



Wildlife migrations highlight importance of both private lands and protected areas in the Greater Yellowstone Ecosystem

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ARTICLE INFO

Keywords:

Disturbance
Easements
Elk
Greater Yellowstone Ecosystem
Land use
Protection
Zoning

ABSTRACT

Formally protected areas are an important component of wildlife conservation, but face limitations in their effectiveness for migratory species. Improved stewardship of working lands around protected areas is one solution for conservation planning, but private working lands are vulnerable to development. In the Greater Yellowstone Ecosystem (GYE), ungulates such as elk (*Cervus canadensis*) use both protected areas and private lands throughout their annual migrations. We studied patterns of landownership, protection, and conservation challenges within the ranges of migratory elk in the GYE. We used GPS data from 1088 elk in 26 herds to define herd-level seasonal ranges, and extracted covariates related to landownership and protection, land use, and human infrastructure and development. All elk herds used land encompassing >1 ownership type. Most elk herds (92.3 % of herds, $n = 24$) used the highest proportion of private land in the winter (mean = 36.2 % private land). Most elk herds' winter ranges contained the highest building densities (mean = 1.24 buildings/km²), fence densities (mean = 1.02 km fence/km²), and cattle grazing (mean = 1.9 cows/km²), compared to migratory and summer ranges. Out of all ranges, 36.5 % of ranges did not have any zoning regulations, indicating the potential for future development. Our results show that elk in the GYE rely on habitat outside of protected areas, and face landscape-scale conservation challenges such as habitat fragmentation from human development, particularly in winter ranges. Future conservation strategies for wildlife in this system need to encompass coordination across both public and private land to ensure migratory connectivity.

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1. Introduction

Globally, one of the most effective strategies for wildlife conservation has been the establishment of protected areas, which serve to protect habitats, species, and ecological processes (Geldmann et al., 2013). As conservation challenges such as land use change, habitat fragmentation, and climate change continue to threaten the world's biodiversity (de Chazal and Rounsevell, 2009), there have been recent calls to increase the amount of land protected globally. For example, the 30 by 30 initiative aims to have 30 % of global land and waters protected by the year 2030 (Convention on Biological Diversity, 2020), a goal adopted by several US states, the current US administration as the “America the Beautiful challenge” (United States Department of the Interior, 2021), and 84 other governments worldwide (Worldwide Fund for Nature, 2020).

Despite clear conservation benefits, protected areas face several limitations in safeguarding biodiversity, including often being too small to meet the needs of wide-ranging species, (Maiorano et al., 2008), having limited connectivity with other protected areas (Saura et al., 2018), and having high levels of human development immediately beyond protected area boundaries (Wittemyer et al., 2008; Martinuzzi et al., 2015). Additionally, protected areas often preclude traditional economic activity and cultural practices (West et al., 2006). Improved protection and stewardship of working lands around protected areas is increasingly seen as a solution (Kremen and Merenlender, 2018) but requires a strong understanding of key ecosystem elements and human land uses which may impact those elements, in order to inform development of policy instruments and needed multi-stakeholder coordination.

The limitations of protected areas can be especially pronounced for wide-ranging or migratory species whose life histories require them to move across landscape gradients and beyond the borders of protected areas. For example, wildebeest (*Connochaetes taurinus*) in the Serengeti-Mara ecosystem spend much of the year in protected areas, but use migration routes through unprotected lands that are threatened by land use change (Thirgood et al., 2004). Likewise, nomadic Mongolian gazelles (*Procapra gutturosa*) use both protected and unprotected areas because they have large home ranges, and face threats outside of protected areas such as fences and conversion of land to oil fields (Nandintsetseg et al., 2019). Migratory wildlife can also face threats associated with conversion of land outside of protected areas to agriculture due to competition with domestic livestock for forage, disease transmission, and crop predation (Hegel et al., 2009; Rayl et al., 2021). Although protected areas might conserve part of the annual cycle for migratory species, threats outside of protected areas can reduce or fragment habitat and even lead to population declines or loss of migratory behavior (Bolger et al., 2008). Thus, ensuring the persistence of migratory species in the future will likely depend on conservation efforts involving both protected areas and surrounding working lands (Thirgood et al., 2004; Middleton et al., 2020).

The Greater Yellowstone Ecosystem (GYE) in western North America harbors important migratory ungulate populations, but some migrations in this landscape have already been truncated or lost (Kauffman et al., 2021b) and there are concerns about the persistence of others because of land use change and fragmentation (Berger, 2004; Kauffman et al., 2021b). Although the GYE encompasses large protected areas (e.g., Yellowstone and Grand Teton National Parks and surrounding national forests), migratory species must exploit landscape gradients on multi-use and private lands, which often are not formally protected and therefore are likely vulnerable to future land use change. Areas throughout the GYE are currently experiencing development booms, as the COVID-19 pandemic and increased remote work opportunities have led to more people moving to small mountain towns and surrounding rural areas (Dimke et al., 2021). Current land uses, as well as future land use changes, could be particularly challenging for long-distance migratory ungulates such as elk, mule deer, and pronghorn (Middleton et al.,

2020). Impacts on elk (*Cervus canadensis*), which make round-trip migrations up to 226 km each year in the GYE, could have particularly broad consequences because they are a primary food source for large carnivores (Husseman et al., 2003) and can influence food webs by affecting predator space use and behavior (Nelson et al., 2012; Middleton et al., 2013), plant growth (Brice et al., 2022), and nutrient cycling (Singer and Schoenecker, 2003). Elk are also important culturally and economically within this system (Middleton et al., 2020). Because elk play an important role in this ecosystem, understanding current land protection and conservation issues within elk ranges can offer insight into the challenges associated with the land use change in the GYE. Despite the value of such work, no systematic analysis of land use associated with migratory ungulates in the GYE has been conducted, and only recently do we have the landscape-scale animal movement data needed to execute this type of analysis.

