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Declining pronghorn (*Antilocapra americana*) population productivity caused by woody encroachment and oil and gas development

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ABSTRACT

Conservation is increasingly focused on preventing losses in species' populations before they occur. Tracking changes in demographic parameters that can impact a population's resilience in response to drivers of global change can support early conservation efforts. We assessed trends in population productivity (late summer juveniles per 100 females) relative to drivers of global change in 40 pronghorn (Antilocapra americana) herds across sagebrush (Artemisia spp.) steppe in Wyoming. Pronghorn are an iconic rangeland species that have been exposed to increasing levels of anthropogenic, climatic, and land-use change. Using data collected across the state of Wyoming, we (1) assessed long-term trends in population productivity, (2) identified patterns in large-scale drivers of global change (i.e., climate, land cover change) across pronghorn habitat, and (3) determined the relationship between drivers of global change and population productivity over a 35-year (1984-2019) period. While Wyoming hosts some of the most abundant populations of pronghorn in North America that have been largely stable in recent years, we found many herds are experiencing long-term declines in productivity. Long-term declines in productivity were associated with increases in oil and gas development and woody encroachment. Although increasing across almost all herd units, woody vegetation cover remains at low levels, suggesting that pre-emptive management may help to prevent losses in pronghorn populations.

1. Introduction

Global species diversity continues to decline in response to factors such as anthropogenic development and resource use, changing

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climate, and biological invasions (Butchart et al., 2010; Pimm et al., 2014; Pimm and Raven, 2000). Conservation efforts often focus on species that are most endangered or at risk, leading to a conservation triage approach to balance limited resources (Bottrill et al., 2008; Gerber, 2016; McCarthy et al., 2008; Scott et al., 2010). However, it is often more economical and effective to focus on long-term preventative conservation rather than short-term 'crisis management' to optimize conservation and keep common species common (Joseph et al., 2009; Schneider et al., 2010; Wilson et al., 2011). Thus, there is a need to understand species' responses to external changes before drastic declines in populations occur (Capdevila et al., 2021, 2020).

Changes in demographic structure within a population are increasingly being recognised as an indicator of stress on populations in response to global change (Capdevila et al., 2021, 2020). Environment-driven demographic rates such as reproduction and survival are highly sensitive to environmental deterioration that can drive changes in populations (Drake and Griffen, 2010). For instance, Gasaway et al., (1983) found that high juvenile mortality in moose (*Alces alces*) driven by wolf (*Canis lupus*) predation in Alaska helped to sustain population declines initiated by hunting and severe winter, leading to heightened risk for species extirpation. Tracking trends in components of population demographics can be used to signal potential changes in population resilience to disturbances within their range (Clements and Ozgul, 2018).

Productivity, the number of surviving offspring produced during a given year, is highly responsive to environmental changes (Britten et al., 2016; Gaillard et al., 1998). It can be one of the first population parameters to indicate resource limitation (Bishop et al., 2005; Eberhardt, 1977) and is sensitive to changes in predator abundance (Brown and Conover, 2011). Declines in population productivity have been associated with lowered population resilience in a number of species (Fujiwara et al., 2014; Graham et al., 2007; Kruszynski et al., 2021) and can lead to declines in population numbers, particularly when paired with disturbances that drive adult mortality (Bender et al., 2013; Bonnot et al., 2017; Hatter and Janz, 1994). Because annual productivity tends to be easily quantified compared to other demographic rates like survival, they can be used as a broad indicator of the impacts of changing environment on populations (Gaillard et al., 1998).

We assessed long-term trends in productivity for pronghorn (*Antilocapra americana*) relative to drivers of global change across the state of Wyoming. Pronghorn are an iconic species of western North American rangelands. The Wyoming Basin shrub steppe, one of the most intact rangeland ecoregions on the planet (Scholtz and Twidwell, 2022), provides habitat to approximately half of the worldwide pronghorn population (Yoakum and O'Gara, 2000). However, environmental stressors are increasing across the region. Oil and gas development and associated roads and fencing have expanded rapidly in recent decades leading to loss and fragmentation of sagebrush habitat (Finn and Knick, 2011; Walston et al., 2009). Neighbouring regions are experiencing rapid encroachment of woody species that lead to the conversion of rangeland to woodland (Fogarty et al., 2020; Roberts et al., 2021; Twidwell et al., 2013) and invasion by non-native annuals that can increase fire frequency and damage some sagebrush ecosystems (Balch et al., 2013; Knapp, 1996). It is not clear how rapid large-scale changes to pronghorn habitat (Allred et al., 2015; Christie et al., 2015; D'Antonio and Vitousek, 1992; Fogarty et al., 2020) are impacting population demographic trends across Wyoming.

