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White-tailed deer population dynamics in a multipredator landscape shaped by humans

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Abstract

Large terrestrial mammals increasingly rely on human-modified landscapes as anthropogenic footprints expand. Land management activities such as timber harvest, agriculture, and roads can influence prey population dynamics by altering forage resources and predation risk via changes in habitat, but these effects are not well understood in regions with diverse and changing predator guilds. In northeastern Washington state, USA, white-tailed deer (*Odocoileus virginianus*) are vulnerable to multiple carnivores, including recently returned gray wolves (*Canis lupus*), within a highly human-modified landscape. To understand the factors governing predator–prey dynamics in a human context, we radio-collared 280 white-tailed deer, 33 bobcats (*Lynx rufus*), 50 cougars (*Puma concolor*), 28 coyotes (*C. latrans*), and 14 wolves between 2016 and 2021. We first estimated deer vital rates and used a stage-structured matrix model to estimate their population growth rate. During the study, we observed a stable to declining deer population ($\lambda = 0.97$, 95% confidence interval: 0.88, 1.05), with 74% of Monte Carlo simulations indicating population decrease and 26% of simulations indicating population increase. We then fit Cox proportional hazard models to evaluate how predator exposure, use of human-modified landscapes, and winter severity influenced deer survival and used these relationships to evaluate impacts on overall population growth. We found that the population growth rate was dually influenced by a negative direct effect of apex predators and a positive effect of timber harvest and agricultural areas. Cougars had a stronger effect on deer population dynamics than wolves, and mesopredators had little influence on the deer population growth rate. Areas of recent timber harvest had 55% more forage biomass than older forests, but horizontal visibility did not differ, suggesting that timber harvest did not influence predation risk. Although proximity to roads did not affect the overall population growth rate, vehicle collisions caused a substantial proportion of deer mortalities, and reducing these collisions could be a win-win for deer and humans. The influence of apex predators and forage indicates a

dual limitation by top-down and bottom-up factors in this highly human-modified system, suggesting that a reduction in apex predators would intensify density-dependent regulation of the deer population owing to limited forage availability.

KEYWORDS

agriculture, *Canis lupus*, carnivore, *Odocoileus virginianus*, population dynamics, predator–prey interactions, *Puma concolor*, survival analysis, timber harvest, ungulate

INTRODUCTION

Human activities are increasingly affecting wildlife and their habitats (Fischer & Lindenmayer, 2007), influencing prey, predators, and the interactions therein (Guiden et al., 2019). However, much of the existing research on predator–prey interactions comes from protected areas where human activities are regulated, limiting inference on the multiple pathways through which humans can influence prey population dynamics (Kuijper et al., 2016). Humans have reduced and extirpated many predator populations worldwide, which can decrease predation rates and increase prey abundance (Estes et al., 2011). However, conservation efforts have allowed some predator species to re-establish in parts of their historic ranges, raising questions about the potential for predator recovery to negatively affect prey populations (Marshall et al., 2016). At the same time, humans can cause substantial prey mortality through vehicle collisions (Cunningham et al., 2022) and hunting (Ballard et al., 2000). Furthermore, human activities, such as timber harvest, can improve forage for herbivores (Hull et al., 2020; Monzingo et al., 2023) but are often associated with the construction of linear features that facilitate the movement of some predators and human hunters, increasing prey mortality risk (DeMars & Boutin, 2018; Neilson & Boutin, 2017). Thus, investigations of prey population dynamics in human-modified systems are necessary to identify the role of predators when humans are present and guide conservation and management decisions in increasingly human dominated landscapes.

Managing prey populations can be challenging because the effects of predators depend on system-specific factors, including the composition of the wildlife community and the forage resources available to prey. Moreover, many studies of carnivore–ungulate interactions overlook the complexity of multipredator systems, tending to focus on predator–prey dyads (Montgomery et al., 2019). Yet the overall composition of the wildlife community may be the strongest factor in determining how predation influences prey populations because prey life stage can affect vulnerability to different predator

species and because apex predators can suppress mesopredator populations (Elbroch et al., 2015; Elbroch & Wittmer, 2013; Gervasi et al., 2012; Prugh et al., 2009; Prugh & Arthur, 2015). Generally, ungulate population growth rates (λ) are most sensitive to adult female survival because their reproductive output determines potential recruitment of young (Ballard et al., 2001; Gaillard et al., 1998). However, juvenile recruitment tends to be more variable, so juvenile mortality usually has a stronger influence on population growth across years and populations (Ballard et al., 2001; Forrester & Wittmer, 2013; Gaillard et al., 1998). Apex predators such as cougars (*Puma concolor*) and wolves primarily eat wild ungulates and are capable of killing deer of all age classes (Elbroch & Wittmer, 2012; Newsome et al., 2016), giving them greater potential to influence deer population growth rates compared to mesopredators that eat more diverse diets and kill adult ungulates more rarely (Ballard, 2011; Jensen et al., 2022).

Predation effects also differ across systems because primary productivity and abiotic factors moderate predator impacts (Ballard et al., 2001). Indeed, forage quality and availability are the primary factors governing ungulate population dynamics (McCullough, 1999), and ungulate populations are more resilient to predation in areas with high primary productivity and mild climates (Donadio & Buskirk, 2016; Melis et al., 2009). Prey with more nutritional resources relative to energetic output should be in better condition, in turn improving predator evasion capabilities as well as survival, pregnancy, and fetal rates (Eberhardt, 2002). For example, in the US state of Colorado, mule deer (*Odocoileus hemionus*) provided with supplemental feed experienced lower predation rates, higher survival, and increased population growth relative to deer without food supplementation (Bishop et al., 2009). Thus, the dynamic interplay between diverse carnivore guilds and forage resources in variable climates make predation impacts on prey populations difficult to predict.

Land modifications by humans, such as timber harvest, conversion of land to agriculture, and creation of roads, can likewise have uncertain effects on prey populations because changes to landscape structure can

alter forage resources while also influencing the mortality risk of prey (Kuijper et al., 2016). Removal of the overstory canopy via timber harvest increases light penetration to the understory, triggering increased forage biomass favored by ungulates up to 20 years after harvest (Hull et al., 2020; Monzingo et al., 2023). Timber harvest has led to booming white-tailed deer (*O. virginianus*) populations in Alberta, Canada, presumably owing to increased forage (Latham et al., 2011). Timber harvest also has the potential to influence predation risk for ungulates by shaping prey escape capabilities and, subsequently, predation rates (Wirsing et al., 2021). For white-tailed deer that escape predators by galloping (Dellinger et al., 2019), the dense understory vegetation of early seral habitat could hinder escape from predators. Recent work also suggests that wolves in human-dominated systems target prey by chasing them into complex, forested habitats (Barker et al., 2023), counter to Yellowstone National Park, USA, where wolves hunted in open landscapes (Kauffman et al., 2007). Similarly, deer could be vulnerable to cougars in early seral habitats that create hiding cover for cougars to approach undetected (Ruth & Murphy, 2010). Like timber harvest, agriculture may benefit ungulates by providing abundant, high-quality forage during the growing season (Barker et al., 2019), when nutritional demands peak for reproductive females because of the energetic requirement of lactation (Moen, 1978; Tollefson et al., 2010, 2011). Additionally, open fields associated with agriculture could create a “human shield,” further benefiting ungulates by reducing predation risk from human-averse carnivores (Berger, 2007; Muhly et al., 2011). High-speed roads that are frequented by people could likewise induce a human shield effect, but these roads could also increase ungulate mortality risk through vehicle collisions (Cunningham et al., 2022).

The factors driving prey population dynamics in multipredator landscapes should depend on the extent to which populations are influenced by top-down (i.e., direct causes of mortality including predation, hunting, and vehicle collision) and bottom-up (i.e., the quality and availability of forage) factors and how humans alter these pathways (Kuijper et al., 2016). Since 2008, wolves have returned to Washington, USA (Wiles & Hayes, 2011), joining a sympatric community of predators that includes black bears (*Ursus americanus*), bobcats (*Lynx rufus*), cougars, and coyotes. The return of wolves to this highly altered landscape raises concerns about whether an additional predator could lead to declines in the white-tailed deer population. Across our study area, approximately a quarter of the forested area (~16%–18% of the total area) has been harvested for timber since 2000 (Hansen et al., 2013), with the potential to influence deer vulnerability to predators and enhance ungulate

forage, both of which may shape prey population dynamics (Hull et al., 2020). Thus, our goal was to identify the primary factors governing white-tailed deer population dynamics within a human-modified landscape recently recolonized by wolves. Such dynamics can be difficult to predict because humans can affect prey and their interactions with predators through multiple pathways (Guiden et al., 2019; Kuijper et al., 2016).

