

## ARTICLE

# Logging, linear features, and human infrastructure shape the spatial dynamics of wolf predation on an ungulate neonate

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## Abstract

Humans are increasingly recognized as important players in predator-prey dynamics by modifying landscapes. This trend has been well-documented for large mammal communities in North American boreal forests: logging creates early seral forests that benefit ungulates such as white-tailed deer (*Odocoileus virginianus*), while the combination of infrastructure development and resource extraction practices generate linear features that allow predators such as wolves (*Canis lupus*) to travel and forage more efficiently throughout the landscape. Disturbances from recreational activities and residential development are other major sources of human activity in boreal ecosystems that may further alter wolf-ungulate dynamics. Here, we evaluate the influence that several major types of anthropogenic landscape modifications (timber harvest, linear features, and residential infrastructure) have on where and how wolves hunt ungulate neonates in a southern boreal forest ecosystem in Minnesota, USA. We demonstrate that each major anthropogenic disturbance significantly influences wolf predation of white-tailed deer fawns ( $n = 427$  kill sites). In contrast with the “human shield hypothesis” that posits prey use human-modified areas as refuge, wolves killed fawns closer to residential buildings than expected based on spatial availability. Fawns were also killed within recently-logged areas more than expected. Concealment cover was higher at kill sites than random sites, suggesting wolves use senses other than vision, probably olfaction, to detect hidden fawns. Wolves showed strong selection for hunting along linear features, and kill sites were also closer to linear features than expected. We hypothesize that linear features facilitated wolf predation on fawns by allowing wolves to travel efficiently among high-quality prey patches (recently logged areas, near buildings), and also increase encounter

Sean M. Johnson-Bice, Thomas D. Gable, and Austin T. Homkes contributed equally.

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rates with olfactory cues that allow them to detect hidden fawns. These findings provide novel insight into the strategies predators use to hunt ungulate neonates and the many ways human activity alters wolf–ungulate neonate predator–prey dynamics, which have remained elusive due to the challenges of locating sites where predators kill small prey. Our research has important management and conservation implications for wolf–ungulate systems subjected to anthropogenic pressures, particularly as the range of overlap between wolves and deer expands and appears to be altering food web dynamics in boreal ecosystems.

#### KEY WORDS

anthropogenic disturbance, boreal forest, *Canis lupus*, ecological trap, habitat fragmentation, human shield hypothesis, movement, *Odocoileus virginianus*, off-highway vehicles, olfaction, predator–prey dynamics, white-tailed deer

## INTRODUCTION

Human-induced changes to animal behavior through both direct and indirect pathways have been documented across a wide variety of ecosystems. Humans directly alter wildlife behavior through top-down forces such as hunting (Ciuti et al., 2012; Hertel et al., 2016; Lone et al., 2015), and through less invasive activities such as hiking and ecotourism (Coppes et al., 2017; Larm et al., 2021). Indirect effects of humans on wildlife behavior can also occur through physical alterations to the environment, such as anthropogenic noise and light pollution (Sanders et al., 2021; Shannon et al., 2016), residential development (Wang et al., 2017), and resource extraction practices (Blum et al., 2015; Johns, 1986). These forces, in turn, alter wildlife behavioral traits (Doherty et al., 2021; Sih et al., 2011; Wilson et al., 2020).

Wildlife often exhibit different behavior in and around human settlements and infrastructure relative to conspecifics in less disturbed areas. For instance, mammalian movements are generally shorter near human-modified areas (Doherty et al., 2021; Tucker et al., 2018). Although one meta-analysis found mixed support for smaller home ranges in disturbed areas among mammalian species (Doherty et al., 2021), other studies have documented these traits across gradients of human influence (Main et al., 2020; O'Donnell & delBarco-Trillo, 2020). Indeed, one global analysis demonstrated mammalian population densities are greater near human-modified areas (Tucker et al., 2021), probably due largely to anthropogenic resource subsidies (Tucker et al., 2018). Animals also adjust their space use and activity patterns in response to human presence (Gaynor et al., 2018; Moll et al., 2018; Wang et al., 2015). However, some prey and subordinate predators benefit from top predator sensitivity to humans, or the displacement of predators by

humans (Hebblewhite et al., 2005; Leighton et al., 2010). These behavioral patterns have informed the “human shield hypothesis” (Berger, 2007; Muhly et al., 2011), which postulates that lower trophic levels can benefit from human activity by using human-modified areas as a refuge. Support for the human shield hypothesis appears context dependent. For example, studies from different cities have demonstrated that subordinate predators may or may not use urban areas as refuge from dominant predators (Gámez & Harris, 2021; Moll et al., 2018; Parsons et al., 2019). Nonetheless, numerous prey species have shown significant behavioral and space-use shifts toward human landscape features in response to predation risk (Atickem et al., 2014; Berger, 2007; Gaynor et al., 2022; Hebblewhite & Merrill, 2009; Rogala et al., 2011; Shannon et al., 2014).

Anthropogenic development and resource extraction practices often spawn linear features across landscapes (e.g., roads, seismic lines, power lines) that alter predator–prey dynamics. Predator functional responses (i.e., foraging efficiency) are driven by predator searching and handling times, the former of which is influenced by the rate that predators encounter prey. Theoretical predictions and results from simple model systems indicate predators increase encounter rates when they make directed (or ballistic) movements compared with sinuous movements (Bartumeus et al., 2008; Noonan et al., 2023; Visser & Kiørboe, 2006). Thus, the addition of linear features to a landscape should theoretically increase predator encounter rates with prey by facilitating directed movements. Predators can also move faster and cover more ground while traveling on linear features, thereby increasing their foraging efficiency (Dickie et al., 2017; Zimmermann et al., 2014).

Previous work has demonstrated that predators such as wolves (*Canis lupus*) and American black bears

(*Ursus americanus*) show strong selectivity for linear features in North American boreal forests (e.g., Kittle et al., 2017; Latham, Latham, Boyce, & Boutin, 2011; McKenzie et al., 2012; Newton et al., 2017), probably because linear features increase their foraging efficiency (Dickie et al., 2017, 2020; McKenzie et al., 2012). At the same time, timber harvest practices have created large stands of early successional forest, which contains the preferred forage for ungulates such as moose (*Alces alces*) and deer (*Odocoileus* spp.) (Alverson et al., 1988; Courtois et al., 2002; Litvaitis, 2001). Moose and deer density have increased in many systems due to the greater forage supply from timber harvesting and climate change (Dawe & Boutin, 2016; Frelich et al., 2012; Fuller et al., 2023; Laurent et al., 2021; Street et al., 2015), leading to apparent competition with the rarer endemic woodland caribou (*Rangifer tarandus caribou*) by subsidizing predators like wolves (Frenette et al., 2020; Latham et al., 2013; Serrouya et al., 2021). The combined effects of development and resource extraction practices have thus greatly altered local predator-prey dynamics (Boucher et al., 2022; Courbin et al., 2014; DeMars & Boutin, 2018; McKay et al., 2021; McKay & Finnegan, 2022; Whittington et al., 2011). However, previous studies that evaluated the effects of linear features on predator-prey dynamics have predominately focused on large-scale features (e.g., oil pipelines, transmission lines) and less on smaller-scale features often found in boreal forests (e.g., all-terrain vehicle [ATV] and hiking trails, logging roads). Understanding how generalizable these effects of human activity are to other predator-prey systems is also unclear, particularly during times when small prey such as ungulate neonates are the dominant food sources for predators.

Wolves in southern boreal forests primarily travel as packs and hunt adult ungulates during fall and winter months (Mech & Boitani, 2003; Mech, Smith, & MacNulty, 2015), but during the ice-free season they rely heavily on small prey (ungulate neonates, beavers [*Castor canadensis*]) and forage largely individually (Barber-Meyer & Mech, 2015; Gable, Windels, Romanski, & Rosell, 2018). Because deer fawn parturition dates are synchronized within landscapes, deer fawns are a resource pulse that wolves and other predators can rapidly capitalize on (Kunkel & Mech, 1994). However, survival rates of fawns increase greatly by ~8 weeks of age when they are more mobile and thus better able to evade most predators (Carstensen et al., 2009; Grovenburg et al., 2011; Nelson & Woolf, 1987; Rohm et al., 2007), which corresponds with a dramatic decrease in fawns in wolf diets in northern Minnesota (Fuller, 1989; Gable, Windels, & Bruggink, 2017; Gable, Windels, Bruggink, & Barber-Meyer, 2018). During this

period of vulnerability (hereafter the “early fawning season”), fawns rely on hiding and cryptic coloration, in addition to grooming behavior from their mothers to reduce odorants (Conover, 2007; Jackson et al., 1972), to avoid detection by predators (Nelson & Woolf, 1987). Fawn “hiding spots” are determined by a two-level selection process (Bowyer et al., 1998; Michel et al., 2020). The first level is where the dams (mothers) select to forage during summer within their home ranges, and the second is where fawns select to bed within dam foraging patches (Grovenburg et al., 2010). During summer, dams in the boreal forest preferentially use upland deciduous and mixed forest stands (Kohn & Mooty, 1971), and fawns generally select for bed sites with dense and tall vegetative cover that provides visual concealment from predators within forest stands (Grovenburg et al., 2010; Michel et al., 2020; Uresk et al., 1999). Predation risk for deer during the summer can be very high, with one study indicating fawns can be at risk for predation nearly daily (Mech, Morris, & Barber-Meyer, 2015). However, the exact strategies wolves and other predators use to locate hidden fawns are not well known (Ruprecht et al., 2022). Because deer fawns primarily remain motionless while bedding during the early fawning season, wolves probably use active searching strategies to seek out and locate fawns in contrast with the cursorial strategies wolves use when hunting large ungulates (i.e., out-running and outlasting prey). Moreover, because fawns hide in concealed areas, wolves probably rely on nonvisual sensory cues (e.g., olfaction) to locate fawns.