To better understand the state of landscape conservation for migratory ungulates in the GYE, we examine land protection and land use within the seasonal ranges of 26 elk herds across the GYE, comprising the most comprehensive elk spatial dataset to date and spanning multiple-use public and private lands. We seek to understand: a) current landownership, land protection, and land use within elk ranges in the GYE, and b) spatial variation in land use within ranges of migratory elk, particularly as it pertains to human development and infrastructure, agriculture, and livestock grazing. We highlight the challenges and opportunities associated with conserving migratory species within a matrix of land protections and land uses, which is relevant to many systems globally where wide-ranging wildlife use a matrix of landownership types.

2. Methods

2.1. Study area

We studied migratory elk within the GYE, an approximately 10.8 million ha ecosystem centered around the Yellowstone plateau and surrounding mountain ranges in Idaho, Montana, and Wyoming (Noss et al., 2002). The GYE contains a mix of landownership including federally-protected Yellowstone National Park, Grand Teton National Park and several national forests and wilderness areas, as well as land managed by the Bureau of Land Management (BLM), state-owned lands in Idaho, Montana, and Wyoming, tribal lands, and private land (both protected from development through easements and without easements) which includes working lands, amenity ranches, and suburban developments. Habitat types within the GYE include high elevation alpine forests, mid-elevation coniferous and deciduous forests, and low elevation shrub-step and grasslands, with riparian areas scattered throughout.

2.2. Elk spatial data

We defined winter, summer, and migration ranges for 26 herds within the GYE that spend at least a portion of the year in Yellowstone and Grand Teton National Parks and adjacent public lands. We compiled existing elk GPS datasets from previous research in the GYE spanning 2000–2020. All elk included in this analysis had GPS collar data with fix rates from 45 min to 24 h. For elk that were monitored for more than one year, we selected the most recent year of data. Because elk herds can contain thousands of animals, we only collared a subset of individuals within a herd; thus, we assumed that the coarse-scale space use of individual elk was representative of that of the entire herd, even though finer-scale space use might vary for individual animals.

For each individual elk, we delineated seasonal and migratory ranges by using both net squared displacement and elevation change over time to generate movement timing graphs (Bunnefeld et al., 2011; Spitz et al., 2018; Lowrey et al., 2020). We visually inspected the curves to manually identify spring and fall migration events and determine start and end dates for each individual elk. We estimated seasonal occurrence

distributions using Brownian bridge movement models (BBMM; Horne et al., 2007) to define the seasonal ranges of elk herds. We did not incorporate variation in intensity of use within ranges since we were interested in estimating the overall spatial extent of elk space use.

We estimated herd-level winter ranges by taking the 99 % isopleth of a BBMM for each individual elk fit to the 60 days of data before the spring migration or the entire year of data for resident elk (Sawyer et al., 2009). We then merged each individual elk's 99 % isopleth to form a single herd-level winter range encompassing the entire area used by the herd in the winter season. Summer ranges were estimated by fitting individual BBMMs to the movement data between migration events, or to the 60 days after the spring migration for elk with only a single migration, and then merging the 99 % isopleths to form herd-level ranges encompassing the entire area used by the herd in the summer. We estimated migratory ranges by fitting separate BBMMs for spring and fall migrations, and then merging the individual 99 % isopleths of both the spring and fall migration ranges to form a single herd-level migratory range that encompassed the total area used by the herd during both migrations. We selected the 99 % isopleth because it provided us with the maximum estimates of land use and potential conservation challenges for elk, which could prove useful for connecting these results to management (Allen and Singh, 2016), and because low use areas can still be essential for ensuring migratory connectivity in this system (Sawyer et al., 2009).

2.3. Landownership data

We extracted spatial covariates related to landownership from all herd-level ranges. Because many habitat conservation and management efforts depend on coordination among public and private landowners, we sought to quantify the proportion of elk ranges falling within different landownership categories, the proportion of elk ranges currently under protection, and the number of private landowners within elk ranges. We used land management data from the BLM National Surface Management Agency Area Polygons (<https://data.doi.gov/dataset/blm-national-surface-management-agency-area-polygons-national-geospatial-data-asset-ngda>), which separated land into state, National Park Service, US Forest Service, BLM, other federal, tribal, and private lands, and calculated the proportion of all elk herd ranges under each land jurisdiction.

We identified the level of guaranteed permanency of habitat protection using the U.S. Geological Survey (USGS) US Protected Areas Database (<https://www.usgs.gov/programs/gap-analysis-project/science/protected-areas>) for public conservation areas, or the National Conservation Easement Database (<https://www.conservationeasement.us/>) for conservation easements. Both the US Protected Areas Database and the National Conservation Easement Database use the same ranking system to characterize protection level (1 = managed for biodiversity and natural disturbances are permitted, 2 = managed for biodiversity, but natural disturbances are suppressed, 3 = managed for multiple use and extraction is permitted, 4 = protected but no known mandate for biodiversity protection). We calculated the percentage of each protection category within elk herd ranges, as well as the overall proportion of land protected vs. not protected within herd ranges.

For private land, we estimated the number of individual landowners based on parcel ownership data publicly available from individual counties, or purchased from outline databases (LandGrid: <https://landgrid.com/>; ReportAll: <https://reportallusa.com/>). Within each county, we merged parcels registered to the same name, and summed the number of unique landowners within all the elk seasonal ranges. While we recognize that parcel ownership might not perfectly reflect the actual number of landowners because of variation in the names that parcels are registered under, we consider this metric an informative coarse-scale approximation of landownership in the GYE.