We tested two hypotheses about the factors driving white-tailed deer population dynamics in northeastern Washington from 2017 to 2021 by linking habitat use and survival of collared deer to model population dynamics. First, we expected that the deer population would be influenced by predator exposure (H1: predator effects hypothesis). According to this hypothesis, we expected that mortality risk would increase with greater exposure to predators and that simulated increases in predator exposure would decrease λ . Second, we predicted that human landscape-modification effects (H2) could impact deer interactions with predators and deer survival, translating to changes in λ via bottom-up or top-down effects. If the predominant effect of human landscape modification was to improve forage available to deer and the population was limited or colimited by nutrition, then we predicted that deer mortality risk would decrease with increased use of timber harvest areas and agriculture (H2a: landscape modification influences forage) and that simulated increases in the use of areas of timber harvest and agriculture would result in an increase in λ . It was alternatively possible that landscape modification influenced predation (H2b) primarily, such that deer using recent timber harvest would be subject to increased predation risk from apex predators. According to this hypothesis, deer survival, and subsequently λ , would decrease with increased use of timber harvest areas. Proximity to high-speed roads could also influence top-down effects if deer spending more time near these roads were at increased risk of deer–vehicle collisions, or these roads could reduce predation risk if human activity along roads induced a human shield. Because managers have the potential to manipulate predator densities (Clark & Hebblewhite, 2021), forage resources (Bishop et al., 2009), and mitigate wildlife–vehicle collisions, understanding the comparative roles of these influences in the population growth rate of ungulates is critical to effective wildlife management.

METHODS

Study area

We defined the study area (Figure 1) as the range of the white-tailed deer that were marked with global

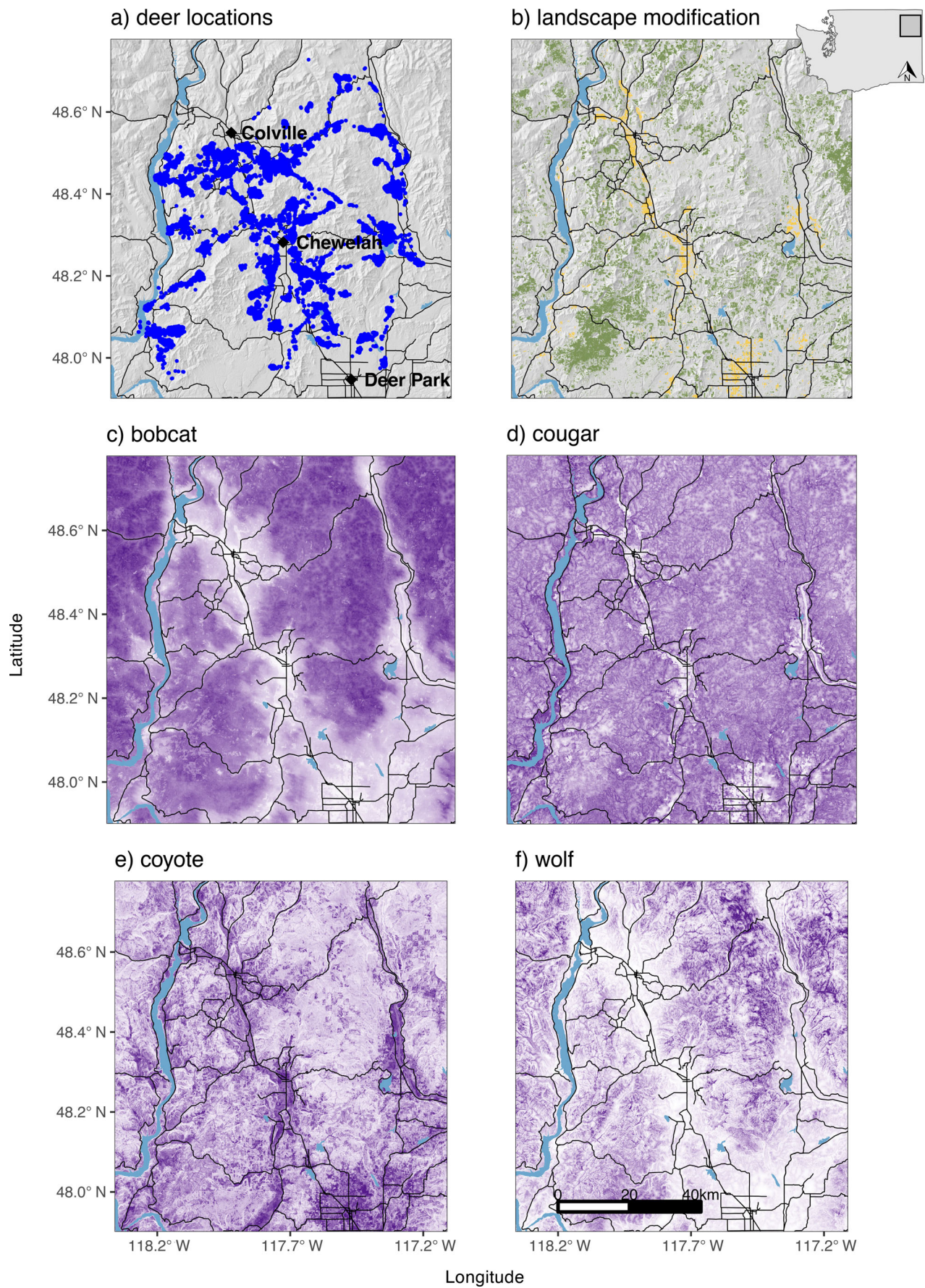


FIGURE 1 Legend on next page.

positioning system (GPS) or radio transmitters for our study, which primarily occurred within Stevens and Pend Oreille Counties of northeastern Washington state, USA (latitude: *c.* 47.900° to 48.720°; longitude: *c.* −118.300° to −117.200°, ~5200 km²). Elevations ranged from 370 to 2080 m. Cool winters (average low of −6°C, average high of 4°C from December to March) and warm summers (average low of 7°C to average high of 27°C from June to September) were typical of the region with an estimated 152 cm of rainfall and 114 cm of snow annually (values estimated for Chewelah, WA, USA, at the center of the study area; <https://www.usclimatedata.com/climate/chewelah/washington/united-states/uswa0074>).

Forests (51.9%) and shrub and grassland (38.7%) dominated the study area, and agriculture (3.5%), wetland (2.7%), open water (2.1%), and developed areas (1.1%) accounted for the remainder of the land-cover types (summary data for 2019; <https://www.cascadiapartnerforum.org/terradapt>). Potential vegetation types indicated that the area was historically 70.0% forest, 24.3% shrub and grassland, and 2.9% open water, and wetland, barren, and unmodeled areas made up the remaining potential habitat types (Oregon State University Libraries & Press and Institute for Natural Resources, 2021). Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), and western red cedar (*Thuja plicata*) were the primary tree species, and snowberry (*Symphoricarpos albus*), Oregon grape (*Mahonia repens*), common St. John's-wort (*Hypericum perforatum*), shinyleaf spiraea (*Spiraea lucida*), and hawkweed (*Hieracium* spp.) were common understory species that were acceptable to white-tailed deer as forage (Berry et al., 2019). Of the agricultural area, which primarily occurred in valley bottoms, 52% produced alfalfa (*Medicago sativa*), 25% was used to grow other, nonalfalfa hay, 6% was fallow crop land, 6% produced winter wheat (*Triticum aestivum*), 4% produced spring wheat, 3% was allocated to barley (*Hordeum vulgare*), and >30 other crops accounted for the remaining 4% (USDA National Agricultural Statistics Service Cropland Data Layer, 2019). The US Forest Service manages 16% of the land, and US Fish and Wildlife Service, the Washington Department of Natural Resources, and the Bureau of Land Management manage 7%. Most of the region (77%)

was privately owned and primarily managed for timber harvest. Since 2000, 18% of the total area and 25% of the forested area have lost canopy cover (Hansen et al., 2013), with forest management practices ranging from small-scale selective thinning to large-scale clear-cuts.

Elk (*Cervus canadensis*), moose (*Alces alces*), and mule deer occur across the area at low densities relative to white-tailed deer, suggesting that interspecific competition for resources likely has limited impact on white-tailed deer. Four wolf packs occupied the study area for the duration of the project (Washington Department of Fish and Wildlife et al., 2022). Black bears, bobcats, cougars, and coyotes are also native to the area and prey on white-tailed deer. White-tailed deer in this area are within the Selkirk White-tailed Deer Management Zone, which has the highest densities of white-tailed deer in the state (Hoenes et al., 2016). The local population experienced several weather and disease-related declines due to severe winters during 2008–2011 and an outbreak of hemorrhagic disease in the fall of 2015. Generally, white-tailed deer populations rebound after such events owing to their high reproductive potential (DeYoung, 2011), but the impact of these events is largely unknown because formal population surveys to determine abundance were not conducted for this herd (Hoenes et al., 2016). During this study, there was a general season harvest of antlered deer from October to November, limited antlerless opportunities from 2017 to 2018, and no antlerless opportunities from 2019 to 2021.

Animal capture and handling

To estimate vital rates and determine the factors influencing survival of white-tailed deer (hereafter: deer), we fit GPS and very high frequency (VHF) collars to deer, bobcats, coyotes, cougars, and wolves. We conducted all wildlife captures and monitoring between February 2016 and June 2021. We captured 6-month-old and older deer in the winter between December 2016 and March 2020 using a suspended net gun (Wildlife Capture Services, Flagstaff, AZ, USA) and clover traps (Clover, 1954; Hawkins et al., 1968). Yearling and adult deer were also captured by ground darting. We fit GPS radio collars

FIGURE 1 (a) Locations (blue) of collared white-tailed deer in northeastern Washington state, USA from 2017 to 2021 with the three largest towns labeled. (b) Human landscape modification was primarily caused by timber harvest (green; identified from Hansen et al. [2013] as areas of forest cover loss), agriculture (yellow; identified from TerrAdapt: Cascadia [<https://www.cascadiapartnerforum.org/terradapt>]), and paved roads where risk of vehicle collision was highest (black lines—all plots). Relative likelihood of predator use, modeled from resource selection functions (RSFs) using GPS collar data, was higher where colors are darker. The RSFs were constructed for each season of each year, and layers for summer 2018 are shown for (c) bobcats, (d) cougars, (e) coyotes, and (f) wolves. Each RSF layer was scaled between 0 and 1 for best resolution. Light blue (all plots) indicates major water bodies.