We evaluate how the combined effects of all major human landscape modifications in a southern boreal forest ecosystem influence wolf-ungulate neonate predator-prey ecology. Specifically, we investigate the relative influence that human-created linear features, timber harvest practices, and human infrastructure have on spatial patterns of wolf predation on white-tailed deer fawns (*Odocoileus virginianus*). Our objectives were to evaluate (1) whether wolves hunt or kill white-tailed deer fawns nearer to human-modified landscape features than would be expected based on spatial availability, (2) whether wolves hunt or kill fawns more often in recently logged areas, (3) whether any human-modified landscape features influence the relative probability of wolf hunting success by comparing kill site locations with typical hunting locations, and (4) whether fawn kills were located in areas with denser-than-average vegetation. Collectively, this evaluation enabled us to investigate how human-altered landscapes shape wolf-ungulate neonate dynamics, and assess under what conditions the human shield hypothesis may break down.

Assuming wolves adjust their foraging strategies during the early fawning season, optimal foraging theory

suggests they will selectively hunt deer fawns in high-quality resource patches to minimize time spent searching for fawns (Demma et al., 2007; Demma & Mech, 2009). We would also expect wolves to use available human-created linear features to travel between these patches because linear features allow wolves to travel more efficiently and probably increase their encounter rates with fawns. Dickie, Serrouya, et al. (2022) hypothesized that linear features may be particularly beneficial for predators hunting small prey. Small prey require short handling times, so being able to travel efficiently between high-quality resource patches may be even more important for predators to acquire sufficient food compared to when they hunt large prey. Therefore, we predicted that wolves hunt and kill fawns closer to linear features than would be expected based on availability. We also hypothesized that recently-logged areas provide good forage and concealment cover for deer, and therefore predicted that wolves hunt and kill fawns closer to, and more often within, recently logged areas. We hypothesized that wolves primarily detect deer fawns via olfaction because fawns typically hide in densely vegetated areas. We therefore predicted that concealment cover would be greater at fawn kill sites than at paired random sites. Finally, we evaluated support for the human shield hypothesis by evaluating spatial patterns of wolf predation on fawns in relation to human infrastructure. Evidence supporting the human shield hypothesis would demonstrate kill sites and/or hunting locations far from human infrastructure, as reported in other studies (Kaartinen et al., 2005; Kojola et al., 2016; Yovovich et al., 2021). Wolves, like many large predators, often show sensitivity to human influence, and we therefore hypothesized that wolves avoid human structures when moving/hunting to avoid interacting with humans. However, based on direct observations in our study area, we suspected that deer tend to congregate near human structures for either safety from predators or food subsidies from people. Given these observations, we predicted that most hunting locations would be farther from buildings but fawn kills would be closer to buildings relative to spatial availability.

## METHODS

### Study area

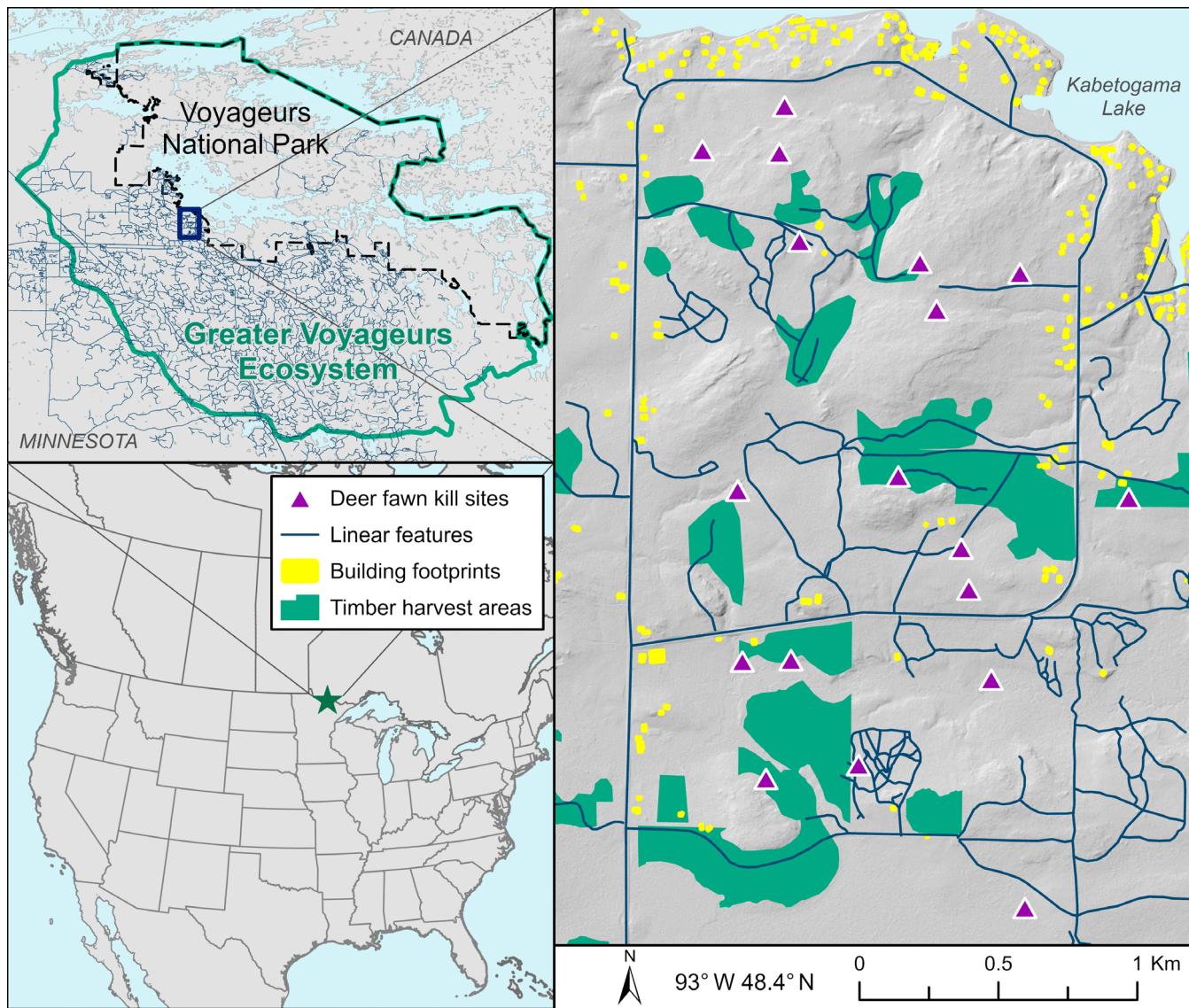
The Greater Voyageurs Ecosystem (GVE) is an ~1960-km<sup>2</sup> study area located in northern Minnesota, USA that contains Voyageurs National Park (VNP) (882 km<sup>2</sup>) and a large area south of the park that consists of the Kabetogama State Forest, the Superior National

Forest, St. Louis County land, timber company land, and privately-owned parcels (Figure 1). The GVE is in the Laurentian Mixed Forest Province and contains four major lakes—Kabetogama, Rainy, Namakan, and Sandpoint—that cover a total of 342 km<sup>2</sup>. The GVE consists of a mix of southern boreal and northern hardwood forests, bogs and swamps, and beaver ponds. Forest management and human development have not been permitted inside the boundaries of VNP since its creation in 1975, although a few linear features associated with these activities still persist in some areas of the park. Timber harvest is prevalent throughout the area south of VNP. Most timber stands in the area are harvested using partial or clearcut harvesting practices, with both methods leaving some fraction of trees uncut to aid in stand regeneration. The result from these practices is a landscape typified with a mosaic of regenerating timber stands, dominated by young aspen (*Populus* spp.), and interspersed with mature mixed forests and wetlands (Gable & Windels, 2018). An extensive network of logging roads fragments the forests and links timber stands to gravel roads. Year-round human population density is low (~1–2 people/km<sup>2</sup>), but the area sees an influx of seasonal tourists and visitors during summer and fall.