2.4. Human development and infrastructure data

We extracted spatial covariates related to human development and infrastructure from all herd-level ranges. We included fence density because of the potential for fences to restrict the movement of elk and other migratory ungulates (Xu et al., 2021), as well as the potential for elk to cause damage to fences (Walter et al., 2010), which in turn could affect landowner tolerance. We estimated private and public fence density in the GYE using county-level parcel ownership shapefiles and US Forest Service grazing allotment boundaries, respectively. Previous studies show that these two datasets approximate potential distributions of private and public fences in the western US, respectively (Poor et al., 2014; McInturff et al., 2020). However, not all parcel and allotment boundaries are fenced in our study area, and data from different counties may have different accuracy. To avoid overestimating fence density, we estimated Type I errors of the datasets by randomly sampling 1200 locations (600 along parcel boundaries and 600 along grazing allotment boundaries) and visually assessing high-resolution satellite imagery (spatial resolution 0.02–0.15 m) to determine if a fence was present. To capture regional differences in fence density and data accuracy, we divided the study area into 5×5 km grids ($n = 90$) and calculated the Type I errors at the grid-level based on the rate that parcel boundaries falsely indicated the presence of fences. The raw private and public fence estimations (km per km²) were multiplied by the Type I error rate of its corresponding grid. We then added the adjusted private and public fence density estimates together to obtain the final estimate for the study area. Finally, we calculated the mean fence density within the seasonal ranges for all elk herds. Although our fence density estimate is likely an underestimate of the true density of fences considering other types of fences that exist in the GYE (e.g. road-side fences, cross-fences within grazing allotments and pastures), it serves as a useful proxy for evaluating coarse-scale differences.

We investigated spatial variation in road density because of the potential for roads to serve as a source of elk mortality and a safety risk to humans through vehicle collisions, and because roads fragment habitat (Trombulak and Frissell, 2000). We estimated road density in the GYE using the US Census Bureau 2020 Tiger/Lines shapefile (<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>). We considered all roads, and interstate-only roads separately, given that interstates might represent greater barriers for migratory elk because of higher traffic volumes, speeds, and surface widths. For both road groupings, we estimated the road density (km/km²) across our study area and calculated the road density within the seasonal ranges for all elk herds.

We estimated the density of energy infrastructure because oil and gas development fragments habitats and leads to the reduction of habitat use of elk (Buchanan et al., 2014). We used spatial data from the WY Oil and Gas Conservation Commission (<http://pipeline.wyo.gov/legacywogcce.cfm>), the MT Board of Oil and Gas (<http://www.bogc.dnrc.mt.gov/gisdata/WellSurface/>), and the United States Wind Turbine Database (Hoen et al., 2018). We did not include energy infrastructure data from Idaho given the low density of energy development within the state. We considered oil and gas wells (both active and inactive) and wind turbines as sources of disturbance on the landscape. We estimated the infrastructure density (counts of wells and turbines/km²) across our study area and calculated the mean infrastructure density within the seasonal ranges for all herds.

We estimated both current and potential future building densities in the GYE because building development reduces habitat for elk (Gude et al., 2007). For current building densities we used the Microsoft US Building Footprints shapefile (<https://github.com/Microsoft/USBuildingFootprints>). Using this shapefile, we calculated the mean building density (buildings/km²) throughout our study area and calculated the mean building density within the seasonal ranges for all herds. To estimate the potential for future building development, we obtained county zoning regulations from the counties within our study area,

either as shapefiles or PDF maps which we then digitized. We used the maximum allowable building densities from the zoning regulations to characterize the potential maximum number of buildings/km² throughout our study area and calculated the average potential maximum building density within the elk seasonal ranges.

We estimated spatial variation in agriculture and livestock within elk ranges because they can result in human-wildlife conflict due to

competition between elk and livestock for forage, crop damage, and the potential for disease transmission risk (Hegel et al., 2009; Rayl et al., 2021). To characterize agriculture in the GYE, we used U.S. Department of Agriculture (USDA) CropScape data (<https://nassgeodata.gmu.edu/CropScape/>) from 2020. We defined agriculture as any cultivated crop, or any grassland which could be used for grazing. We calculated the proportion of agriculture within each elk herd seasonal range. We also