(Models Vertex Plus or Survey, Vectronic Aerospace, Berlin, Germany) to female yearling and adult deer. Collars were programmed to attempt a fix every 4 h and were equipped with mortality sensors that sent an email and SMS notification after 9 h of inactivity. During capture, we collected blood samples to determine pregnancy from blood serum by analyzing pregnancy-specific protein B concentration (PSPB; Bio-Tracking LLC, Moscow, ID, USA; Duquette et al., 2012). We also tested a subset of adult female deer for pregnancy during capture with a portable ultrasound (Ibex Pro, E.I. Medical Imaging, Loveland, CO, USA) and inserted vaginal implant transmitters (VITs; VERTEX Natal-Link Vaginal Implant Transmitter, Vectronic Aerospace) when pregnancy was detected (Johnson et al., 2006). We administered 1.00 cc of butorphanol-azaperone-medetomidine to all deer receiving VITs during winter captures (Miller et al., 2009).

Expulsion of the VITs triggered an email and SMS notification, allowing us to target neonates for capture (Rice, 2016). From May 2017 to June 2020, we captured neonatal white-tailed deer by searching the area around a VIT expulsion, opportunistically, and by observing the behavior of adult female deer and searching the area if a neonate was suspected (White et al., 1972). Neonatal and 6- to 8-month-old deer were equipped with expandable VHF radio collars (Model M4210, Advanced Telemetry Systems, Isanti, MN, USA and Model Vertex Natal-linked, Vectronic Aerospace). Neonates were weighed during capture to account for neonate condition in the summer survival model, as larger neonates may have lower risk of mortality (Griffin et al., 2011). VHF collars were set to a 6-h mortality delay, and juvenile deer were monitored with VHF radio telemetry on a daily basis from capture to September, twice per week from October through December, and weekly from January until reaching 1 year of age around June. We assumed that 6- to 8-month-old deer that survived 365 days after the mean date of neonate captures the previous spring/summer reached 1 year of age. If any juvenile had a collared mother, we assumed their locations were the same as the mother. For juveniles with unmarked mothers, locations were triangulated ~ weekly. We censored the first 3 weeks after capture for all deer captured >6 months old to minimize the effects of capture on movement and survival estimates (Northrup et al., 2014; van de Kerk et al., 2020).

We investigated mortalities as rapidly as possible upon detection to determine the cause of death. The investigations included a necropsy of the carcass and mortality scene inspection during which we collected DNA swabs associated with the potential predator when relevant (Ganz, DeVivo, Reese, & Prugh, 2022). We confirmed predation by skinning the carcass to identify

lethal hemorrhage associated with bite marks (Williams et al., 2003) or by finding clear signs of a chase or struggle that indicated a kill site. Because these criteria might have eliminated true predation mortalities that were mostly consumed, we also classified likely or possible predation mortalities, though ultimately the cause of death was unconfirmed in these cases. “Likely predation” mortalities were cases where predation could not be confirmed and scavenging could not be ruled out, but there was no other apparent cause of death and the evidence pointed to a single potential predator. “Possible predation” mortalities were cases where predation could not be confirmed and scavenging could not be ruled out, but there was no other apparent cause of death, and the evidence revealed signs from multiple potential predators or vague evidence for a single predator. In these cases, we assigned the possible predator as the one that was most likely based on our investigation. Additionally, we classified “likely vehicle collisions” as cases where the carcass was found adjacent to a road with no other apparent cause of death but where vehicle collision could not be confirmed. We had no cases where disease or illegal harvest was the suspected but unconfirmable cause of death. When predation was determined to be the confirmed, likely, or possible cause of death, we evaluated the predator tracks and signs and patterns of consumption following Elbroch (2003), Washington Department of Fish and Wildlife (2014), Stonehouse et al. (2016), and Elbroch and McFarland (2019) to determine the species of predator responsible for the kill. Our survival analyses do not account for the cause of death (Cox, 1972), so assignment of a likely or possible cause of death only provides context. To determine the fetal rate, we recorded the number of fetuses at the mortalities of collared deer when possible and for opportunistically encountered dead deer (e.g., roadkill).

Bobcats were captured using baited cage traps and fit with GPS collars (Model Gen4 GPS-Iridium, Telonics, Mesa, AZ, USA). We captured cougars using trained dogs or baited cage traps (Kertson et al., 2011) and fit them with GPS collars (Model Vertex Lite, Vectronic Aerospace and GPS-enabled accelerometer collars, Advanced Telemetry Systems, Inc., Isanti MN, USA). Coyotes and wolves were captured with padded foot-hold traps and by aerial darting (Frame & Meier, 2007; Jessup, 1982) and then fit with GPS radio collars (Model Gen4 GPS-Iridium, Telonics for coyotes, Models Vertex Lite and GPS Plus, Vectronic Aerospace for wolves). Carnivore collars were also programmed to record a fix every 4 h. White-tailed deer, bobcat, cougar, and coyote capture and handling followed protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol 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 wolf capture and handling protocols (Washington Department of Fish and Wildlife, 2019) and the guidelines of the American Society of Mammologists for the use of live animals in research (Sikes et al., 2016).

Estimating population growth

We created a female-only post-birth-pulse matrix, including juvenile (0- to 12-month-old deer), yearling (1- to 2-year-old deer), and adult (>2-year-old deer) age classes as follows to estimate λ across the population (Kendall et al., 2019):

$$\begin{bmatrix} N_f(t+1) \\ N_y(t+1) \\ N_a(t+1) \end{bmatrix} = \begin{bmatrix} 0 & P_y \times F_y \times S_y & P_a \times F_a \times S_a \\ S_j & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix} \times \begin{bmatrix} N_f(t) \\ N_y(t) \\ N_a(t) \end{bmatrix}.$$

Annual stage-specific survival rates (S_j : juvenile survival, S_y : yearling female survival, S_a : adult female survival) were determined using the staggered entry Kaplan and Meier (1958) technique. Pregnancy rates of yearling females (P_y) and adult females (P_a) were determined via blood serum analysis or ultrasound at time of capture. We did not test juveniles for pregnancy and assumed their pregnancy rate was 0 (DeYoung, 2011). We calculated the female-only fetal rate (F_y : yearling fetal rate, F_a : adult fetal rate) by halving the total number of fetuses found per pregnant deer during post mortem sampling of collared deer and opportunistically encountered dead deer (e.g., roadkills), and we verified an equal sex ratio of juveniles with a χ^2 test. We also used a χ^2 test to confirm that the mortality rate of juveniles did not differ by sex. Here and throughout, we interpreted p -values as indicators of the strength of evidence, as recommended by Muff et al. (2022), such that covariates with p -values <0.05 were considered strong evidence of an effect, covariates with p -values between 0.05 and 0.15 indicated weak evidence for an effect, and covariates with p -values >0.15 indicated no evidence for an effect.

We calculated λ as the dominant eigenvalue of the matrix and used Monte Carlo simulation with 10,000 repetitions to determine the mean and variance of λ . For each Monte Carlo simulation, we drew a random value for S_j , S_y , S_a , P_y , and P_a from the beta distribution

describing that vital rate, using moment matching to translate the appropriate means and variances that were obtained from survival or pregnancy analysis to the parameters of the beta distribution (Appendix S1). We evaluated the elasticity (the relative influence of a matrix element on λ) and the sensitivity (how much λ would change in response to a change in that matrix element) of the matrix to determine the relative importance of the vital rates to population dynamics. All analyses were conducted in R version 4.1.2 (R Core Team, 2021).

Factors influencing mortality risk

To evaluate the factors potentially influencing deer survival that may subsequently affect population growth, we modeled survival as a function of covariates describing predator exposure, human landscape modification, winter severity, and neonate mass. Then we used these equations to parameterize the matrix model and simulated changes to the covariates to evaluate whether changes in predator exposure, landscape modification, winter severity, and neonate mass might influence λ .

Predator exposure

We used resource selection functions (RSFs) (Manly et al., 2002) adapted from Basing (2022) to describe an individual deer's exposure to bobcats, cougars, coyotes, and wolves for the period under consideration. The RSFs were based on telemetry data collected from carnivores collared within this study area and in a similar system in north-central Washington. Although RSFs describe habitat selection or the relative probability of use rather than abundance per se, predation risk increases with the increased likelihood of encountering a predator (Boyce et al., 2016; Hebblewhite & Merrill, 2007; Lima & Dill, 1990). Therefore, we assumed areas predators were relatively more likely to select reflected areas of higher predation risk relative to other locations on the landscape. We created RSFs for winter (December–February), spring (March–May), summer (June–September), and fall (October–November) and included covariates describing terrain (elevation and slope), environmental factors (distance to nearest water, canopy cover, land-cover type, and distance to nearest habitat edge), and a human-modification index. The human-modification index incorporated data on human population density, urban development, transportation and electrical infrastructure, and resource extraction into a single indicator of human impacts on the landscape (Kennedy et al., 2019), allowing us to consider the effects of humans on predators without

duplicating the covariates used in the deer survival models. We constructed RSFs to describe predator activity within the home range (i.e., third-order habitat selection; Johnson, 1980) because we expected cougars to be the primary predators of deer, and recent research suggests cougars occupied all available habitat within the study area. Specifically, Beausoleil et al. (2021) estimated 1.96 cougars per 100 km² (SD = 0.20) directly north of this study system (i.e., one cougar per 51.0 km²), and annual home range estimates of collared cougars within the study area well exceeded this threshold (females: 124 km², SD = 78, $n = 11$; males: 390 km², SD = 99, $n = 8$; Washington Department of Fish and Wildlife, unpublished data). Construction of the RSFs is detailed in Appendix S2.

