beausoleil et al., 2021), cougars may have represented a chronically high background of risk that elk could not avoid via habitat selection. It may also be that elk were effectively able to reduce predation risk from cougars by using open habitats at night when cougars hunt. By contrast, elk apparently avoided wolves by using areas outside core wolf pack territories.

Differences in predator distribution may have ultimately reflected human activities. Bassing (2022) and Prugh et al. (2023) found that wolves consistently avoided anthropogenic activities in this system regardless of the indices considered (i.e., roads, human landscape modification) or scale of analysis. In contrast, cougar avoidance of humans depended on the index considered and scale of analysis, suggesting that cougars are somewhat more tolerant of anthropogenic activities (c.f., Bassing, 2022), perhaps due to strong nocturnality. The difference in response to humans may additionally explain why elk appear to leverage a human shield (H_{3b}) against wolves but not cougars (Figure 3). It is also possible that differences in elk response to cougars and wolves reflected the modeling frameworks we used as indices of predator presence. Cougars likely fully occupied the landscape, so we used RSFs (Manly et al., 2007) to describe their habitat associations within the home range (Johnson, 1980). In contrast, wolf distributions were patchy, so we used LDDs to represent the location of pack territories and the intensity of use within them (Kittle et al., 2016). Cougars and wolves may have additionally responded to each other, and to the human footprint contingent on the time of day, but we could not account for these interactions when modeling wolf LDDs. Additionally, elk's response to cougars, wolves and humans could reflect the landscape features (e.g., water bodies, habitat type, alternate prey) ultimately governing the distribution of predators. However, we controlled for the effects of topography by including elevation and slope covariates, and we did not find concerning correlations between predator distributions and landscape features in other analyses of this system (Bassing, 2022), so we think it is more likely that elk are responding to predators rather than landscape correlates.

We had predicted that in areas of higher wolf activity, elk would reduce the use of open habitat (H_{1a}) to avoid areas where wolves hunt most effectively, but this was not consistently the case. Instead, elk chose more open habitats with higher wolf use in the fall, as did elk without calves in the summer (H_{1b}). Elk also used more open habitats at night at nearly all levels of wolf and cougar use. Using Hidden Markov Models to examine the same data, Bassing (2022) evaluated changes in elk movement behavior and likewise found that elk in this system responded similarly to cougars and wolves, rather than responding depending on predator hunting mode. Similarly, Barker et al. (2023) found that wolves primarily killed elk in more forested areas within the anthropogenic landscape of Jackson Hole, WY, USA, counter to the prevailing notion that prey is most vulnerable to wolves in open habitat (Kohl et al., 2018, 2019). Unlike in many areas, wolves in this system preferred forested habitat across seasons, perhaps to avoid humans (Bassing et al., 2023), and diet analysis suggests that wolves were targeting moose within these forests (L. Satterfield; unpublished data). Thus, by shifting toward open habitats in areas of higher wolf presence, elk may have reduced the risk of a wolf encounter. Collectively, these findings indicate that outcomes of predator–prey interactions based on the hunting mode of the predator and their habitat associations may differ between protected areas and human-modified landscapes and in landscapes with abundant alternate prey.

Humans play a critical role shaping predator–prey dynamics in this system via multiple mechanisms. We found support for the human super predator hypothesis (H_{3a}), because humans caused 80% of the mortalities of adult female elk (mainly through hunting), and elk consistently avoided human-impacted areas during the day. Human activities may have additionally contributed to elk avoiding open areas in the day, because ungulates in harvested populations have been shown to perceive higher risk from humans where visibility is greater (Gaynor et al., 2022). Indeed, elk avoided open areas during the day more strongly in the fall hunting season than in the summer. We also found evidence that elk leveraged the human shield (H_{3b}) against wolves at night, but not against cougars. By shifting toward areas with a relatively high human footprint at night, elk may have exploited agricultural food subsidies associated with human landscape modification (Rouleau & Ouellet, 2002). Because lactation requires a high caloric intake, elk may have preferred areas with higher human presence in the summer to utilize the relatively nutritious agricultural areas (Rouleau & Ouellet, 2002).

Our approach to quantifying the influences of people and predators has some limitations. The human footprint index encompasses many aspects of anthropogenic activities, including urbanization, transportation infrastructure, agriculture, and forestry, and human impacts on ecosystems are myriad and operate through many pathways (Guiden et al., 2019), which we were unable to fully capture here in a single indicator. It is possible that more specific measures of human impacts and activities shape predator–prey interactions in different ways from the generic approach we used. We did not collar black bears during this study, and thus we were not able to account for bear presence within the step selection functions. Although black bears may have been responsible for up to ~50% of neonatal mortalities, only very young elk are vulnerable to black bear predation (Griffin et al., 2011) and all elk calves were born (and collared) within a 3-week window, so the time period when bears should have affected elk movement would have been limited to a brief period. We also only investigated the movement of female elk, and male elk may display different movement patterns.

This work yields critical insights for understanding and managing predator–prey dynamics in human-dominated systems. Our findings build on prior research showing that ungulates use temporally dependent habitat selection to manage risk from multiple nonhuman predators (Kohl et al., 2018, 2019) by incorporating humans into the dynamic landscape of fear. By accounting for differences in habitat use between day and night, our results suggest that humans can function as super predators (Darimont et al., 2015) while also shielding elk against predation (Berger, 2007; Prugh et al., 2023). Although the elk population was increasing in this system (Ganz, 2022), the consequences of humans simultaneously acting as a shield and super predator have the potential to be detrimental and may be important to consider for conservation (Prugh et al., 2023). For example, differences in elk responses to cougars and wolves suggest that accounting for interactions between the predator species and humans will be key to predicting the degree to which humans have the potential to function as a shield for prey. However, elk leveraging the human shield could increasingly come into conflict with humans. Thus, continued research on the effects of humans on predator–prey interactions is vital to sustaining wildlife populations outside of protected areas.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Anonymized data (Ganz et al., 2024) are available in Dryad at http://doi.org/10.5061/dryad.sj3tx96br. Complete data supporting this research are sensitive and not available publicly; telemetry relocations of collared elk are available to qualified researchers by contacting the Washington Department of Fish and Wildlife and requesting elk telemetry data from the Washington Predator–Prey Project.

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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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