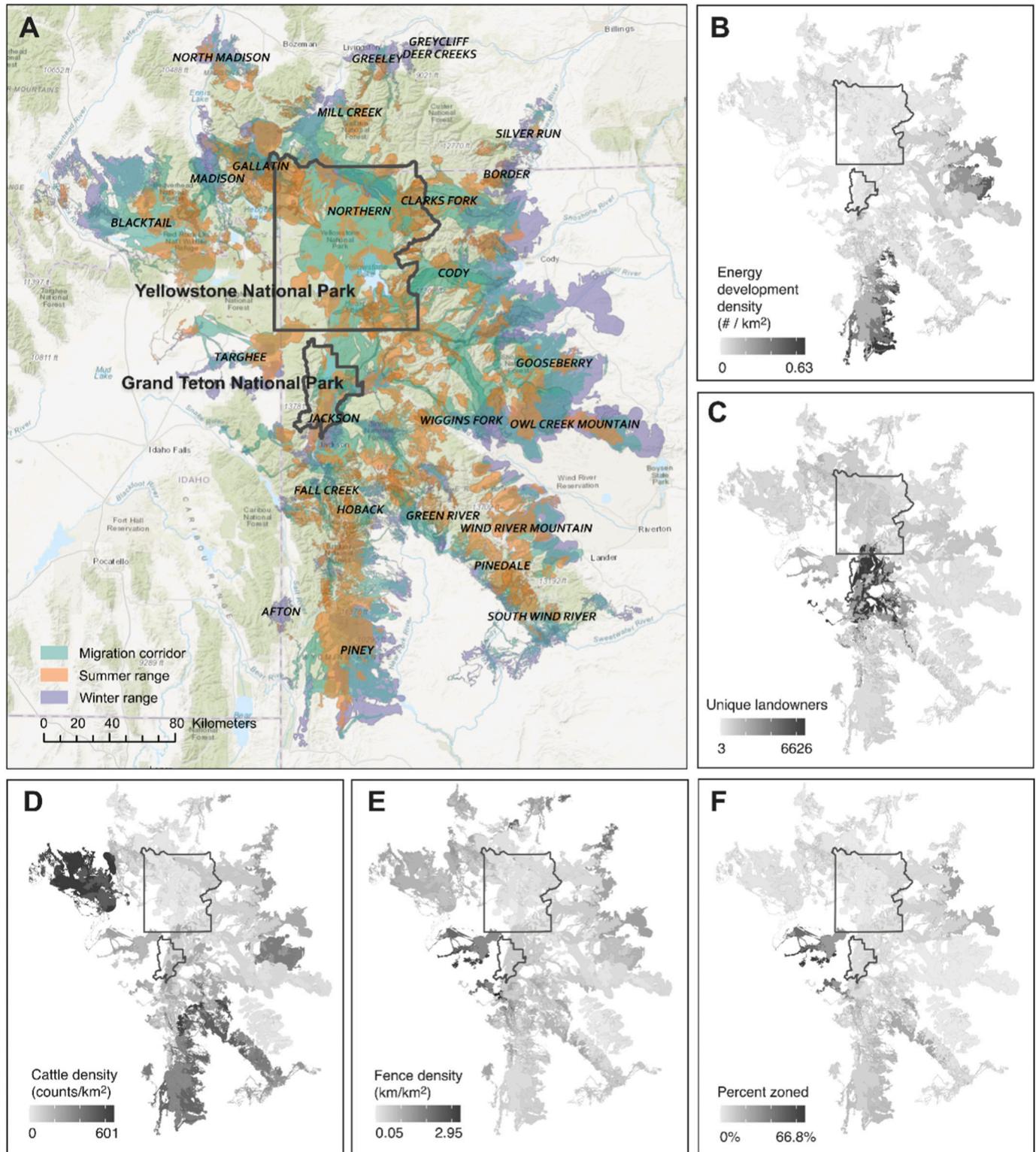


Fig. 1. A) Ranges of the 26 elk herds included in this study, and spatial variation in B) energy development (counts/km²), C) number of unique landowners, D) cattle density (counts/km²), E) fence density (km/km²), and F) percent zoned land within elk ranges, Greater Yellowstone Ecosystem, 2000–2020.

estimated livestock grazing intensity in the GYE using grazing allotment data from the BLM Rangeland Administration System (<https://reports.blm.gov/reports/RAS>) and individual US Forest Service Forest offices. Because grazing can vary seasonally, we used the maximum number of each individual species that were permitted to use an allotment each year. We calculated the average cattle density (number of individuals/km²) within a 1 × 1 km grid in our study area and used this to calculate the average livestock density within all elk seasonal ranges. Although the available livestock data do not always include grazing on private lands, we believe these data are a useful proxy for coarse-scale spatial variation in livestock grazing within the GYE.

3. Results

We used 1088 individual elk from 26 herds within the GYE to define herd-level seasonal ranges and migratory ranges (Fig. 1A). Twenty-four herds exhibited migrations ranging from 1 to 113 km, whereas two herds (Greycliff and Deer Creeks) were comprised of only non-migratory individuals. For the two non-migratory herds, we only present winter range statistics.

3.1. Landownership and protection

Landownership and protection associated with the elk ranges that we included in our analyses varied both seasonally, and among individual elk herds. All elk herds used land encompassing >1 ownership type during all three seasonal ranges (Fig. 2A), with herds ranging from primarily using private land (e.g. North Madison herd) to primarily using federal lands (e.g. Afton herd). The majority of migratory herds

used the highest proportion of private land in the winter (92.3 % of herds; *n* = 24), with only 8.3 % of herds (*n* = 2) using the highest proportion of private land in migratory ranges, and no herds using the highest proportion of private land in summer ranges. The average percentage of private lands within elk herd ranges ranged from 3.3 % to 85.4 % of winter ranges (mean = 36.2 % private land), 3.2 % to 91.3 % of migratory ranges (mean = 21.3 % private land), and 0.4 % to 86.3 % of summer ranges (mean = 11.4 % private land). Across all elk herds we included in our analysis, 1.88 million acres of easement-free private lands overlap elk ranges.

When only considering private lands, elk herds included in our analyses experienced differing numbers of private owners within their winter, summer, and migratory ranges (Fig. 1C; Table S1). Migratory elk herds experienced the highest number of private owners either in winter ranges (54.2 % of herds; *n* = 13), or migratory ranges (45.8 % of herds; *n* = 11), with no herds experiencing the highest number of private owners in summer ranges. The number of private owners within elk herd ranges ranged from 21 to 5657 private owners in winter ranges (mean = 616), 10 to 6626 private owners in migratory ranges (mean = 662), and 3 to 2612 private owners (mean = 269) in summer ranges.