The GVE has supported a stable wolf population (average density of 57.5 wolves/1000 km<sup>2</sup>) for the past 8 years and probably several decades (Gable et al., 2022). Wolves were federally listed as an endangered species throughout the duration of this study, so no legal harvesting or hunting of wolves occurred. However, illegal killing by humans is a common source of wolf mortality in the parts of the study area outside of VNP (Cassidy et al., 2023). White-tailed deer are the primary annual prey for wolves in the GVE with beavers an important secondary prey (average beaver density of 1.0–1.6 colonies/km<sup>2</sup>). White-tailed deer are common in the GVE with pre-fawn densities of 2–4 deer/km<sup>2</sup> during 2014–2021 (Gable, Windels, & Olson, 2017). Moose are relatively rare in VNP (<0.15 moose/km<sup>2</sup>) and south of the park (<0.05 moose/km<sup>2</sup>; Gable, Windels, & Olson, 2017; Windels & Olson, 2019).

### Wolf capture and collaring

We captured 28 wolves during 2016–2021 using rubber-padded foothold traps and fitted them with GPS-collars set to record locations every 20 min. All capture and handling of wolves was approved by the Institutional Animal Care and Use Committees for the National Park Service (MWR\_VOYA\_WINDELS\_WOLF: Appendix A) and University of Minnesota (1905-37051A). For additional



**FIGURE 1** Map of the Greater Voyageurs Ecosystem (GVE), in northern Minnesota, USA. The upper left panel shows the GVE (green outline), Voyageurs National Park (dashed black line), and all linear features within and around the GVE (thin blue lines). The panel on the right shows a subset of fawn kills included in this study (purple/white triangles) in an area surrounded by linear features, timber harvest areas, and human structures (building footprints).

details on capture and handling of wolves, see Gable et al. (2020).

### Wolf hunting locations and finding wolf-killed fawns

During 2016–2021, we visited clusters of locations from GPS-collared wolves to locate kills. We defined a cluster as two or more consecutive locations within 200 m of the first location, and >500 m from the current home site (Gable et al., 2020). At clusters, we systematically searched a 20-m radius around every GPS location in the cluster for evidence of a kill or bedding (Gable et al.,

2016; Metz et al., 2011). Evidence of a kill included presence of bone fragments, prey hair, teeth, fresh blood, and/or drag marks (Cristescu et al., 2022). We considered a fawn to have been killed by a collared wolf if: (1) the estimated age of the fawn remains and disturbance were consistent with when a collared wolf was at the site, (2) there was no evidence of predators in addition to wolves, and (3) there was clear evidence of a struggle at the site. Once identified, we recorded the specific location of kills using handheld GPS receivers. Wolves are almost always hunting when traveling and are highly-flexible predators that readily exploit opportunistic encounters with prey when moving (Mech, Smith, & MacNulty, 2015). Therefore, all GPS locations not part of a GPS

cluster and >500 m from the home site represent “hunting locations” (DeCesare, 2012).

## Habitat and landscape covariates

### Data sources

We assessed wolf hunting and kill locations in relation to human-created linear features, human structures, timber harvest areas, and land cover types. We generated an extensive linear features layer from our field work in the GVE. The linear features layer included dirt and paved roads, recreational trails (ATV trails), snowmobile trails, hiking trails, powerlines, and hunting lanes (cleared paths radiating out from a hunting blind). Many, if not most, of the linear features in the area were created for timber harvest practices but have since been maintained by recreational users (ATV users, hunters), which prevents regeneration on these features. It is also common for local residents to create linear features for recreational purposes. Our objective was to assess wolf use of all human-created and -maintained linear features available to them, not simply those accessible to vehicles or visible from aerial imagery, and therefore included minor features (e.g., hiking trails, hunting lanes) in our linear feature network.

To evaluate the role human infrastructure had on wolf-deer fawn spatial dynamics, we combined the Microsoft US building footprints layer (Microsoft, 2018) with the OpenStreetMap building footprints layer (OpenStreetMap contributors, 2022; [openstreetmap.org](https://openstreetmap.org)).

We mapped all timber harvest activity in the area by creating polygonal features of every area harvested in the GVE from 2000 to 2021 using a combination of aerial imagery and timber sale records from the United States Forest Service, Minnesota Department of Natural Resources, Koochiching County, and Saint Louis County. This method allowed us to identify the approximate age ( $\pm 1$  year) of each harvested area. Harvested areas  $\leq 15$  years old were dominated by early successional forest (largely aspen), which deer select preferentially (Darlington et al., 2022). We binned the harvest areas into three age-since-harvest categories: 0–5 years post-harvest, 6–10 years post-harvest, and 11–15 years post-harvest.

We classified the dominant land cover type around each location using the harvest polygonal data and the 2019 National Land Cover Data (NLCD) (Dewitz, 2021), which was obtained during the middle of our study period. We first removed all areas classified as “open water” in the NLCD layer, and then reclassified the remaining categories into six different cover types:

“Herbaceous” (Herbaceous, Hay/Pasture, Cultivated Crops types), “Developed” (Barren Land, all Developed classes, which generally represent paved and gravel roads in the area), “Wetlands” (Woody Wetlands, Emergent Herbaceous Wetlands), “Deciduous Forest” (Deciduous Forest, and Shrub/Scrub classes that were largely in harvested areas), “Mixed Forest,” and “Evergreen Forest.” We then replaced the NLCD cover type with the corresponding age-since-harvest group (0–5, 6–10, or 11–15 years post-harvest) for the harvested areas for each year 2016–2021, which resulted in annual land cover layers for each year. Land cover type for each hunting location was extracted at each GPS point, whereas land cover for kill sites was determined by taking the dominant cover type (greatest percentage among all types) within a 30-m buffer of the kill site.

## Assessing visibility at kill sites

We assessed concealment cover at a subset of kill sites by measuring horizontal visibility at two different spatial scales: within-patch and among-patch. We assessed within-patch concealment by comparing horizontal visibility at kill sites (where we assumed the fawn was bedded when it was killed) with locations 50 m from kill sites in each cardinal direction (Appendix S1: Figure S1). Among-patch concealment was assessed by comparing visibility at kill sites with visibility at random locations within each wolf’s territory (one random location for each kill identified from that wolf). At each location, we measured horizontal visibility by placing a 30.5 cm  $\times$  10.0 cm cover board on the ground (which was approximately the size of a bedding fawn; Appendix S1: Figure S1; Alldredge et al., 1991; Griffith & Youtie, 1988). We recorded the maximum distance at which any part of the cover board could be seen from each cardinal direction at 1 m above the ground to represent the perspective of a standing wolf. We also recorded visibility at 5, 10, and 15 m from the cover board in each direction. We only assessed visibility during 2016 and 2017 (data from seven wolves) due to logistic constraints.

## Statistical analyses

### Assessing landscape characteristics of wolf kill sites and hunting locations

We applied a used-available study design to evaluate landscape characteristics that influenced where wolves hunted fawns (“hunting model”), landscape characteristics influencing where wolves killed fawns (“kill site

model”), and a comparison of how landscape characteristics may influence the relative probability of wolf hunting success by comparing kill site and hunting locations (i.e., comparing “successful” vs. “unsuccessful” hunting locations; “kill vs. hunting location comparison”; Smith et al., 2020). We restricted our analysis to only the “early fawning season,” which represented the time when fawns are most vulnerable to predation and frequently rely on concealment cover within dense vegetation for protection. Average parturition date is 26 May or 27 May (Carstensen et al., 2009), so we defined the early fawning season as 27 May to 15 July of each year.

We assessed availability in the hunting model by generating 10 random (“available”) locations within the territory of each collared wolf for every one hunting location recorded for that individual using ArcGIS Pro (version 2.8; Esri, 2021). Similarly, we generated 100 random locations within each wolf’s territory for every one kill location for the kill site model. Summer territory boundaries (defined as 1 May to 31 October) for each wolf were created using a 99% kernel density estimator from GPS locations (Gable et al., 2022). Land cover types for random locations were assigned using the same methods as for kill and hunting locations (detailed earlier). We measured the Euclidean distance from each kill site, hunting location, and random location to the nearest linear feature, human structure, and timber harvest area (all age classes combined) using ArcGIS Pro 2.8.