Human impacts

We sought to investigate the primary components of human modification of the landscape that were likely to impact deer, specifically paved roads, agriculture, and timber harvest. We evaluated distance to paved roads based on data from TerrAdapt:Cascadia (freeways, highways, and secondary highways—generally areas of higher traffic and higher speeds; <https://www.cascadiapartnerforum.org/terradapt>) as a metric of collision risk. We identified agricultural areas from TerrAdapt:Cascadia at a 30 × 30-m resolution. To identify areas of timber harvest, we used the Global Forest Cover Change data set (Hansen et al., 2013), a remotely sensed data set that indicates whether canopy cover has been lost since 2000, and the percentage canopy cover in 2000 (though not proportion of cover loss) at a 30 × 30-m resolution. Forest cover loss indicated a stand-replacement disturbance (Hansen et al., 2013). It was possible that some loss was due to fire, but only 3% of the study area has burned since 2000 (MTBS Project, 2022), and within the canopy cover loss areas only 12% of the loss could potentially be attributed to a fire (i.e., a wildfire occurred in the area in the year of or years preceding the loss), so it was reasonable to assume timber harvest was the predominant driver of forest loss. Forest management practices ranged from small-scale selective thinning to large-scale clear-cuts, but given the multitude of landowners and large portion of private land, we were unable to evaluate the impacts of different management strategies. Instead, we conducted vegetation surveys to coarsely determine whether recently (<20 years) harvested areas differed from forested areas not harvested in the last 20 years and open areas in (1) visual cover that may influence predation risk and (2) biomass of forage acceptable to deer.

We selected 188 unique sites by stratified random sampling across elevation, aspect, and forest harvest

history, categorized as open (<50% forest cover in 2000; $n = 67$), forested ($\geq 50\%$ forest cover in 2000 and no subsequent loss; $n = 58$), and timber harvest ($\geq 50\%$ forest cover in 2000 and subsequent canopy cover loss; $n = 63$). Surveys were conducted from July to September in 2019 and 2020 to capture the season when female ungulates are under high nutritional demands because of lactation and with the strongest effects on ungulate survival and reproductive success (Moen, 1978; Tollefson et al., 2010, 2011). Each 30 × 30-m site was oriented to the cardinal directions and placed in an area of contiguous habitat as close as possible to the randomly selected location. For each site we validated the aspect, elevation, and harvest history by which the site was chosen. As an indicator of habitat structure that may influence predation risk, we measured horizontal cover by placing a cover pole 10 m from site center in each of the cardinal directions and recorded the percentage of the 1.5-m pole that was obscured from 0 to 0.5 m and 0.5–1.0 m to 1.0–1.5 m, yielding 12 measures of horizontal cover per site (Pierce et al., 2004; Rearden et al., 2011; Toledo et al., 2008). The 12 measures were averaged, creating a single metric of horizontal cover for the site. We then used an ANOVA to test whether horizontal cover differed by site type, allowing us to infer whether these areas might confer differences in predation risk.

Nine 1 × 1-m quadrats were spread evenly across the site in which we documented the species and percentage cover of each plant species with at least 1% cover and >1 cm and <2 m in height, as this is the forage available to deer as food (Rowland & Vojta, 2013). Percentage cover of the quadrat was estimated for each species independently such that total cover could exceed 100%. To estimate the biomass of forage considered “acceptable” for white-tailed deer at each quadrat, we classified each plant species measured in plots as avoided (significantly negative Ivlev’s electivity index; Ivlev & Scott, 1961), neutral (95% confidence intervals [CIs] for Ivlev’s index overlapped 0), or selected (significantly positive Ivlev’s index) based on studies with tractable deer and elk (i.e., captive individuals habituated to observation) in similar habitats (Berry et al., 2019; Cook et al., 2016; Hull et al., 2020; Ulappa et al., 2020; Wagoner et al., 2013). For all acceptable plant species (neutral or selected), we used equations developed by Monzingo et al. (2022) for a similar study area to convert percentage cover of acceptable forage to biomass (in kilograms per hectare). Species-level equations were used when available, or else we used equations developed for the growth form of the plant, which generally performed comparably to species-specific equations (Monzingo et al., 2022). We averaged values across the nine quadrats to estimate the biomass of acceptable forage (in kilograms per hectare) at each

of the 188 sites. Finally, we used an ANOVA to determine whether biomass of acceptable forage differed among forested, recently harvested, and open sites.

Winter severity

Abiotic factors such as precipitation and temperature can play a critical role in ungulate population dynamics (Forrester & Wittmer, 2013). In North American ungulate populations, predation and winter severity are the primary drivers of juvenile mortality, and adult female mortality is most affected by winter severity across populations (Gaillard et al., 1998; Griffin et al., 2011). To account for the influence of climate on deer winter/spring survival, we created a winter severity index (WSI) for the period from December to February, as described by Johnson et al. (2013). First, we averaged the monthly minimum temperatures and total monthly precipitation within the study area from winter 1965–1966 to winter 2020–2021 based on the Parameter-elevation Regressions on Independent Slopes Model (PRISM; <https://prism.oregonstate.edu/>; Daly et al., 2008). Next, we standardized temperature and precipitation for each year such that the mean = 0 and standard deviation = 1. Finally, WSI was computed as the standardized precipitation – standardized temperature.

Survival modeling

We used Cox proportional hazard models with staggered entry (Cox, 1972; Pollock et al., 1989) to test the effects of exposure to predators, human impacts, and winter severity on survival of individual adult female and juvenile (male and female) white-tailed deer using the survival package (Therneau, 2022) in R. This model identifies factors influencing the time to an event (in our case, death) but does not incorporate the cause of death (Cox, 1972). We chose this approach because the causes of mortality for many of the deer were unknown, and we suspected that some causes of death (e.g., wolf predation) were more likely to remain unidentified than others (e.g., cougar predation and vehicle collision; Ganz, DeVivo, Reese, & Prugh, 2022), which would lead to biased estimates of cause-specific mortality rates. Additionally, we were only able to identify the proximate, rather than the ultimate, cause of mortality for deer, and this approach allowed us to account for factors influencing deer beyond the documented proximate causes of mortality. Cox proportional hazard models assume that the baseline hazard and the effects of model covariates are constant over the model timeframe (Fieberg &

DelGiudice, 2009), which we checked by inspecting diagnostic plots of the residuals and testing the proportionality assumption (Therneau, 2022; Therneau & Grambsch, 2000). To meet these assumptions, we created five separate models: (1) juveniles 0–6 months old, (2) juveniles 6–9 months old, (3) juveniles 9–12 months old, (4) adult females in the summer and fall (June–November), and (5) adult females in the winter and spring (December–May). Because juveniles entered the model on the day of capture whereas the annual period for adults started June 1, the periods for 0- to 6-month-old deer and adults in the summer and fall were closely, but not exactly, temporally aligned. Likewise, the period for the adult female model from December to May was approximately aligned with the juvenile 6- to 9- and 9- to 12-month-old models.

All models included exposure to coyotes, cougars, and wolves to describe predation risk, use of agriculture and areas of timber harvest, and distance to paved roads to account for human impacts. We did not expect bobcats to influence survival of adult female deer, so we included them in the models of juvenile deer only (Ballard, 2011). Winter/spring models also included winter severity (Eacker et al., 2016). The 0- to 6-month-old model additionally included body mass at capture because larger neonates tend to have higher survival rates (Bergman et al., 2014; Bishop et al., 2009). We used data from neonates captured with VITs to compare survival between individuals captured at 0 days old to those captured 1–3 days old (assuming birth occurred the day of VIT expulsion), to determine whether left-censoring influenced survival estimates (Gilbert et al., 2014). Survival did not differ between these neonates ($n_{\text{captured day 0}} = 23$; $n_{\text{captured day >0}} = 11$; $\chi^2 = 0.6$, $df = 1$, $p = 0.44$), so all neonates entered the survival models on the day of capture.

We monitored deer for varying lengths of time, which prohibited the estimation of annual home ranges, so we averaged the values of the spatially varying predictors (predator RSFs, distance to roads, use of agriculture, and use of timber harvest) at each of their telemetry locations over the period of interest to parameterize the models (Eacker et al., 2016; Shuman et al., 2017; White et al., 2010). For all spatial covariates except distance to roads, deer locations were buffered with a 200-m radius moving window using the “focal” function in the raster R package (Hijmans et al., 2015). We chose a 200-m buffer to reflect the resources available to each deer across each step (median distance between 4-h deer relocations = 188 m, mean = 265 m) and their vulnerability to wider ranging predators. Distance to road was calculated as the Euclidean distance from each telemetry location to the nearest paved road, where vehicle collisions were most likely to occur.