Across all migratory herds, winter ranges in the majority of herds (87.5 % of herds; *n* = 21) had the lowest proportion of permanently protected areas, followed by migratory ranges (12.5 % of herds; *n* = 3). The average percentage of permanently protected areas within elk herd ranges ranged from 12.4 % to 95.2 % of winter ranges (mean = 62.1 % protected), 19.0 % to 96.6 % of migratory ranges (mean = 73.0 % protected), and 27.5 % to 100 % of summer ranges (mean = 81.8 % protected). The majority of permanently protected areas within elk ranges were public conservation areas, rather than conservation

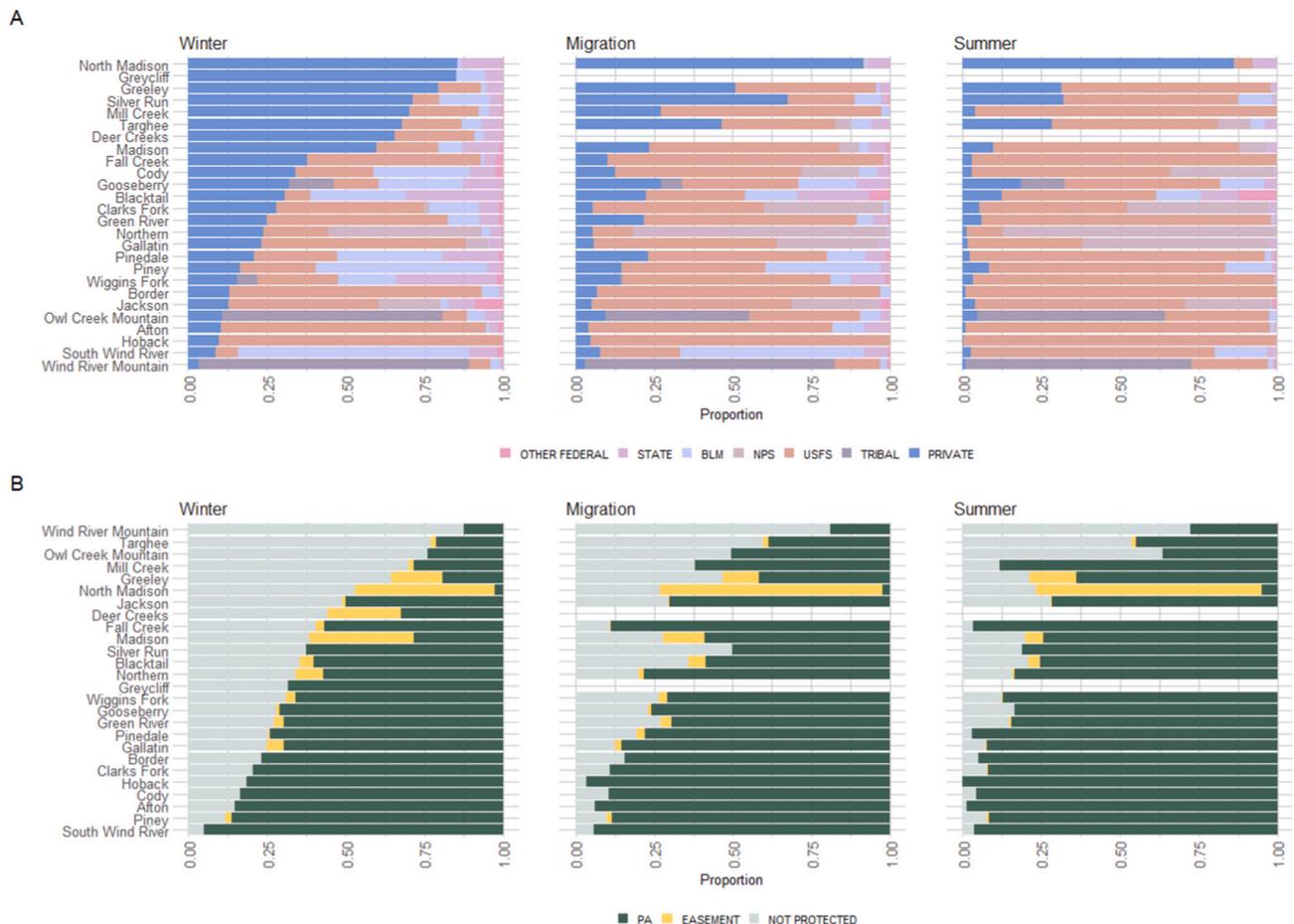


Fig. 2. Proportion of elk herd seasonal ranges in relation to A) land ownership (BLM = Bureau of Land Management, NPS = National Park Service, USFS = US Forest Service), and B) land protection (public protected areas (PA) vs. easements vs. not protected), Greater Yellowstone Ecosystem, 2000–2020.

easements (Fig. 2B). The percentage of ranges protected by conservation easements ranged from 0 % to 44.3 % of winter ranges (mean = 7.3 % in conservation easements), 0 % to 70.6 % of migratory ranges (mean = 5.9 % in conservation easements), and 0.08 % to 71.9 % of summer ranges (mean = 6.7 % in conservation easements). Collectively, only 1.6 % of all elk ranges are protected by conservation easements. When considering both public conservation areas and easements combined, the level of formal protectedness varied seasonally and among herds (Fig. 2B). Areas with the highest level of permanent protection (1 = managed for biodiversity and natural disturbances are permitted) comprised an average of 6.8 % of elk winter ranges, 19.4 % of migratory ranges, and 35.6 % of summer ranges.

3.2. Current and future building densities

Similar to private owner numbers, the elk herds that we included in our analyses experienced differing numbers of current building densities and potential future building densities within their seasonal ranges (Table S2). Migratory elk herds experienced the highest mean building densities either in winter ranges (58.3 % of herds; $n = 14$), or migratory ranges (33.3 % of herds; $n = 8$), with only 8.3 % of herds ($n = 2$) experiencing the highest mean building densities within summer ranges. Average building densities ranged from 0.03 to 7.75 buildings/km² in winter ranges (mean = 1.24 buildings/km²), 0.05 to 2.05 buildings/km² in migratory ranges (mean = 0.69 buildings/km²), and 0 to 1.31 buildings/km² in summer ranges (mean = 0.30 buildings/km²). Overall, there were 27,841 buildings within all elk ranges, with 19,457 buildings in migratory ranges alone.