We compared hunting and kill site locations with their respective random locations using generalized linear mixed models (GLMM) with a logit link (i.e., logistic regression) using the “glmer” function from the *lme4* R package (Bates et al., 2015). Available locations were given a weight of 1000, while used locations had a weight of 1 (Fieberg et al., 2021); weighting available locations in this manner provides similar results as to fitting a model with a much larger sample size of available locations but in a computationally efficient manner (Northrup et al., 2022). Similarly, we used a GLMM with a logit link to evaluate how each variable of interest affected hunting and kill site locations (kill vs. hunting location comparison), in which kills were coded as 1 and hunting locations as 0. In each model, we log + 1 transformed the continuous covariates (distance to nearest harvested area, linear feature, and human structure) because the data were heavily skewed. When evaluating distance to nearest harvested area, we did not distinguish among the different age groups (0–5, 6–10, 11–15 years post-harvest) due to high collinearity among distances to each of these age classes. Land cover type was a categorical variable in all models with “Deciduous Forest” set as the reference level. We included a random intercept term for wolf ID for each model to account for nonindependence of

individual wolves (Fieberg et al., 2021; Fieberg & Johnson, 2015). Although including both random slope and random intercept terms may account for greater uncertainty in coefficient estimates (Muff et al., 2020), we did not include random slope terms due to model convergence issues. Variance inflation factor values were  $<4$  for all covariates, which indicated collinearity was not a concern (Dormann et al., 2013). We evaluated the importance of individual covariates with an  $\alpha = 0.05$  and 95% confidence intervals (CIs) that did not overlap 0. We carried out all analyses using R version 4.2.0 (R Core Team, 2022). All data and code are available from the figshare data repository (Johnson-Bice et al., 2023).

### Spatial predictions of the average effect of model variables

For each model tested, we generated spatial predictions at a  $30 \times 30$  m pixel resolution based on the relative probability of use for each pixel in the study area (excluding areas identified as “Open Water” in the 2019 NLCD data) using the terra R package (Hijmans, 2022). We calculated the relative selection strength (RSS) for each pixel, which is a quantitative measure of the relative magnitude of selection for a given location calculated as:  $\exp(\beta_1 \times X_1 + \beta_2 \times X_2 + \beta_3 \times X_3 + \dots)$ , where  $\beta_1$  is the coefficient estimate for variable  $X_1$ ,  $\beta_2$  is the coefficient estimate for variable  $X_2$ , and so on from each fitted model (Avgar et al., 2017; Fieberg et al., 2021; Northrup et al., 2022).

Predicting RSS values throughout the full study area allowed us to visualize wolf selection/use of areas in two ways. First, we created maps to visualize areas in the GVE where wolves are more or less likely to hunt and/or kill deer fawns. Second, by extracting the predicted RSS value along with the land cover type and metrics related to distance to human-modified landscape features (nearest timber harvest area, linear feature, and human structure) for each pixel, we were able to visualize the change in the probability of use for each variable tested in each model. In other words, predicting RSS values throughout the full study area accounted for both the selection and full availability of each variable tested, and allowed us to plot the population-level effect of each independent variable while averaging over all values of other variables (Avgar et al., 2017). This approach complemented our logistic modeling analyses because it provided an additional way to evaluate the data by generating population-level predictions (i.e., predictions from only estimates of fixed effects). It also helped elucidate the effects of land cover type in each model by generating spatial predictions, since interpreting

categorical variables in resource selection models can be notoriously difficult (Fieberg et al., 2021).

For each of the continuous covariates tested in each model (distance to nearest harvested area, linear feature, and human structure), we plotted the population-level relative probability of use using generalized additive models with cubic regression splines. We used boxplots to visualize the distribution of RSS values for each land cover type in each model, and compared these plots to the median RSS value for each model throughout the full study area. Prior to making the maps and plotting the average effect of each variable, we re-scaled RSS values to have a minimum of 0 and maximum of 1 for better cross-model comparison. We used 2019 as the reference year for this process.

## Kill site visibility analysis

Visibility (averaged from all cardinal directions) was highly correlated at 5, 10, and 15 m from the cover board. Thus, we formally compared only the average maximum distance (in meters) that the cover board was visible at the subset of kills and paired random locations for both the within and among-patch analyses. We used linear mixed-effects models with “wolf ID” as a random intercept term to account for multiple kills from the same individuals.

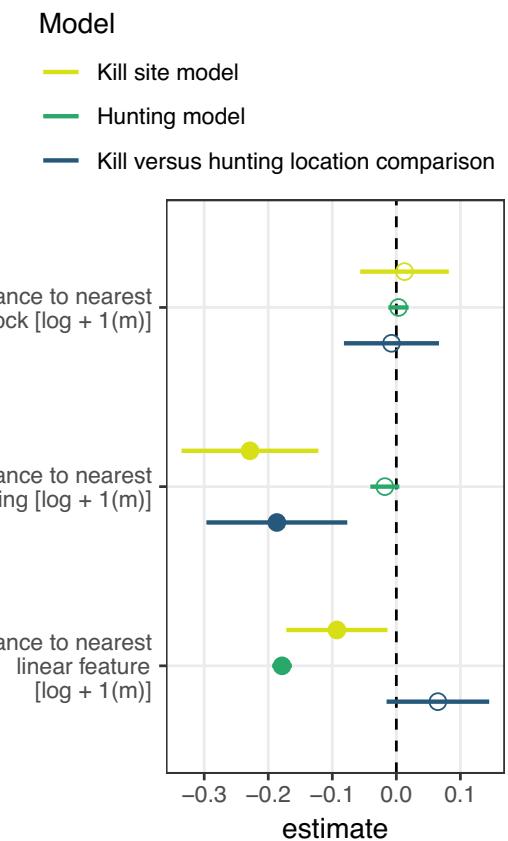
## RESULTS

During 2016–2021, we searched 21,725 clusters from 28 wolves and identified 570 fawns killed by wolves. Of those, 427 kills from 26 wolves (31 wolf-seasons; we collected multiple seasons of kill site data from five wolves) occurred during the early fawning season (27 May to 15 July). We collected 11,185 “hunting locations” from these 26 wolves during the early fawning season.

### Assessing landscape characteristics of wolf kill sites and hunting locations

#### Hunting and kill site models

Wolves hunted closer to linear features than would be expected based on spatial availability (i.e., closer to linear features on average than the “available” points used for comparison;  $\beta = -0.178$ , 95% CI =  $-0.194$ ,  $-0.163$ ,  $p < 0.001$ ; Figure 2, Table 1). Relative to the NLCD deciduous forest cover type, wolves selected for 0–5 years post-harvest areas, and developed cover types, and herbaceous



**FIGURE 2** Coefficient estimates describing the influence of proximity to anthropogenic landscape features (nearest timber harvest area, nearest human structure, nearest linear feature) from three different models evaluating wolf–deer fawn spatial dynamics in the Greater Voyageurs Ecosystem in northern Minnesota, USA. Estimates where 95% CIs overlapped 0 have an open point. Wolves hunted and killed fawns closer to linear features than would be expected based on availability. Wolves also killed fawns closer to human structures than expected based on availability, and relative to where wolves typically hunted fawns. Proximity to timber harvest areas had no effect on hunting or kill locations.

cover types when hunting fawns (Table 1) (NLCD developed cover types largely correspond to roads and parking lots in the area). However, distance to nearest harvested area and human structure had no influence on wolf hunting selection (Figure 2, Table 1).

Wolves killed fawns closer to linear features ( $\beta = -0.093$ , 95% CI =  $-0.172$ ,  $-0.014$ ,  $p = 0.021$ ) and human structures ( $\beta = -0.229$ , 95% CI =  $-0.335$ ,  $-0.122$ ,  $p < 0.001$ ) than would be expected based on availability (Figure 2, Table 1). Relative to deciduous forest cover type, wolves were less likely to kill fawns in evergreen forest (Table 1). We also found that wolves appeared to kill fawns more often in 0–5 year post-harvest areas than deciduous areas, although this pattern did not reach statistical significance ( $p = 0.063$ ). However, similar to hunting model results, proximity to the timber harvest

**TABLE 1** Results from logistic generalized linear mixed models evaluating wolf (*Canis lupus*) selection of land cover types and proximity to human created linear features, human structures, and recently harvested areas when hunting and killing white-tailed deer (*Odocoileus virginianus*) fawns from late May to mid-July of 2016–2021 in Minnesota, USA.