All covariates in the survival models were scaled within each model data set to have a mean of 0 and standard deviation of 1. Because adult deer surviving >1 year were included in multiple rows of the model, we calculated robust standard errors that accounted for the lack of independence between multiple records of the same individual (Therneau & Grambsch, 2000). We checked Pearson's correlations among covariates within the model and eliminated covariates with $|r| > 0.7$ (Dormann et al., 2013). If covariates were highly correlated, we used Akaike's information criterion corrected for small sample size (AIC_c) to compare the two versions of the full models, excluding each of the correlated covariates, and selected the model with better predictive performance (Anderson & Burnham, 2002). We verified that models met the assumptions of proportional hazard, and we adjusted model periods and included polynomial forms of the covariates if necessary to meet model assumptions (Fieberg & DelGiudice, 2009).

Simulating population growth

We used the Cox proportional hazard models to parameterize stage-specific survival rates in the matrix and simulated changes to the considered covariates to determine how λ would respond. Specifically, we parameterized S for each period such that $S(t) = 1 - \text{hazard}(t)$, where t is the time period, $\text{hazard}(t) = h_0 e^{\beta X}$, and h_0 is the baseline hazard (Murray, 2006). The exponentiated βX represents the matrix of coefficients (β) and covariates (X). Annual survival was the product of the time periods for each age class, that is, $S_a = S_{\text{June–November}} \times S_{\text{December–May}}$ and $S_j = S_{0–6\text{months}} \times S_{6–9\text{months}} \times S_{9–12\text{months}}$. To align simulations with the null estimate of λ , we set h_0 to 1—the Kaplan Meier survival estimate for the survival period.

We simulated changes to λ by independently varying each model covariate from -0.5 to 0.5 standard deviations of the mean in 0.01 standard deviation increments, with 1000 repetitions at each value. Each simulation therefore represented a counterfactual scenario where the average predator exposure, land use, or winter severity value changed across the population. For instance, setting agriculture to 0.2 represented a scenario where deer on average used agricultural areas 0.2 standard deviations above the study period mean. Assuming a normal distribution, changes of 0.1 , 0.2 , 0.3 , 0.4 , and 0.5 standard deviations equate to 4.0% , 7.9% , 11.8% , 15.5% , and 19.1% changes, respectively, which was a realistic range that managers could influence (Proffitt et al., 2020). We did not simulate changes to harvest rates because antlerless harvest was limited during the study, our population model was female only, and no collared deer died by

harvest. Simulations incorporated stochasticity from pregnancy rates and yearling survival, as previously described, because the sample size of yearlings was too small to model survival as a function of covariates. We additionally accounted for uncertainty in survival for each time period based on h_0 and coefficient estimates in the Cox proportional hazard model. As $h_0 = 1 - S_{\text{Kaplan Meier}}$, we used draws of survival based on the mean and standard error of the beta distribution for the period. We stochastically generated coefficient values, assuming coefficient estimates followed a normal distribution with the mean and standard error derived from model estimates.

Finally, we used simple linear regression to evaluate how changes in predator exposure, human impacts on the landscape, winter severity, and neonate body mass influenced λ . Linear regression allowed us to directly compare the variable coefficients to one another to determine which factors influenced λ most strongly. We also visually inspected plots displaying the effect of each variable on λ to determine whether a nonlinear response should be considered. We did not evaluate the significance of the potential predictors of λ because significance would depend on the arbitrary choice of the number of simulations run.

RESULTS

We captured 280 white-tailed deer, of which 148 were juveniles. We found an additional two neonates dead during searches. Hoof wear indicated that these dead neonates were born alive such that 150 (73 female, 77 male; $\chi^2 = 0.06$, $df = 1$, $p = 0.81$) total juveniles were tracked. Of these, 108 were located as neonates (76 opportunistically and 32 from VITs), and 42 were captured in the winter at 6–8 months old. Neonate capture dates (CDs) ranged from 26 May to 1 July but generally occurred in early to mid-June ($\overline{CD}_{2017} = 11$ June, $SD_{2017} = 3.7$ days; $\overline{CD}_{2018} = 13$ June, $SD_{2018} = 5.2$ days; $\overline{CD}_{2019} = 15$ June, $SD_{2019} = 6.1$ days; $\overline{CD}_{2020} = 7$ June, $SD_{2020} = 5.8$ days). After censoring data from the first 3 weeks after capture (Northrup et al., 2014; van de Kerk et al., 2020) for 6- to 8-month-old juveniles, a total of 144 juveniles were included in the analysis (68 females, 76 males). Annual survival of juveniles did not differ by sex ($\chi^2 = 0.4$, $df = 1$, $p = 0.51$), so both male and female juveniles were included when estimating survival rates and factors influencing survival. We captured 131 deer as yearlings and adult females. After censoring post-capture data, 117 individual deer (266 deer-years) informed the models of adult female survival. Female juveniles that survived beyond 1 year ($n = 18$), as well as deer collared

as yearlings ($n = 17$, $n = 14$ with post-capture censor), were used to estimate yearling survival ($n = 31$).

Predation ($n = 45$) and vehicle collisions ($n = 21$) were the primary confirmed causes of mortality of collared deer ($n = 72$ documented juvenile mortalities, 48 documented adult female mortalities, one documented yearling female mortality), and 50 mortalities were due to unknown cause (Table 1). Of these unknown mortalities, 23 juveniles and 11 adult females likely or possibly died due to predation, and two adult females likely died from vehicle collisions. Juvenile deaths were due to a range of predators. Cougars were the primary confirmed predator of juveniles (11 of 30 confirmed predations), but coyotes were the primary predators when also including likely and possible predation mortalities (20 of 53 confirmed, likely, and possible predations). Cougars were the primary predator of adult female deer when considering both confirmed (11 of 15) and confirmed, likely, and possible (17 of 26) predations. We did not find evidence of bobcats killing adult female deer. Wolves may have been involved in three mortalities: a juvenile where predation was confirmed and both bobcat and wolf DNA were detected on lethal bite wounds, a juvenile where wolf was the possible cause of death, and an adult where predation was confirmed but it was unclear if the mortality was due to wolves or coyotes.

Annual survival was estimated to be 0.356 (95% CIs: 0.279, 0.455) for juveniles, 0.900 (95% CIs: 0.732, 1.00) for

yearlings, and 0.728 (95% CIs: 0.665, 0.798) for adult females. Yearling pregnancy rates are typically lower than those of adults (DeYoung, 2011), yet all tested yearlings were pregnant at capture ($n = 11$). To avoid overestimating yearling pregnancy, we pooled yearling and adult pregnancy data and estimated a combined pregnancy rate of 0.958 (SE: 0.019, $n = 113$). Yearlings averaged 1.33 fetuses per pregnant female ($n = 3$), whereas adults averaged 1.60 ($n = 20$). Incorporating these demographic rates into the population matrix model, the estimated population growth rate (λ) was 0.97 (95% CIs: 0.88, 1.05) with 74% of simulations resulting in $\lambda < 1$ and 26% of simulations resulting in $\lambda \geq 1$ (Appendix S3: Figure S1). Estimates of λ were most sensitive to adult female survival (mean sensitivity = 0.615, SD = 0.035), followed by juvenile survival (mean sensitivity = 0.526, SD = 0.047). Rescaled for proportional changes, adult female survival (mean elasticity = 0.464, SD = 0.044) still had the largest effect on λ , followed by juvenile survival (mean elasticity = 0.193, SD = 0.017).

Factors influencing mortality risk

Predator RSFs (Figure 1) incorporated data from 33 bobcats, 50 cougars, 28 coyotes, and 14 wolves (model outputs provided in Appendix S2: Tables S1–S4). Locations

TABLE 1 Proximate causes of death for white-tailed deer with global positioning system or very high frequency collars in northeast Washington state, USA, from 2017 to 2021.

Cause of death	Juveniles				Adult females			
	Confirmed ($n = 72$)	Likely ($n = 8$)	Possible ($n = 15$)	Total ^a	Confirmed ($n = 48$)	Likely ($n = 8$)	Possible ($n = 5$)	Total ^a
Unknown COD	29	0	0	29	21	0	0	21
Vehicle/other accident	10	0	0	10	10	2	0	12
Disease	3	0	0	3	1	0	0	1
Illegal harvest	0	0	0	0	1	0	0	1
Total predator	30	8	15	53	15	6	5	26
Bear	2	0	0	2	1	1	0	2
Bobcat	6	1	2	8	0	0	0	0
Cougar	11	3	2	17	11	4	2	17
Coyote	8	4	8	20	1	1	1	3
Wolf	0	0	1	1	0	0	0	0
Unknown predator	3	0	2*	5	2	0	3**	5

Note: Predation was confirmed at mortality sites if the carcass had lethal bite marks with hemorrhage or clear signs of a chase or a struggle. In cases where there were no clear signs of hemorrhage due to consumption of the carcass but all evidence clearly indicated a single species of predator responsible for the mortality, we further classified the mortality as due to “likely predation.” If there were no clear signs of hemorrhage due to consumption of the carcass and the evidence weakly indicated a single species of predator, we further classified the mortality as due to “possible predation.” For juveniles, one unknown (*) predation was identified as felid, but it was unclear whether a cougar or a bobcat was the predator. For adult females, one unknown (**) predation was identified as canid, but it was unclear whether wolf or coyote. One yearling died during the study, and the mortality was attributed to vehicle collision.

^aTotal confirmed, likely, and possible.

used by predators were strongly correlated with areas of high predicted selection (Spearman's rank-order correlation coefficient, ρ , ranged from 0.87 to 1.00; Appendix S2: Table S5), indicating that the RSFs performed well as predictors of the relative probability of predator use (Boyce et al., 2002).