Future potential building development based on zoning regulations also varied among herds and seasons (Fig. 1F). Out of all herd seasonal ranges, 36.5 % of ranges did not have any type of zoning regulations in place, and ranges with zoning ranged from 0.37 % zoned (Hoback herd summer range) to 66.8 % zoned (Targhee herd winter range). For the ranges that included zoned areas, the maximum allowable building density ranged from 0.03 to 40 (Gallatin herd in all seasons) buildings/km², with winter, summer and migratory range averages of 3.9, 3.2, and 4.1 buildings/km² respectively.

3.3. Human infrastructure

Based on our validation, 65.5 % ± 25.5 % estimated fences represent actual fences on the landscape. The adjusted fence density showed that elk herds experienced differences in the densities of fences (Fig. 1E) and roads within their ranges (Table S3). Elk ranges collectively contained an estimated 25,562 km of fences, and 1442 km of interstate roads, with 1217 km of interstate roads just within migratory ranges.

All herds had higher mean fence densities within winter ranges (mean = 1.02 km fence/km², range = 0.16 to 2.95 km fence/km²), compared to migratory ranges (mean = 0.60 km fence/km², range = 0.15 to 1.74 km fence/km²) and summer ranges (mean = 0.33 km fence/km², range = 0.05 to 1.24 km fence/km²). Road densities within ranges also varied seasonally and by herd. Out of the 24 migratory herds, 91.7 % of herds ($n = 22$) experienced the highest densities of all road types combined within their winter ranges, and 8.3 % of herds ($n = 2$) experienced higher densities of all road types combined within their migratory ranges. Mean road densities of all roads combined ranged from 0.44 to 1.59 km road/km² in winter ranges, 0.25 to 1.25 km road/km² in migratory ranges, and 0.13 to 1.10 km road/km² in summer ranges. Interstate road densities exhibited more seasonal variation than all roads, with 54.2 % of migratory herds ($n = 13$) exhibiting the highest interstate densities within winter ranges, 20.8 % of migratory herds ($n = 5$) exhibiting the highest interstate densities within summer ranges, and 4.2 % of migratory herds ($n = 1$) having no interstates within any of their seasonal ranges.

Energy infrastructure density varied for the elk herds that we included in our analyses (Fig. 1B). Out of the 24 migratory herds, 83.3 %

of herds ($n = 20$) experienced the highest mean energy infrastructure densities within their winter ranges, 8.3 % of herds ($n = 2$) experienced the highest mean energy infrastructure densities within their migratory ranges, and 8.3 % of herds ($n = 2$) experienced the highest mean energy infrastructure densities within their summer ranges. Mean infrastructure densities ranged from 0.00002 infrastructures/km² (Northern herd summer range) to 0.63 infrastructures/km² (Piney herd winter range).

3.4. Agriculture and livestock grazing

Elk herds within the GYE experienced different levels of agriculture and livestock grazing within their seasonal ranges (Table S4). Overall, agriculture did not comprise a large proportion of elk seasonal ranges, with 90.5 % of ranges comprised of <10 % agricultural land. However, several herds experienced higher agriculture in their ranges, in particular the Targhee herd (36.4 % agriculture in winter range, 21.4 % agriculture in migratory range, and 14.6 % agriculture in summer range). Compared to agriculture, livestock grazing within elk ranges exhibited more seasonal and among-herd variation (Fig. 1D). Migratory herds varied in which range contained the highest cattle grazing, with 45.8 % of herds ($n = 11$) with winter ranges containing the highest cattle grazing, 33.3 % of herds ($n = 8$) with migratory ranges containing the highest cattle grazing, and 20.8 % of herds ($n = 5$) with summer ranges containing the highest cattle grazing. Across all herds, mean cattle density ranged from 0 to 5.9 cows/km² in winter ranges (mean = 1.9 cows/km²), 0.03 to 6.0 cows/km² in migratory ranges (mean = 1.9 cows/km²), and 0 to 5.9 cows/km² in summer ranges (mean = 1.6 cows/km²).

4. Discussion

Our results show that elk in the GYE rely heavily on private lands beyond protected areas. Additionally, we found that elk face a variety of potential landscape-scale conservation challenges such as habitat fragmentation from human development and infrastructure. Given that elk play an important role ecologically, economically, and culturally in this ecosystem, our results highlight the importance of private lands, in addition to formally protected areas, in conserving migratory ungulates and the habitats that they rely on, a scenario which recurs around the globe in African savanna (Thirgood et al., 2004), Arctic tundra (Taillon et al., 2012), Patagonian and central Asian steppe (Olson et al., 2010; Iranzo et al., 2018), and other ecosystems where large migratory herbivores range well beyond protected area boundaries.

4.1. Landownership and protection

Although protected areas form the core of the GYE, all elk herds used land comprising more than one ownership type, with some elk herds spending the majority of the year on private lands. Simply using private lands is not necessarily detrimental to elk, and in fact, elk herds can thrive on private lands because of forage availability and security from hunting on public lands (Proffitt et al., 2013; Barker et al., 2019). However, compared with formally protected areas, private lands are more vulnerable to future habitat modifications, and even when elk thrive on private lands, their large body size, large herd sizes, and susceptibility to disease can lead to conflicts that greatly complicate conservation efforts. Additionally, most elk herds used the highest proportion of private land in their winter ranges, during which time elk are under higher physiological stress (Cook et al., 2013). Therefore, private land conservation and efforts to mitigate human-wildlife conflicts will be essential for the continued persistence of migratory elk populations within this system, since protected areas alone cannot conserve these populations.