Variable	Kill site model				Hunting model				Kill versus hunting location comparison			
	Estimate	Conf. low	Conf. high	p	Estimate	Conf. low	Conf. high	p	Estimate	Conf. low	Conf. high	p
Intercept	<b>-9.604</b>	<b>-10.35</b>	<b>-8.862</b>	<0.001	<b>-8.296</b>	<b>-8.480</b>	<b>-8.112</b>	<0.001	<b>-2.351</b>	<b>-3.169</b>	<b>-1.532</b>	<0.001
Distance to linear feature	<b>-0.093</b>	<b>-0.172</b>	<b>-0.014</b>	0.021	<b>-0.178</b>	<b>-0.194</b>	<b>-0.163</b>	<0.001	0.065	-0.015	0.145	0.113
Distance to building	<b>-0.229</b>	<b>-0.335</b>	<b>-0.122</b>	<0.001	-0.018	-0.041	0.005	0.12	<b>-0.187</b>	<b>-0.297</b>	<b>-0.077</b>	<b>0.001</b>
Distance to harvest area	0.013	-0.056	0.082	0.72	0.003	-0.012	0.019	0.68	-0.008	-0.082	0.067	0.84
Harvest 0–5 years	0.592	-0.031	1.216	0.063	<b>0.55</b>	<b>0.424</b>	<b>0.676</b>	<0.001	0.012	-0.628	0.652	0.97
Harvest 6–10 years	-0.145	-0.692	0.403	0.61	-0.02	-0.128	0.088	0.72	0.014	-0.545	0.573	0.96
Harvest 11–15 years	0.274	-0.316	0.864	0.36	-0.045	-0.176	0.085	0.49	0.293	-0.322	0.909	0.35
Developed	-0.742	-1.758	0.274	0.153	<b>0.576</b>	<b>0.455</b>	<b>0.696</b>	<0.001	<b>-1.062</b>	<b>-2.083</b>	<b>-0.041</b>	<b>0.041</b>
Evergreen forest	-0.448	-0.928	0.032	0.067	-0.079	-0.165	0.007	0.070	-0.310	-0.799	0.180	0.22
Herbaceous	-0.608	-1.768	0.552	0.304	<b>0.649</b>	<b>0.514</b>	<b>0.784</b>	<0.001	-1.108	-2.272	0.057	0.062
Mixed forest	0.115	-0.158	0.389	0.408	0.031	-0.024	0.086	0.27	0.073	-0.207	0.354	0.61
Wetland	0.029	-0.255	0.313	0.841	0.041	-0.015	0.096	0.15	0.007	-0.282	0.296	0.96

Note: The “kill site” and “hunting” models evaluated the influence of the variables tested on deer fawn kill sites and wolf hunting locations relative to available locations within each wolf’s territory (i.e., used-available habitat selection study design). The “kill versus hunting location comparison” model compared how landscape characteristics may influence the relative probability of wolf hunting success by comparing kill site and hunting locations. “Deciduous forest” was set as the reference level for the categorical land cover variable. Parameters in bold had 95% CIs (conf. low, conf. high) that did not overlap 0, and  $p < 0.05$ .

area had no influence on kill locations ( $\beta = 0.013$ , 95% CI =  $-0.056$ ,  $0.082$ ,  $p = 0.72$ ; Figure 2).

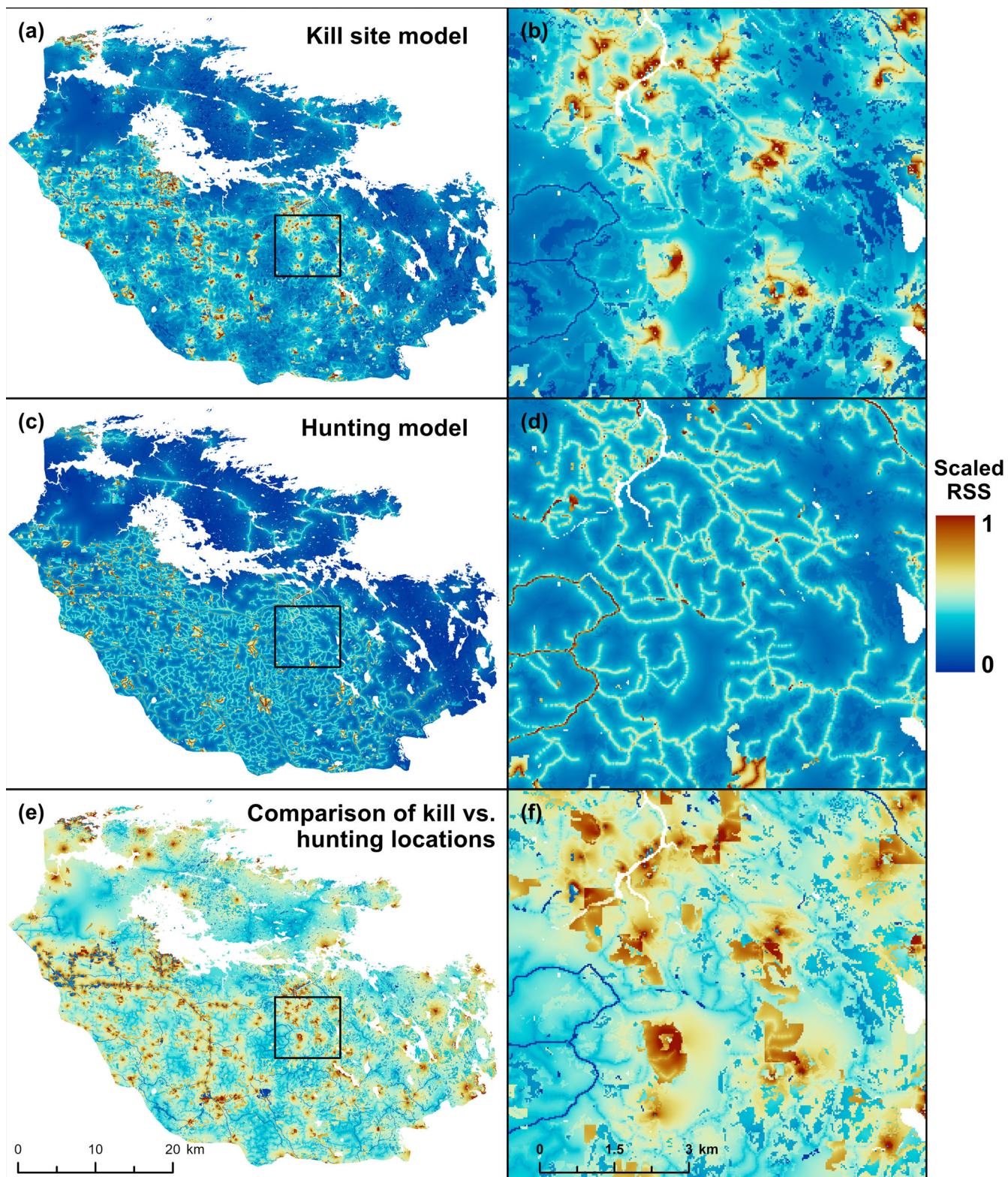
Several landscape features influenced kill sites and hunting locations differently. Specifically, kills were closer to human structures than where wolves typically hunted fawns ( $\beta = -0.187$ , 95% CI =  $-0.297$ ,  $-0.077$ ,  $p = 0.001$ ; Figure 2, Table 1). Wolves also tended to have lower relative hunting success near linear features, and within herbaceous and developed (generally paved and gravel roads) cover types (i.e., kill locations were rare in these areas in relation to the frequency that wolves hunted in them; Table 1). The random effect term for “wolf ID” had minimal influence within each model (intraclass correlation coefficients ranged from 0 to 2.9).