We documented 303 individual species of understory vegetation across the 188 sites investigated. Horizontal cover was lower in open areas (mean = 40.2%, SD = 30.4%) compared to forested (mean = 59.1%, SD = 26.6%) and harvested (mean = 54.4%, SD = 24.7%) areas ($F_{2,185} = 8.17$, $p < 0.001$), but there was no meaningful difference in horizontal cover between forested and timber harvest areas ($F_{1,119} = 1.01$, $p = 0.32$). The biomass of acceptable forage was higher in sites with recent timber harvest (mean = 334.6 kg/ha, SD = 150.9, range = 23.0–852.4) compared to forested sites (mean = 215.9 kg/ha, SD = 165.2, range = 0.3–796.1) and open sites (mean = 248.9 kg/ha, SD = 183.0, range = 0.0–761.1) ($F_{2,185} = 8.24$, $p < 0.001$). Forage biomass was comparable between open sites and forested sites ($F_{1,123} = 1.01$, $p = 0.30$). Winters were slightly more severe than average during the study ($\overline{\text{WSI}} = 0.58$), relative to all winters since 1965–1966. Winter conditions were most severe the first year of the study ($\text{WSI}_{2016-2017} = 2.07$), the mildest during 2019–2020 ($\text{WSI}_{2019-2020} = -0.31$) and relatively moderate in other years of the study ($\text{WSI}_{2017-2018} = 0.39$, $\text{WSI}_{2018-2019} = 0.68$, $\text{WSI}_{2020-2021} = 0.08$).

Survival modeling

Bobcats were highly correlated with wolves in the model for 0- to 6-month-old deer ($\rho = 0.85$), and the model for 9- to 12-month-old deer ($\rho = 0.80$), so we used AIC_c to compare models excluding bobcats and wolves (covariate correlations for all models are available in Appendix S3: Tables S1–S5). In both cases, the model with bobcats performed slightly better than the model with wolves (52% of model weight and 0.2 AIC_c points lower in the 0- to 6-month-old model and 57% of model weight and 0.6 AIC_c points lower in the 9- to 12-month-old model), so we removed wolves from both of these models. Although differences in AIC_c score between the models were small, bobcats kill far more juvenile deer than wolves where sympatric (Carstensen et al., 2009), which we also observed (Table 1), further justifying the inclusion of bobcats over wolves. In the 0- to 6- and 9- to 12-month-old models, the effect of timber harvest was nonlinear, so we included a quadratic term for timber harvest. Likewise, the effect of cougars in the adult model of summer–fall survival was nonlinear, so a quadratic term for cougars was included.

Cox proportional hazard models (Figure 2, Appendix S3: Table S6) indicated that exposure to bobcats did not influence mortality risk for juvenile deer. Cougar exposure increased mortality risk for 0- to 6-month-old deer. Though the evidence of an effect of cougar exposure on adult deer survival in the summer–fall was weak, the quadratic effect of cougars indicated that deer were most vulnerable to mortality in areas of the highest cougar activity. We only detected weak evidence for an effect of cougar exposure on the survival of adult deer in the winter–spring, and cougar exposure did not influence survival of 6- to 12-month-old deer. Coyote exposure did not affect the mortality risk of 0- to 9-month-old deer or adult deer in any season, but higher coyote exposure increased the survival of 9- to 12-month-old deer. Wolf exposure increased the mortality risk of adult females in the summer–fall, but not in winter–spring, and there was weak evidence that wolf exposure increased the mortality risk of 6- to 9-month-old deer in the winter.

The use of timber harvest areas reduced the mortality risk of 0- to 6-month-old deer, but there was no effect of use of timber harvest for deer 6–12 months old. Because of the nonlinear effect of timber harvest, the lowest mortality risk for deer 0–6 months old occurred for juveniles using timber harvest ~ 1 SD above the mean. Timber harvest did not affect the mortality risk of adult deer in any season. The use of agriculture did not influence juvenile mortality risk, nor did it affect adult mortality in the summer–fall. We found weak evidence that the use of agriculture reduced mortality risk for adult deer in the winter–spring. Distance to paved roads did not influence deer survival in any model. There was weak evidence that more severe winters increased the mortality of adult females in the winter–spring, but not for deer 6–12 months old. Mortality risk was lower for neonates with larger body mass at capture.

Simulating population growth

Simulating changes to predator exposure, landscape modification and winter severity all influenced λ to varying degrees, and responses were generally linear (Figure 3). A simulated increase in the use of timber harvest areas had the strongest effect on λ and led to positive population growth. Use of agriculture was likewise positively associated with λ , as was exposure to bobcats, increased distance to roads, and the capture mass of neonates, though these effects were smaller. Simulated increases in cougar exposure, followed by wolf exposure, most strongly decreased λ . Winter severity and coyote exposure additionally decreased λ , but the effect was small.

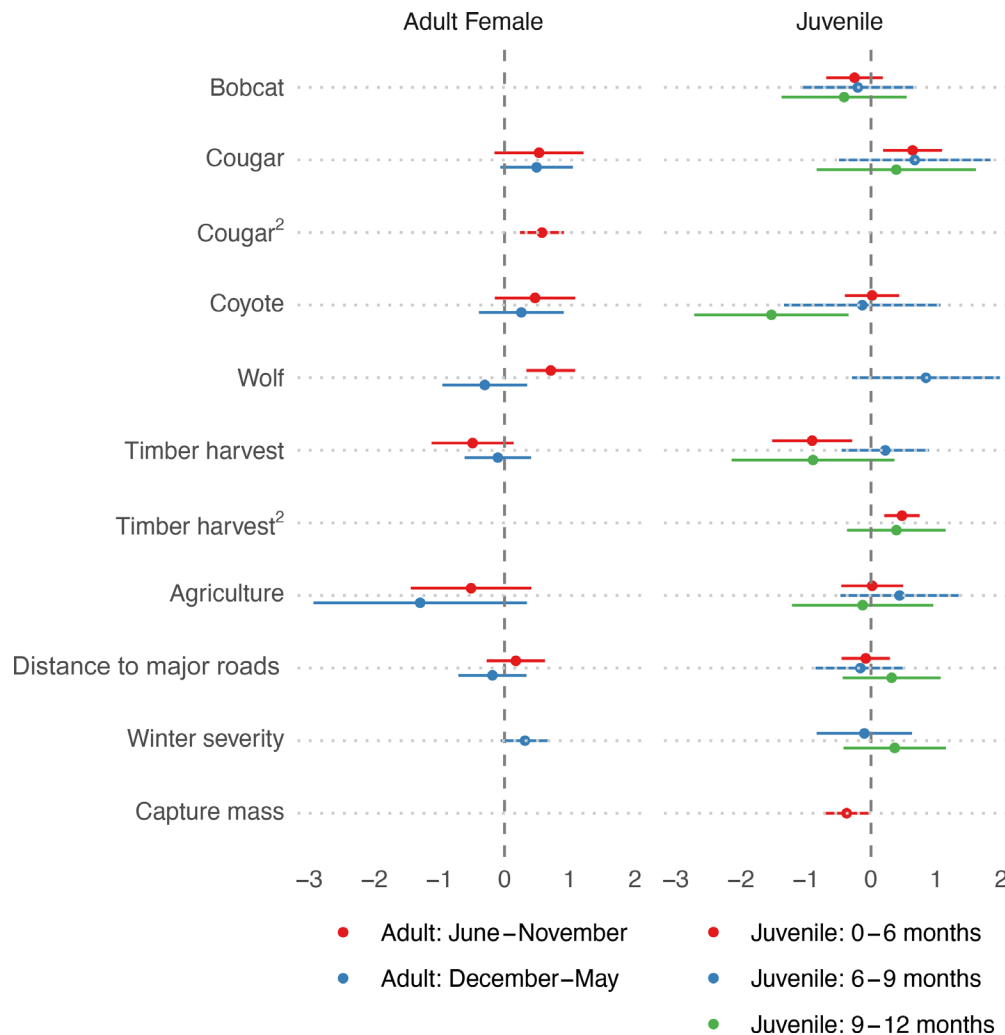


FIGURE 2 Factors influencing risk of mortality for adult female and juvenile white-tailed deer in northeastern Washington state, USA from 2017 to 2021. Covariate estimates >0 increase the risk of mortality, while covariate estimates <0 reduce the risk of mortality. On the x-axis, dots indicate coefficient estimates and corresponding lines display the 95% confidence intervals. Because juveniles entered models on the day of capture, the 0- to 6-month period and June–November period are closely, but not exactly, aligned. Likewise, the 6- to 9- and 9- to 12-month models approximate the same time span as the adult December–May model. Only neonates were weighed at capture. Covariate estimates are included in Appendix S3: Table S6.