One opportunity for formalizing private land conservation is the use of conservation easements, in which landowners agree to limits on future development of their property in exchange for a tax advantage or

payment. As a voluntary, incentive-based approach to conservation, easements are a more effective approach for private lands conservation in some areas than regulatory based approaches (Langpap, 2006). Although conservation easements have been used widely in the US (Fishburn et al., 2009), we found that their use has been limited to only a small proportion of the elk ranges within the GYE. We suggest that conservation organizations seeking to conserve wildlife in the GYE could seek to understand limitations on the use of easements to date, and seek to ameliorate outreach, organizational capacity, and financing bottlenecks (Bennett et al., 2018). Beyond easements, other private land incentives such as habitat improvement incentives or habitat leases could provide additional opportunities to expand conservation efforts on private land.

The utility of both public and private lands in conserving migratory populations has been highlighted in diverse systems ranging from the Northern Great Plains (Tack et al., 2019), to the savannas of East Africa (Morrison and Bolger, 2014); however, coordinating landscape-scale conservation efforts to extend wildlife habitat protections across both public and private lands can be challenging (Scarlett and McKinney, 2016). In areas with significant private ownership, community-based collective goal setting and public commitment-making can be beneficial in helping to facilitate conservation actions across multiple private properties (Niemic et al., 2019). However, high numbers of landowners could complicate coordination efforts, as different landowners might have widely differing understanding, values and opinions related to wildlife conservation (Haggerty et al., 2018; Leonard and Parker, 2021). Indeed, some elk herds had seasonal ranges in areas with extremely high numbers of individual owners (max = 6626 private landowners). The variation we observed suggests that regional agencies or NGOs will need to carefully consider tailoring different landowner engagement approaches even within the same elk herd's range.

4.2. Human infrastructure and land use change

Potential threats related to human infrastructure and development varied spatially in the GYE, but the majority of human infrastructure was associated with elk winter ranges. Not only can human infrastructure fragment habitats and reduce migratory connectivity (Hobbs et al., 2008; Theobald et al., 2011), but the change from natural landscapes to built environments can alter the migratory behaviors (Wyckoff et al., 2018), feeding behavior (Ciuti et al., 2012), and survival (Webb et al., 2011) of elk. Relatedly, conversion of land to cultivated agriculture can lead to changes in elk space use (Hinton et al., 2020) and reduce their propensity to migrate (Barker et al., 2019). Although elk can be adept at navigating landscapes with roads, fences, and buildings, efforts to reduce barriers to movement such as wildlife-friendly fencing or road overpasses and underpasses could benefit all migratory ungulates in this system.

One potential method of attempting to limit future detrimental effects of expanding human infrastructure and agriculture is the use of zoning regulations. Although the majority of elk seasonal ranges included some level of zoning regulations, the majority of ranges had very small proportions of their total area currently zoned. Both the human population density, as well as the associated housing density within the GYE are projected to steadily increase in the next few decades (Hansen and Phillips, 2018). Therefore, a lack of zoning regulations in core elk ranges could lead to increased levels of human infrastructure which could prove to be detrimental to the persistence of some migratory elk in the GYE, given that migratory ungulates have been found to avoid areas with high human infrastructure during migration (Wyckoff et al., 2018; Sawyer et al., 2020). Zoning policies that encourage new building near established development, rather than in areas with no or low development could help control urban and suburban sprawl within the GYE (Gude et al., 2007). Additionally, conservation developments - development areas that incorporate protected open space - could be a useful tool for land use planning (Mockrin et al., 2017). However, it is

important to note that zoning regulations may not be effective for wildlife conservation if allowable building densities exceed disturbance thresholds, or if regulations are not effectively enforced. Additionally, county zoning proposals are often opposed by local private landowners. Therefore, other incentive programs to reduce human infrastructure and development and maintain habitat connectivity for wildlife could also be beneficial.

Although our research indicates variation in the amounts of human infrastructure within elk ranges in the GYE, little information exists on the levels of infrastructure that elk and other migratory ungulates can tolerate before experiencing negative consequences. For example, a study of mule deer in western Wyoming found that mule deer rarely used areas comprised of >3 % energy development (Sawyer et al., 2020). More research is needed to better understand if elk exhibit similar habitat use thresholds in relation to energy development, and if similar thresholds exist for other forms of disturbance such as buildings, roads, and fences. Additionally, we took a coarse-scale approach to investigating elk space use; therefore, finer-scale studies would be useful in determining how land use change or human infrastructure might be affecting elk movement paths or high use areas.

Conserving migratory elk herds within a public-private matrix can bring challenges and costs. Migratory elk herds can be large and elk are gregarious (Proffitt et al., 2012) and can consume native forage that would otherwise be available to livestock (Hobbs et al., 1996). Elk are also a reservoir for the disease brucellosis which can be transmitted between elk and cattle (Cross et al., 2010). Additionally, elk can cause property damage such as knocking down fences (Walter et al., 2010), and consuming crops such as irrigated hay and alfalfa (Hegel et al., 2009), and can be a public safety concern because of the potential for vehicle collisions. Although habitat protection is a crucial component of elk conservation in the GYE, complementary tools to mitigate human-wildlife conflict such as reducing or reimbursing costs associated with damage, and providing technical support for landowners is needed. In addition, building social tolerance towards elk could prove useful in managing elk on private lands (Pooley et al., 2021). University and state extension programs, or other ways of engaging private landowners in wildlife conservation could be beneficial in helping enhance human-wildlife coexistence in this area (Messmer, 2009).