### Spatial predictions of relative probability of use

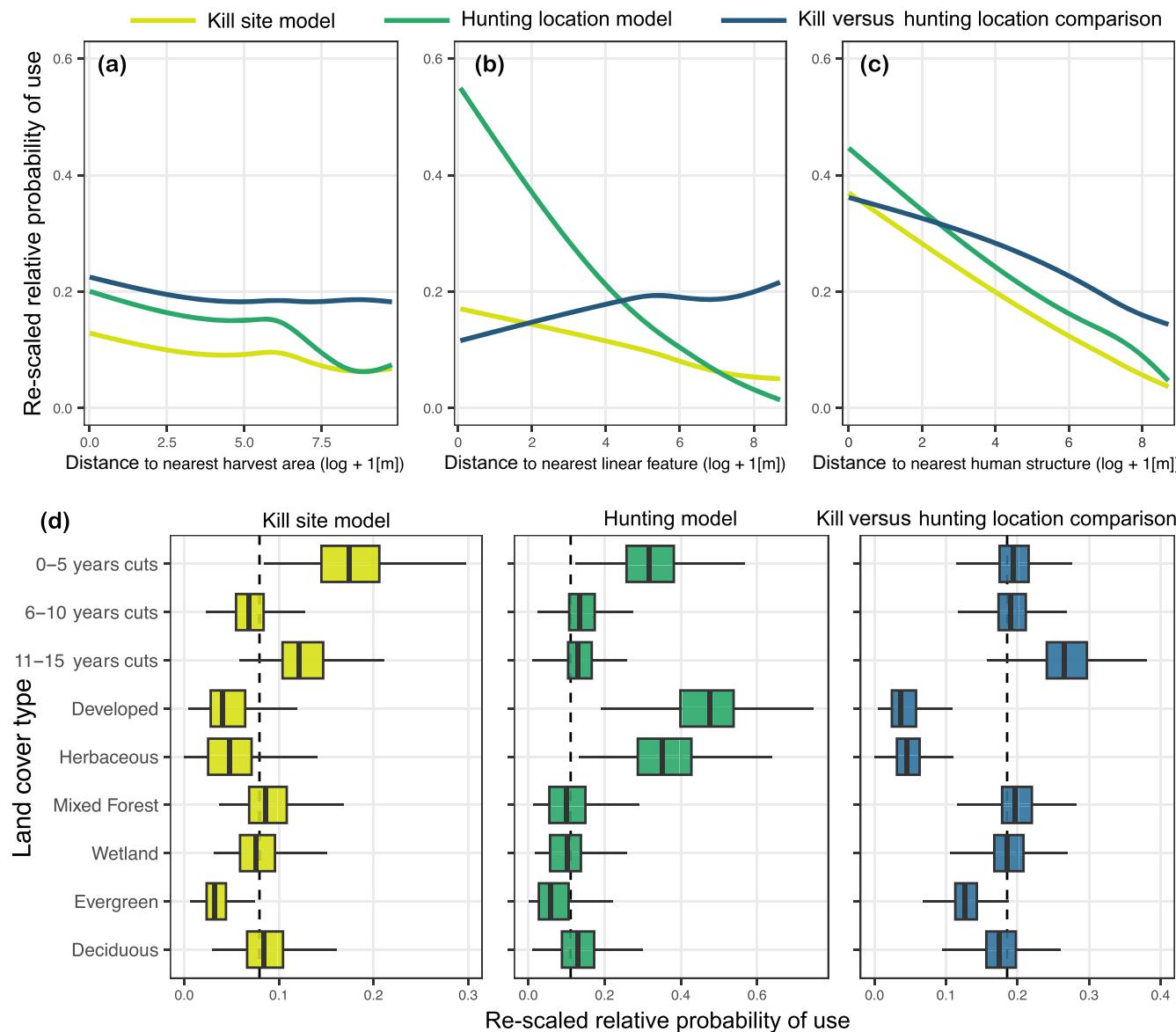
Spatial predictions of RSS for each of the three models evaluated (kill model, hunting model, kill vs. hunting location comparison) throughout the entire study area yielded RSS estimates from 1,787,034 grid cells

(Figure 3). The average population-level effect of each continuous variable (distance to nearest harvested area, linear feature, and human structure) on wolf hunting and kill site selection is presented in Figure 4a–c. The figure panels generally reflect the patterns found in each model evaluated (i.e., wolves hunted and killed fawns close to linear features, wolves killed fawns close to human structures, and proximity to the nearest harvested area had no effect on kill site or hunting locations). However, we found that at the population level, and after averaging over the full availability of each variable throughout the study area, wolves tended to also hunt closer to buildings than would be expected based on spatial availability (Figure 4c).

Based on the full availability of land cover types in the study area, our analysis indicated that wolf kill RSS values were greater for timber harvested areas (0–5-year post-harvest, and slightly greater in 11–15-year post-harvest areas) than average RSS values (Figure 4d). Kill model RSS values were lower than average in developed, herbaceous, and evergreen forest cover types (Figure 4d). Hunting model RSS values largely reflected the modeled



**FIGURE 3** Predicted relative selection strength (RSS) for each of the three models evaluating wolf-deer fawn spatial dynamics in the Greater Voyageurs Ecosystem (GVE) in northern Minnesota, USA (kill [a, b], hunting [c, d], and kill site vs. hunting location model comparison [e, f]). Predictions throughout the full GVE are shown in left panels (a, c, e), while panels on the right (b, d, f) are model predictions at a finer spatial scale that correspond to the area within the indicator boxes in the left panels. RSS values were scaled to a minimum of 0 and maximum of 1 for these plots to aid in visualization/comparison among the models tested. In panels (a-d), RSS values closer to 1 (red) indicate areas of greater selection, while values closer to 0 (blue) indicate areas not selected by wolves. In panels (e, f), values closer to 1 correspond with areas where wolves had relatively high success killing fawns compared with the frequency these areas were used for hunting, whereas values closer to 0 correspond to areas where wolves killed fawns less frequently compared with their use of these areas for hunting.



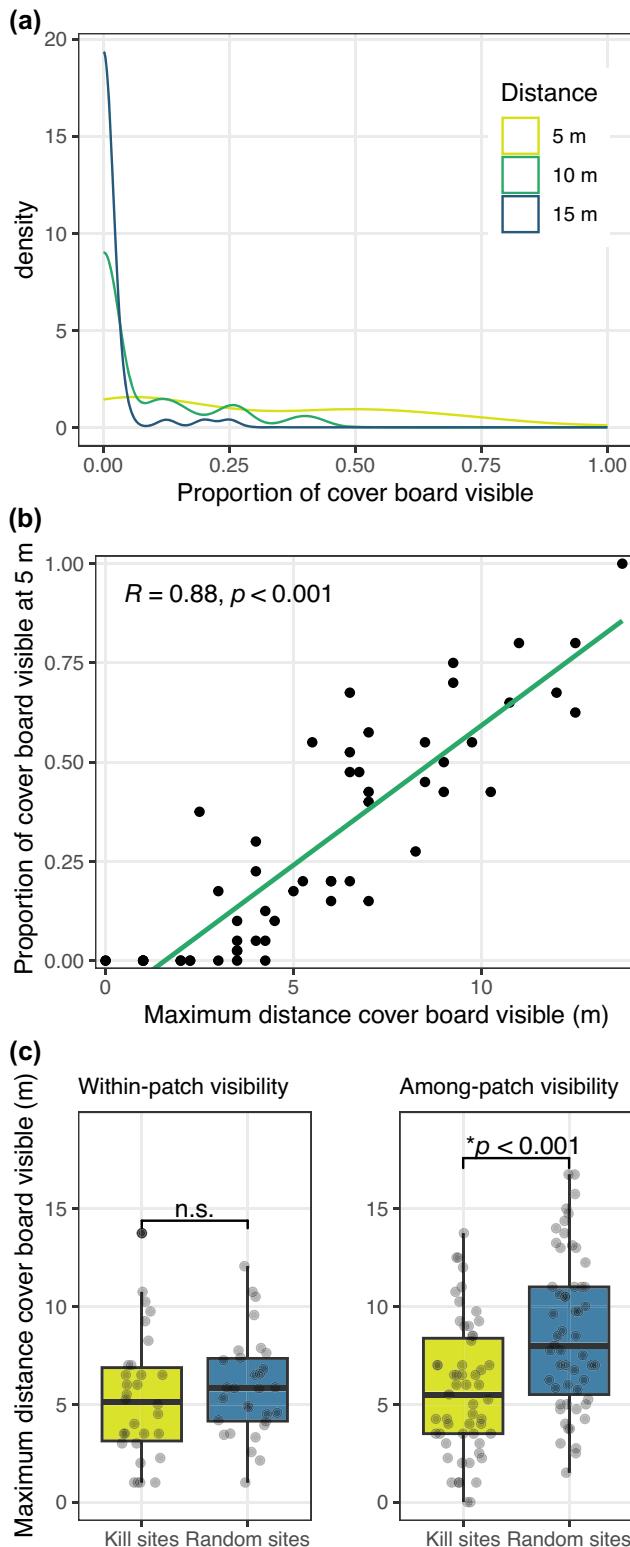
**FIGURE 4** Average population-level relative probability of use for each variable assessed in the kill model, hunting model, and model comparing hunting and kill locations, extracted from predictions generated throughout the Greater Voyageurs Ecosystem in northern Minnesota, USA at a  $30 \times 30$  m pixel resolution ( $n = 1,787,034$  pixels). Panels (a–c) depict the re-scaled relative selection strength (RSS) values across the full distribution of each variable evaluated, fit here with generalized additive models with cubic regression splines. Panel (d) shows the distribution (boxplot) of RSS values for the nine land cover types evaluated in each model. The dashed black line is the median RSS value throughout the study area as predicted from each model; boxplots toward the right of the line show greater relative selection, while boxplots to the left of the line show reduced relative selection. Outlier RSS values in panel (d) are not shown for easier interpretation and visualization. For the model comparing kill and hunting locations, values closer to 1 correspond with landscape features where wolves had a greater relative probability of killing fawns compared with the frequency these features were used for hunting; values closer to 0 indicate wolves had lower hunting success in these landscape features relative to the frequency they hunted there.

results presented earlier. When comparing kill and hunting locations, RSS values suggested that wolves had greater relative success hunting fawns within 11–15-year post-harvest areas (Figure 4d). RSS values were lower in developed, evergreen forest, and herbaceous land cover types, indicating that wolves had lower relative hunting success in these areas (Figure 4d).