DISCUSSION

As landscapes become increasingly dominated by anthropogenic activities (Fischer & Lindenmayer, 2007), understanding the factors influencing prey population dynamics in the human context will be critical for management and conservation (Carter & Linnell, 2016; Kuijper et al., 2016). In our study area, which supports a diverse carnivore assemblage (including recently returned gray wolves) and is shaped by widespread human impacts such as timber harvest, agriculture, and roads, we found that the growth rate of the white-tailed deer population was influenced by predators (H1) and landscape modification (H2). Cougars were the primary documented predator of adult female white-tailed deer and influenced population growth, as did

wolves, indicating that apex predators were the primary top-down force affecting the population. Simulated increases in deer use of areas of recent timber harvest (<20 years) increased the population growth rate and elicited the largest effect of any considered covariate (Figure 3). Vegetation surveys showed that forests with recent timber harvest had greater forage biomass acceptable to deer but did not differ in horizontal cover relative to older forests, suggesting that landscape modification influences forage (H2a) more so than landscape modification influences predation (H2b). Use of agriculture likewise increased population growth. This dual response of deer to apex carnivores and areas associated with increased forage suggests that the deer population was colimited by bottom-up and top-down effects. Our results

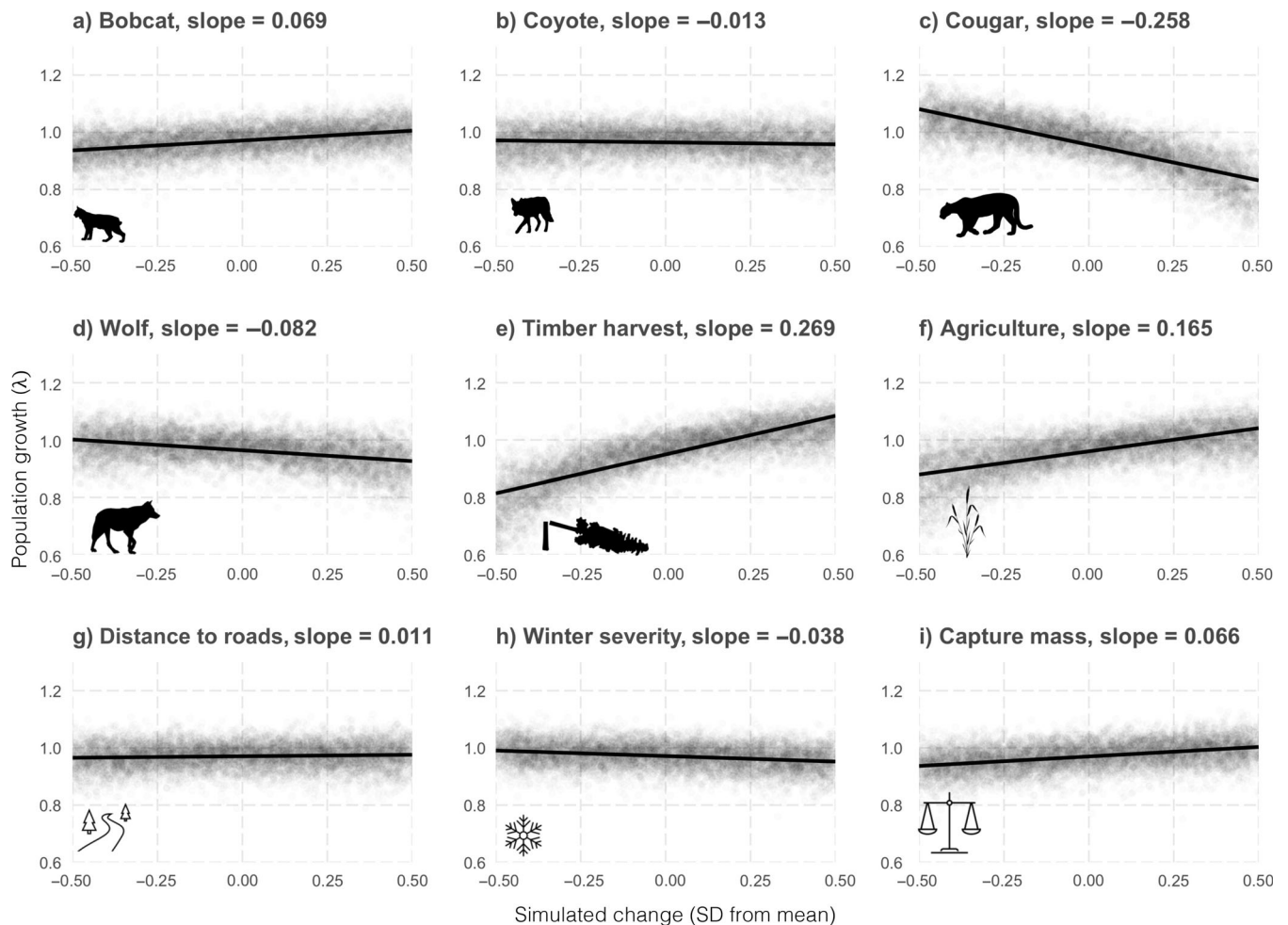


FIGURE 3 Modeled estimates of white-tailed deer population growth in relation to simulated changes to (a) bobcat, (b) coyote, (c) cougar, and (d) wolf exposure, use of (e) timber harvest and (f) agricultural areas, (g) distance from roads, (h) winter severity index, and (i) capture mass of neonates. Assuming a normal distribution, changes of (\pm) 0.1, 0.2, 0.3, 0.4, and 0.5 SDs equate to 4.0%, 7.9%, 11.8%, 15.5%, and 19.1%, respectively. Silhouettes (a–f) were sourced from the R package rphylopic (Chamberlain, 2018) and created by Margot Michaud (a, b, d), Gabriela Palomo-Munoz (c), Michele M. Tobias (e), and Mason McNair (f).

suggest that a reduction in deer exposure to apex predators would likely increase the role of forage in limiting deer due to density-dependent factors (Wang et al., 2009), whereas an increase in the availability of suitable forage would likely increase population performance and could bolster resilience to predators (Bishop et al., 2009).

Apex predators

Despite both species' reliance on wild ungulates as a primary source of prey (Elbroch & Wittmer, 2012; Newsome et al., 2016), simulated changes in cougar exposure had an effect that was more than three times stronger than wolves on population growth rate (Figure 3). This difference likely reflected predator population densities over the study area. In an adjacent area north of our study

system, Beausoleil et al. (2021) estimated 1.96 cougars per 100 km² (SD = 0.20), whereas wolf densities at the time of our study were approximately 0.19 wolves per 100 km² (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). Accordingly, cougars were a primary documented source of mortality for white-tailed deer (Table 1), unlike wolves (Appendix S4). Although the influence of wolves on deer population growth may increase if their densities continue to rise in Washington, our findings indicate they are having weak effects approximately a decade following their return.

In addition to their numerical advantage, cougars may have had stronger annual impacts on deer population growth than wolves because their effects on survival were more seasonally consistent. Hazard models

indicated that wolf exposure tended to increase mortality risk for juvenile deer 6–9 months old (wolves were excluded from 0- to 6- to 9- to 12-month-old models due to correlation with bobcats) and adult female deer in the summer–fall, but wolf exposure did not affect mortality risk for adult females in the winter–spring. Analysis of carnivore diets in the study area suggests that wolf packs increased the use of moose in the winter–spring while continuing to feed on deer, whereas deer were the primary prey of cougars year-round (L. Satterfield, unpublished data). Other studies have likewise shown that wolves prefer moose and elk to deer when available (Popp et al., 2018). Thus, the strength of predation effects on prey in our system and elsewhere are likely influenced not only by predator densities but also by their preferences for other prey in the system as well as alternative prey abundance.

Cougars and wolves responded to humans differently, which may have further affected predation risk for deer. Deer in this area tend to winter in lower-elevation areas close to humans, where the human shield effect may reduce predation pressure from wolves more so than cougars. Specifically, our RSF analysis showed that wolves strongly avoided areas with high levels of human modification (Appendix S2: Table S4), whereas cougars did not (Appendix S2: Table S2). Humans and other predators now occupy much of the landscapes to which wolves are returning, moderating wolf density and habitat use (Prugh et al., 2023). As a result, the effects of wolves on ungulate prey appear to be reduced in human-modified landscapes relative to protected areas or regions lacking sympatric apex predators. Concerns of substantial prey population declines resulting from predator recovery are likely overstated for this system due to the relatively low wolf density, wolf seasonal diet patterns, and wolf avoidance of humans (Marshall et al., 2016). More broadly, our work supports assertions by Kuijper et al. (2016) that the effects of recolonizing wolves on prey can be dampened by human landscape impacts.

Mesopredators

Mesopredators appeared to have little impact on this deer population, perhaps owing to their limited effect on adult female survival. As in other systems with wolves, coyote predation of adult female deer was relatively infrequent (Ballard et al., 2001), and because survival of this age class had the largest influence on the population growth rate, coyotes had limited influence on the population. Unexpectedly, we found that coyote exposure reduced mortality risk for 9- to 12-month-olds. Likewise, bobcat activity tended to reduce mortality risk for juveniles in

the Cox proportional hazard models and apparently led to increased population growth of deer. These counterintuitive results could potentially reflect the suppression of mesopredators by apex predators that we were unable to measure, such that areas of higher mesopredator density reflected lower densities of apex predators (Prugh & Sivy, 2020) and were associated with a net reduction in deer mortality risk. In tightly coupled predator–prey systems, strong suppression of mesopredators by apex predators can increase prey population growth (Prugh & Arthur, 2015). For instance, in Wyoming, USA, the reintroduction of wolves suppressed coyote abundance, leading to increased survival of juvenile pronghorns (*Antilocapra americana*) and increased pronghorn abundance overall (Berger & Conner, 2008). Our findings indicate that mesopredator suppression may be obscured or confounded by human impacts, thereby reducing the impact of these intraguild interactions on shared prey in anthropogenic landscapes.