4.3. Implications for conservation

Collectively, our results highlight a high degree of spatial variation among potential conservation challenges for migratory elk herds within the GYE. Although other research has addressed the importance of considering both public and private land in conserving migratory or wide-ranging populations (Tack et al., 2019), we show that spatial variation in conservation challenges can exist within lands of the same jurisdiction. For example, energy development, cattle grazing, and fences vary spatially within elk ranges in the GYE (Fig. 1). Because of this variation, the conservation of elk migrations within this ecosystem cannot take a "one-size-fits-all" approach and instead should be based on localized knowledge, and degree of social tolerance. Although our research indicates the importance of integrated public and private conservation strategies for a migratory ungulate, similar approaches are likely applicable to non-migratory species worldwide as well.

In the future, successful conservation of migratory ungulate populations within the GYE will require greater coordination across federal, state, county, and local levels. Ultimately, states have the authority to manage wildlife populations, but habitat conservation both on federal and private lands make multi-level coordination imperative. At the national level, the Department of the Interior's Secretarial Order 3362 aims to conserve migratory ungulate habitats and can provide funding for research and habitat conservation, but a simple comparison of the program's past funding levels (~\$10 m over two years) with rough estimates of the potential costs of corridor conservation in the GYE alone (hundreds of millions over many years) suggests enormous unmet needs

(United States Department of the Interior, 2020). Federal efforts could be amplified, and coordination enhanced, through engagement with the USDA, which administers Farm Bill funding for conservation easements, habitat leasing (e.g., Conservation Reserve Program), habitat stewardship, and farm and ranch infrastructure such as fences (United States Department of Agriculture, 2022). For example, a focus by USDA - Natural Resources Conservation Service (NRCS) on the private lands that support year-round sage grouse habitat resulted in 4.4 million acres of conservation over a decade long effort (USDA-NRCS, 2015). Several recent USDA commitments related to private working lands could prove to be beneficial in conserving wide-ranging wildlife populations (USDA, 2022). At the state-level, initiatives such as Wyoming's Migration Corridor Conservation Strategy (State of Wyoming, 2020), and programs related to crop depredation mitigation, brucellosis transmission risk, and hunter access can help target management to key ungulate ranges and help coordinate across state agencies and non-state entities. County-level coordination or regulation represents an important avenue for conserving lands for migratory populations within the GYE since many of the conservation challenges that we address in this paper such as building densities and agricultural land are directly related to local decisions such as zoning regulations or based on decisions of individual property owners.

Although the GYE is often viewed as a conservation success story because of the sheer size of area protected, private lands have been critical to this success as well. However, future development and land use change threaten to upend the role of private lands in sustaining wide-ranging wildlife in the system. As the GYE continues to experience increasing human population and human development, and land use change (Hansen and Phillips, 2018), the need to sustain migratory connectivity is critical. The challenges and opportunities associated with conserving populations across such a large scale can also be applied to other migratory species in the GYE. As wildlife populations globally also face conservation threats and the protection of both public and private lands continues to be a priority, the GYE is a high-profile example of how conservation across landownership is necessary to maintain populations of migratory species. Because protected areas offer incomplete protection for many migratory and wide-ranging species around the world (Thirgood et al., 2004; Middleton et al., 2020; Kauffman et al., 2021a), a global focus on managing these species across matrices of landownership types is critical.

Article impact statement

Protected areas alone are not enough to conserve wide-ranging migratory ungulates; therefore, private lands conservation is essential.

CRedit authorship contribution statement

Laura C. Gigliotti: Conceptualization, Methodology, Formal analysis, Writing – original draft, Supervision. **Wenjing Xu:** Conceptualization, Methodology, Formal analysis, Visualization, Writing – review & editing. **Gabriel R. Zuckerman:** Conceptualization, Methodology, Formal analysis, Visualization, Writing – review & editing. **M. Paul Atwood:** Data curation, Writing – review & editing. **Eric K. Cole:** Data curation, Writing – review & editing. **Alyson Courtemanch:** Data curation, Writing – review & editing. **Sarah Dewey:** Data curation, Writing – review & editing. **Justin A. Gude:** Data curation, Writing – review & editing. **Patrick Hnilicka:** Data curation, Writing – review & editing. **Mark Hurley:** Data curation, Writing – review & editing. **Matthew Kauffman:** Data curation, Writing – review & editing. **Kailin Kroetz:** Writing – review & editing. **Arthur Lawson:** Data curation, Writing – review & editing. **Bryan Leonard:** Writing – review & editing. **Daniel MacNulty:** Data curation, Writing – review & editing. **Eric Maichak:** Data curation, Writing – review & editing. **Douglas McWhirter:** Data curation, Writing – review & editing. **Tony W. Mong:** Data curation, Writing – review & editing. **Kelly Proffitt:** Data curation,

Writing – review & editing. **Brandon Scurlock:** Data curation, Writing – review & editing. **Daniel Stahler:** Data curation, Writing – review & editing. **Arthur D. Middleton:** Conceptualization, Data curation, Writing – review & editing, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The field effort to collect the 26 elk movement datasets used in this analysis came from the Eastern Shoshone and Northern Arapaho tribes, Idaho Department of Fish and Game, Montana Fish, Wildlife, & Parks, National Park Service, USDA-APHIS, US Forest Service, USGS, and Wyoming Game and Fish Department, as well as many field technicians, volunteers, and private landowners. Additional funding for collars and captures was provided by Knobloch Family Foundation, Rocky Mountain Elk Foundation, George B. Storer Foundation, National Geographic Society, Grand Teton Association, and a variety of individual donors. I. Aguilar, K. Dang, and K. Hu assisted with GIS data processing. K. Kroetz, B. Leonard, A. Middleton, and L. Gigliotti received support for this work through Natural Resource Economics (ENRE) Program through grant AWD00035948 from the USDA National Institute of Food and Agriculture. L. Gigliotti and A. Middleton received support for this work from Rocky Mountain Elk Foundation award #WY200444. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109752>.

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