### Assessing visibility at kill sites

Maximum visibility from 1 m above the ground at kill sites ( $n = 55$ ) and random sites (averaged across all four cardinal directions) was generally very low (mean  $\pm$  SD:  $5.75 \pm 3.44$  and  $7.69 \pm 3.79$  m, respectively), reflecting the dense vegetation typical of the study area (Figure 5a). Horizontal

visibility at 5 m from the cover board was strongly correlated with maximum visibility distance (Figure 5b). The within-patch visibility model showed that maximum cover board visibility was not different between fawn kill sites and locations 50 m from kill sites ( $\beta_{\text{random}} = 0.544$ , 95% CI =  $-0.936$ ,  $2.023$ ,  $p = 0.47$ ,  $n = 30$ ; Figure 5c). However, the among-patch model revealed that maximum distance



visibility was lower at fawn kills than at random locations within each wolf's territory ( $\beta_{\text{random}} = 2.924$ , 95% CI =  $1.535$ ,  $4.314$ ,  $p < 0.001$ ,  $n = 55$ ; Figure 5c). The random effect term of wolf ID had no influence in either model.

## DISCUSSION

Our study demonstrates that human-modified landscape features have substantially influenced the strategies wolves use to hunt white-tailed deer fawns and where wolves ultimately kill fawns during the early fawning season. Every major landscape alteration by humans we examined—logging, linear features, and human infrastructure—in the GVE shaped wolf predation of fawns in some manner. Timber harvest practices and human structures appear to affect the spatial distribution of deer, which are likely attracted to these areas for food or perceived safety, and the subsequent locations of wolf-killed fawns. Human-created and -maintained linear features, in turn, create a connected web of travel corridors that wolves selected for while traveling between these high-quality prey patches, which generally had lower horizontal visibility than other similar areas in the GVE. Given that the human alterations we examined are not unique to our area, our results are likely to be generalizable to other southern boreal forest ecosystems. We provide novel insight into the role that human development and resource extraction practices have had on spatial patterns of wolf-ungulate interactions and the strategies wolves use to hunt ungulate neonates.

### Buildings and timber harvesting shape where wolves kill ungulate neonates

Wolves killed fawns close to human structures, which suggests that although large predators are typically thought to avoid human-modified areas, prey availability

**FIGURE 5** Horizontal visibility metrics at fawn kill sites and paired random locations throughout the Greater Voyageurs Ecosystem in northern Minnesota, USA. Panel (a) shows density plots of average coverboard visibility at 5, 10, and 15 m from wolf-killed fawn locations ( $n = 55$ ). Panel (b) depicts the relationship between average maximum distance the cover board was visible at kill (in meters), and the proportion of the cover board visible at 5 m. Panel (c) shows boxplots of the average maximum distance the cover board was visible at kills and paired random locations. There was no difference in maximum visibility from the within-patch analysis (left,  $n = 30$ ) but visibility at kills was significantly less than at random sites in the among-patch analysis (right,  $n = 55$ ).

may override wolf sensitivity to humans at times. Indeed, proximity to human infrastructure (buildings) had the strongest influence of all variables tested on kill site locations (Figure 2, Table 1). Our population-level spatial predictions suggest that wolves generally hunt fawns near buildings, and that they also have relatively high hunting success near buildings (i.e., fawn kill sites were more common near buildings relative to the strength of selection by wolves for these areas when hunting; Figure 4c). These results contrast with the human shield hypothesis, which posits that humans or human infrastructure should provide refuge for prey from predators that are sensitive to human activity (Berger, 2007). Most of the buildings in the GVE, a rural community, are seasonal housing structures (cabins, resorts) interspersed with year-round residences. Thus, it is possible that the level of human activity in our area is not consistently high enough to cause wolves to substantially alter their predation behavior. Support for the human shield hypothesis may therefore depend on the magnitude of human activity, or whether human presence or human footprint is the dominant anthropogenic factor, as these factors may have nonequivalent effects on wildlife (Nickel et al., 2020). Wolves may also selectively hunt closer to buildings during times of day when interactions with humans would be rarer (e.g., during the night) as has been shown with other large carnivores (Valeix et al., 2012; Wang et al., 2017), although such an analysis was outside the scope of our study. Others have shown that wolves are more tolerant of infrastructure when visiting high-quality resource patches (Carricando-Sanchez et al., 2020; Lesmerises et al., 2012), which may also be happening in the GVE. Many year-round residents in the GVE feed deer during winter, and these food subsidies can lead to deer congregating around human infrastructure in the GVE during winter and sometimes summer (T. Gable & A. Homkes, personal observations). Thus, our finding that kills were close to buildings may reflect the spatial response of deer toward buildings. Regardless of the specific mechanism, our results provide evidence that human infrastructure influences spatial patterns of wolf predation on ungulate neonates, probably by attracting ungulates to these areas for opportunities of food and/or safety.

As expected, areas of early successional forest created by timber harvest practices influenced where wolves hunted and killed fawns. Wolves selected for recently logged (0–5 year post-harvest) areas when hunting fawns, and kills were also more likely to be found in these cover types (Figure 4d). Young harvest areas in the GVE are primarily composed of regenerating deciduous trees and dense understory vegetation (primarily aspen), which probably provide ideal forage conditions for adult deer

and hiding cover for fawns (Courtois et al., 2002; Rohm et al., 2007). Indeed, studies from other parts of the boreal forest have demonstrated that deer often select for recently-harvested areas during summer (Lesage et al., 2002; McKay & Finnegan, 2023). Although these patches of high-quality habitat may have benefits for both adult and neonatal ungulates, wolves appear to exploit deer concentrated in them. However, as harvested areas age, browse becomes out of reach of deer within a short period of time (Miller et al., 2009; Oswalt et al., 2006), and is probably why we saw little to no effect of 6–10 and 11–15 year post-harvest areas on kill site locations (Figure 4d). Our findings that wolves selectively hunt in regenerating timber stands are consistent with several other studies from boreal forest environments (e.g., Houle et al., 2010; Muhly et al., 2019). However, despite kills and hunting locations being more likely to occur within recently harvested areas, we found that proximity to harvested area had no influence on wolf predation of deer fawns, in contrast with other wolf-ungulate systems where wolves often move near timber harvest stand edges (Boucher et al., 2022).

Have humans created ecological traps for deer fawns through infrastructure development and resource extraction practices? Given that fawn kills were located in recently logged areas and closer to buildings and human-created linear features than would be expected, it is tempting to suggest that these areas may be a fatal attraction for deer. However, without detailed knowledge of the ecology of deer in the GVE, we cannot say whether deer selection for these areas had maladaptive effects at the population level, which would be indicative of an ecological trap (Robertson & Hutto, 2006; Schlaepfer et al., 2002). In other words, we do not have data on space use or selection of habitats by deer in our study area, nor how these behavioral traits relate to the population dynamics of deer. Assuming wolves hunt deer fawns where fawns are present, we can presume that deer fawns are available and accessible within certain habitats more than others based on our analysis (closer to roads and human infrastructure, within recently harvested forest plots). However, despite the fact that most of these areas are directly impacted by human activity, this does not necessarily imply that these areas are ecological traps: the benefits offered by human activity (food subsidies or safety from humans, high-quality forage from timber harvest) may outweigh the risk of predation when you consider annual life history cycles at the population level. Indeed, other research from the region found no evidence that human development affected deer predation risk (Olson et al., 2021). More information on the movement ecology and demography of deer in the area, including how wolf predation on fawns affects deer

abundance and recruitment, is needed to discern whether these human-modified landscape features function as ecological traps.