Human landscape modification

In our system, human landscape modifications primarily benefited white-tailed deer, and simulated changes to use of areas of recent timber harvest had the largest effect on the deer population growth rate of all considered factors. Although the average acceptable forage biomass at all site types far exceeded the ~50- to 100-kg/ha threshold that is limiting to individual deer (Wickstrom et al., 1984), areas of recent timber harvest had the highest forage biomass relative to forested and open sites during the growing season and should therefore support higher densities of deer. Accordingly, use of timber harvest areas tended to decrease mortality risk for deer in the summer, although not in the winter. This seasonal difference is unsurprising; reproductive females require high-quality forage in summer to meet the energetic demand of lactation, and the influence of forage on body condition leading into winter is more important than forage quality during winter for survival (Cook et al., 2013; Moen, 1978; Tollefson et al., 2010, 2011). Additionally, neonates with larger capture mass were at lower risk of mortality, which reflects the quality of forage available to mothers (Côté & Festa-Bianchet, 2001), providing further evidence for the importance of nutrition in this system. The use of agricultural areas, which are likewise associated with nutritional benefits for ungulates (Barker et al., 2019), also positively affected the overall population growth rate and tended to reduce mortality risk for adult deer. Additionally, or alternatively, agricultural areas may have reduced predation risk via a human shield. These findings corroborate McShea's (2012) argument that white-tailed deer

densities may exceed historic levels across much of North America because of agricultural food subsidies and potentially reduced predation risk.

In addition to the nutrition-enhancing effects of timber harvest, changes to vegetation structure could have increased predation risk for deer by impeding predator evasion (Kuijper et al., 2016), but we found limited evidence for this pathway of effects. This dynamic may explain why juvenile deer with the highest use of logged areas were at greater risk of mortality in summer (Figure 2, Appendix S3: Table S6). However, we found no difference in horizontal visibility between recently harvested and unharvested forest sites, indicating the impacts of this land use on hunting success may have been minimal, and a post hoc analysis showed that predator distributions were not highly correlated with areas of recent timber harvest (Appendix S5: Table S1).

Given that timber harvest and agriculture apparently enhanced nutritional resources for deer and together these bottom-up effects exceeded the effect of apex predators on the population growth rate, forage availability was likely the primary factor ultimately limiting the population. This conclusion is consistent with Forrester and Wittmer's (2013) finding that predation is the primary proximate cause of death in mule deer populations but is generally compensatory, and nutrition is the primary driver of population dynamics. Similarly, Melis et al. (2009) found that the impacts of Eurasian lynx (*Lynx lynx*) predation on population growth of roe deer (*Capreolus capreolus*) were reduced in areas of high primary productivity, and Bishop et al. (2009) determined that forage enhancement could reduce predation rates. Our research illustrates the importance of bottom-up effects even as wolves are recovered and offers a complementary perspective to research showing that predator recovery or removal tends to have a weak effect on ungulate abundance where forage is a limiting factor (Clark & Hebblewhite, 2021).

Although most human modifications of this landscape appear to have benefited deer population growth, roads were not one of them. Vehicle collisions were a common cause of mortality for deer of all age classes (Table 1), yet use of locations closer to roads did not influence survival or subsequently the overall population growth rate. It is possible that distance to the nearest road was not an appropriate covariate to detect differences in risk of deer–vehicle collisions, and instead road density or other road metrics should be investigated. Alternatively, the greater risk of vehicle collision associated with high-speed roads may have been counteracted by reduced predation risk if high-traffic roads induced a human shield, resulting in the apparent lack of effect. If so, measures taken to reduce

vehicle collisions could benefit deer by reducing the lethality of this human shield.

Methodological considerations

Because of the observational nature of this study, we were unable to fully account for all the pathways through which predators and various anthropogenic landscape changes can influence deer population dynamics, which should be considered when interpreting these results (Appendix S4). As with all forms of linear regression, it is possible that the RSFs reflected unmeasured factors affecting deer survival or the direct effects of the landscape features that were used to predict predator activity on deer. The predator RSFs, and therefore our inferences, reflect the order of selection evaluated (*sensu* Johnson, 1980) and the spatial and temporal scales of analysis. In other systems, considering alternate measures of predator activity (e.g., utilization distributions; see Ganz, DeVivo, Kertson, et al., 2022) or modeling RSFs on different scales may be appropriate. Finally, when simulating changes to factors affecting deer survival, we assumed the average exposure to predators, human landscape modification, or winter severity values changed across the population. In reality, managers may only be able to alter factors in specific locations, which may only affect some deer in the population. The influence of a potential management action then depends on the proportion of deer impacted, which should be considered when assessing management strategies.

Forage dynamics and ungulate nutrition are complex processes (Merems et al., 2020) that are shaped by many factors in addition to the land-management practices we considered here, which themselves are multifaceted (Hayes et al., 2022). Specifically, time since harvest and harvest treatment, ranging from selective thinning to clear cutting, play important roles governing the increase in forage biomass following disturbance (Hayes et al., 2022; Hull et al., 2020), which we did not have adequate data to evaluate. As such, we encourage further investigations into the effects of specific timber harvest treatments on deer demographics. Despite these limitations, our finding that the biomass of acceptable forage was higher in timber harvest areas, combined with the positive effects of simulated increases in the use of timber harvest and agricultural areas, highlights the important role of bottom-up effects in this system. This study occurred over a relatively short duration (4 years), so we could not assess the impacts of predation and anthropogenic landscape change on longer-term ungulate dynamics. Continued monitoring and longer-term assessment of these relationships here and in other systems will be key

to understanding ungulate population dynamics in human-modified landscapes.

Management implications

Our findings show that even with strong top-down effects of apex predators, forage biomass is critical to population growth. Drivers of resource dynamics like climate change and active land management, whether by timber harvest, agriculture, or habitat restoration, have especially strong potential to affect ungulate population trajectories in human-altered systems (Bergman et al., 2014; Bishop et al., 2009; Forrester & Wittmer, 2013). Management options come with trade-offs, and managers seeking to increase deer population growth rates should evaluate the economic, social, logistical, ethical, and indirect ecological impacts associated with proposed management strategies (Clark & Hebblewhite, 2021). For instance, short-term predator reduction efforts led to only temporary increases in ungulate population growth rates in a Montana system colimited by forage and predation, and efforts to reduce cougar densities precipitated social controversy within the local community (Proffitt et al., 2020). Habitat-modification effects may persist longer than predator-reduction efforts, with increases in forage biomass lasting for ~20 years following timber harvest (Hull et al., 2020; Monzingo et al., 2023), but may also result in unexpected consequences. For instance, in British Columbia and Alberta, Canada, the creation of early seral habitat due to timber harvest has supported a booming deer population, in turn supporting a larger predator population that is negatively impacting rarer ungulates (i.e., woodland caribou [*Rangifer tarandus*]; Latham et al., 2011; Wittmer et al., 2007). Such indirect effects of landscape change highlight the importance of carefully considering the impacts of management actions beyond the target species and the need for adaptive management to evaluate the efficacy of management implementations. As apex predators return to anthropogenic landscapes, more explicit examination of the influence that humans exert on prey population dynamics by shaping predation risk and altering vegetation dynamics will provide important insights into sustaining wildlife across diverse landscapes.

One promising management strategy to increase deer population resilience in anthropogenic landscapes lies in reducing deer–vehicle collisions, which would benefit both humans and deer. While we did not detect an impact of distance to roads on mortality risk, at least 13.9% (10/72) of juvenile mortalities and a minimum of 20.8% (10/48) adult female mortalities were due to vehicle collisions (Table 1). If these deer had otherwise

survived, annual survival of juvenile deer would have increased from 0.356 to 0.446 and adult female survival would have increased from 0.729 to 0.786, resulting in a predicted population growth rate of 1.06 (95% CI: 0.97, 1.14), with 92% of simulations showing population increase. Collisions may be partially compensatory with other causes of mortality, but even a small increase in adult female survival could positively affect population growth. Because deer–vehicle collisions in the United States cause over 59,000 human injuries and more than 440 human deaths annually (Conover, 2019), costing over \$10 billion (Huijser et al., 2008), efforts to reduce deer–vehicle collisions nationwide would be a win–win, saving human lives and potentially improving deer population performance.

Conclusions

Collectively, our work reveals that top-down effects on ungulates are conserved in predator-rich landscapes shared with humans. Accordingly, apex predators in our system contribute to limiting ungulate population growth, but, as in other systems, forage availability appears to play an even larger role (Bishop et al., 2009; Forrester & Wittmer, 2013). Considering that effects of forage modifications persist longer than altering predator densities (Hull et al., 2020; Monzingo et al., 2023; Proffitt et al., 2020) and that a reduction in predation mortality would likely increase nutrient limitation of the deer population (Wang et al., 2009) and deer–vehicle collision rates (Gilbert et al., 2017; Raynor et al., 2021), efforts to increase the availability of high-quality forage will likely be the most effective strategy to increase deer population growth rates. Despite some concerns that recovering extirpated predators (here, wolves) may lead to additive predation rates on ungulates, human activities limit wolves' distribution (Prugh et al., 2023), and the effect of wolves on deer demographics was relatively weak. As apex predators return to anthropogenic landscapes globally, more explicit examination of the influence that humans exert on prey population dynamics by shaping predation risk and altering vegetation dynamics will provide important insights regarding the ecological impacts of these species and how to sustain wildlife across diverse landscapes.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research are sensitive and not available publicly. Data are available to qualified researchers by contacting the Washington Department of Fish and Wildlife and requesting white-tailed deer 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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