## Wolf hunting strategies and the role of human-created linear features

Studies evaluating fine-scale predation patterns on ungulate neonates have largely been conducted by tagging and following the neonates, rather than the predators, because it is often difficult to locate and identify remains from kill sites of small prey. Deer fawns weigh ~2.8–3.0 kg when born and can be almost wholly consumed by predators in as little as 20–60 min (unpublished data; Carstensen et al., 2009), leaving scant evidence of a kill event to be found when searching clusters of GPS locations from collared predators (Palacios & Mech, 2011). Thus, the behavioral strategies wolves and other predators use when hunting ungulate neonates have remained largely unresolved (Ruprecht et al., 2022). Researchers have shown intensive methods such as using detection dogs can locate kill sites of small prey (Petroelje et al., 2021); however, we have found that the combination of high-frequency GPS-fix intervals and highly trained field personnel can also successfully locate small prey kills (Gable et al., 2016, 2020, 2021; Gable & Windels, 2018), and ultimately help advance our understanding of the strategies wolves (and probably other predators) use to hunt ungulate neonates.

Average horizontal visibility in the GVE is low, and visibility at fawn kills was even lower (Figure 5), indicating that vision is almost certainly not the dominant sense wolves use to locate fawns. We cannot discern whether wolf-killed fawns were bedded in areas with less visual concealment relative to fawns not detected and killed by wolves. Regardless, with such low visibility in the study area (average 7.7 m), the dense vegetation seems to provide little opportunity for predators to visually locate bedded fawns. So how do wolves detect fawns? Given the dense vegetation and their keen sense of smell, wolves are likely to detect fawns from olfactory cues. Mech and Boitani (2003) speculated that while fawns might have some sort of masked scent, it is improbable they are scentless. Alternatively, given the high association between fawns and dams, it is possible that wolves are instead detecting the mother's scent or presence, which ultimately leads wolves to the fawn's location. Despite the increased risk of predation, deer sometimes select for linear features during summer (Darlington et al., 2022), which may lead to increased opportunities for wolves to encounter deer odorants. Our results seem to support one or both of these speculations but future research that

evaluates wind direction patterns (*sensu* Gable et al., 2021; Togunov et al., 2017), for example, may provide better insight into the role olfaction plays in wolf detection of fawns.

Wolves in our study showed strong selection for traveling along human-created linear features while hunting deer fawns, a pattern consistent with numerous other studies that evaluated how linear features influence wolf foraging behavior (e.g., DeMars & Boutin, 2018; Dickie et al., 2017, 2020; Latham, Latham, Boyce, & Boutin, 2011; McKenzie et al., 2012; Newton et al., 2017). Wolves appeared to have relatively lower success killing fawns near linear features relative to their use of linear features while hunting (Figures 2 and 4b), which likely reflects that these features often function more as travel corridors between resource patches. Nonetheless, we found kills were more likely to occur closer to linear features than expected based on spatial availability. We assumed that kills were located in the same spot (or very close to) where fawns were bedded down, as fawns rely on hiding in their first several weeks of life as an antipredator strategy (Grovenburg et al., 2010; Michel et al., 2020). If, however, wolves opportunistically encounter deer fawns while hunting, then it follows that they may encounter fawns, or the scent of fawns, more frequently along linear features and this may be an alternative explanation for why kill sites were disproportionately close to linear features (Gable et al., 2023).

To date, most attention on the role of linear features in predator-prey ecology has focused on linear features created for development or extractive purposes. However, in the GVE, where linear features are ubiquitous south of VNP, a large proportion of linear features are relatively small-scale, low-impact features that are created or maintained for recreational purposes. Many linear features are maintained for ATV and utility terrain vehicle (UTV) recreation, which is an increasingly popular and rapidly growing form of recreation in Minnesota and across North America. Many of the ATV/UTV trails begin as low-impact logging roads but once timber has been extracted, ATV/UTV traffic—which tends to be highest during recreational hunting seasons—prevents regeneration on these linear features (similar to off-highway vehicle use on seismic lines in other boreal systems; Pigeon et al., 2016). In fact, many linear features are actively cleared by ATV/UTV users to prevent regeneration and ensure continued access to remote areas. Additionally, we have observed that many linear features in the GVE are created by recreational ATV/UTV users and hunters (which were accounted for in our study). Thus, it is not just development or resource extraction practices that sustain a vast, connected web of linear features, but also recreational practices that ultimately

facilitate and shape patterns of wolf predation on ungulate neonates. Wolves often avoid traveling along roads with frequent vehicle traffic (particularly during the day; Bojarska et al., 2020; Thurber et al., 1994; Zimmermann et al., 2014), preferring instead to travel on low-use roads. Linear features associated with outdoor recreation activities are generally used infrequently by humans in the GVE, which is probably why wolves showed a strong selection for these features. Our study adds to the growing body of evidence that recreational activities such as riding ATVs/UTVs and hiking can affect wildlife behavior and subsequent predator-prey dynamics in boreal ecosystems (e.g., Naidoo & Burton, 2020; Prock et al., 2022; Sytsma et al., 2022).

When we synthesize all major lines of evidence from our study, a general pattern of the strategies that wolves use to hunt ungulate neonates emerges. Anthropogenic landscape modifications (timber harvest, infrastructure development) appear to alter the spatial distribution of ungulate prey, creating high-quality resource patches that wolves selectively use when hunting. Human-created linear features allow wolves (and other predators) to travel in more directed, straight movements relative to the dense vegetation typical of the area (Dickie et al., 2020), effectively turning linear features into corridors that wolves use to travel between, and often within, these high-quality resource patches. The fact that visibility at fawn kills was so low and that these kills were closer to linear features than would be expected suggest that, if wolves are not encountering fawns directly on linear features, they are likely to encounter cues on linear features that help them locate hidden fawns (e.g., olfactory cues they can pick up while moving along linear features). These findings support the general hypothesis that linear features may be particularly useful for predators that are hunting small prey with correspondingly shorter handling times by providing an efficient way to travel among resource patches and thus increase encounter rates (Dickie, Serrouya, et al., 2022). Collectively, the body of evidence we gathered provides arguably the most detailed understanding of the strategies large predators use to hunt vulnerable, recently-born ungulate neonates and the influence that human landscape modifications have on these relationships.

## Conclusions and future outlook

The combined effects of climate change and human disturbance have facilitated the northward range expansion of white-tailed deer into boreal forest ecosystems (Dawe & Boutin, 2016; Frelich et al., 2012; Fuller et al., 2023). At the same time, moose abundance and distribution have

retracted at their southern edge, while wolf populations have steadily recovered and extended their range southward in Minnesota (Minnesota Department of Natural Resources, 2022) and elsewhere along the temperate forest–boreal forest ecotone (Bowman et al., 2010; Frelich et al., 2012). As the range of overlap between white-tailed deer and wolves expands, understanding wolf predation on deer will become increasingly important. This is particularly true for areas where deer expansion may alter boreal food webs through negative indirect effects on ungulates such as moose and caribou (Fuller et al., 2023), including intensifying predation on other ungulates through apparent competition (Latham et al., 2013; Latham, Latham, McCutchen, & Boutin, 2011). If anthropogenic linear features increase the efficiency with which wolves hunt deer, as our results suggest, the indirect effects of deer expansion on other ungulates will be exacerbated by human activity via mechanisms such as apparent competition. Our work suggests that reversing or mitigating infrastructure development and resource extraction in southern boreal forests is likely to reduce predation pressure on ungulates (Laurent et al., 2021), similar to suggestions and practices used in other North American boreal systems (Dickie, Sherman, et al., 2022; Finnegan et al., 2018; Tattersall et al., 2020).

As human populations continue to expand and fragment habitats through development and resource extraction practices (Haddad et al., 2015), we can expect more pervasive and long-lasting alterations of predator-prey dynamics by human activity. Although one or a few different types of human activity are generally considered at any one time in most studies, it is clear that the many ways in which humans alter landscapes can have cumulative and synergistic effects on predator-prey dynamics (Boucher et al., 2022; Darlington et al., 2022; Nickel et al., 2020). This includes human recreation activities, which are increasingly recognized as drivers of animal behavior change (Larson et al., 2016; Marzano & Dandy, 2012). We demonstrated that evaluating all major aspects of human activity within our study area—resource extraction, residential and tourism development, and outdoor recreation—provides novel insight into understanding how humans have altered the spatial ecology of the dominant predator-prey relationship in this area. Research and conservation and management plans that strive to account for the multifaceted ways humans alter landscapes will likely provide a more complete perspective on the role that humans play in contemporary ecosystems.

## AUTHOR CONTRIBUTIONS

Sean M. Johnson-Bice led the data curation, data analysis, data visualization, and writing and revising of the current version of the manuscript. Thomas D. Gable and

Austin T. Homkes led the data analysis, curation, visualization, and drafting of the initial version of the manuscript, as well as data collection efforts. Steve K. Windels, Joseph K. Bump, and John G. Bruggink helped design and supervise the study, collect data, and contributed substantially to revising and editing the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and R code are available from Johnson-Bice et al. (2023) in the figshare data repository at <https://doi.org/10.6084/m9.figshare.22118423.v3>.

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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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