We tracked long-term trends in productivity (juveniles per 100 females collected during late summer) in 40 pronghorn herds in relation to vegetation change, climate, and anthropogenic development across their range. Low productivity in pronghorn can lead to population decline, particularly when paired with disturbances that impact other vital rates like adult survival (Bender et al., 2013). Pronghorn productivity is also highly sensitive to environmental change, with reproductive success tracking dietary income (Barnowe-Meyer et al., 2011; Bender et al., 2013; Parker et al., 2009) and shifts in predation pressure (Brown and Conover, 2011). We use almost 40 years of pronghorn herd productivity data within and surrounding the Wyoming Basin Shrub Steppe ecoregion in relation to oil and gas well development, roads, fire, annual forb and grass invasion, woody encroachment, and changing precipitation patterns to evaluate (1) if and where there were long-term signals of declining pronghorn productivity, (2) where there were signals of long-term change in pronghorn habitat associated with large-scale drivers of global change (climate, anthropogenic development, vegetation change), and (3) what drivers of global change were associated with changes in pronghorn productivity. We predicted that large-scale global change drivers have increasingly degraded pronghorn habitat during our study period, resulting in long-term declines in pronghorn productivity.

2. Materials and methods

2.1. Study region

The state of Wyoming is an arid region surrounded by mountains in the west, south, and north and prairies to the north and east. Elevations range from 940 to 4200 m. Annual average precipitation ranges from 160 mm to 762 mm (Frankson et al., 2017). The state is dominated by the Wyoming Basin Steppe ecoregion (Dinerstein et al., 2017). Big sagebrush (*Artemisia tridentata* ssp.) dominates the Wyoming Basin Steppe rangelands while mixed grass prairie interspersed with sagebrush patches characterizes rangelands of northeastern Wyoming. Large-scale energy and mineral development along with associated road networks, invasion of exotic annual grasses, increasing wildfire frequency and extent, conifer encroachment, and the conversion of sagebrush to grassland for grazing are substantial threats to habitat across much of the region (Bradley, 2010; Finn and Knick, 2011). Pronghorn herds are distributed across the majority of Wyoming, and represent >50% of the range-wide population (Yoakum and O'Gara, 2000). Wyoming 's pronghorn population numbers have been largely stable in recent years, while harvest rates have declined (Jason Carlisle, Wyoming Game and Fish Department, Personal Communication).

2.2. Data collection and summary

We quantified pronghorn productivity by calculating annual ratios of juveniles to 100 females using data collected by the Wyoming Game and Fish Department between 1984 and 2019. Data were collected across 40 herd units that spanned pronghorn range in Wyoming using aerial and ground surveys following established routes within each herd unit (Emmerich et al., 2007; Grant Frost, Wyoming Game and Fish Department, Personal Communication). Surveys were conducted in the late summer (typically August 1–31st) before hunting season. Females typically give birth during late May and early June, meaning juveniles are ~2–3 months old at the time of surveys. Herd units were delineated by Wyoming Game and Fish Department based on geographic or man-made barriers that restrict interchange among populations (Emmerich et al., 2007). In some cases, herds that were originally monitored separately were aggregated to form one larger herd by the Wyoming Game and Fish Department. In these instances, we took the average number of juveniles per 100 females across both herd units before the time they were merged to obtain the longest possible data sets for each unit.

We assessed large-scale changes in vegetation across each herd unit using annual, Landsat-derived, 30-m resolution percent cover (1984–2019) and herbaceous biomass estimates (1986–2019) for multiple vegetation functional groups using the Rangeland Analysis Platform (Jones et al., 2018). Within each herd unit we summarized tree cover, shrub cover, the cover and biomass of perennial and annual forbs and grasses, and total herbaceous biomass inclusive of all herbaceous functional groups.

We assessed the impacts of climate on pronghorn productivity using changes in winter and spring precipitation. We evaluated changes in annual winter and spring total precipitation per herd unit using PRISM 4-km resolution monthly precipitation data from 1984 to 2019 (https://prism.oregonstate.edu/). We defined winter from November-March (Reinking et al., 2019; Smith et al., 2020; Taylor et al., 2016) and spring from April to June (Canon and Bryant, 1997; Collins, 2016) based on past assessments of pronghorn in Wyoming.

We quantified anthropogenic disturbance patterns by calculating the length of roads in Wyoming and the cumulative number of oil and gas wells through time. We collected road data mapped across Wyoming in 2009 from the U.S. Geological Survey (O'Donnell et al., 2014). We calculated the total road length within each herd unit, and then standardised the measure by dividing it by total herd unit area. While there was no temporal component to road data within Wyoming, we included this variable to indicate the general level of fragmentation that occurred among herd units. We obtained oil and gas well data from 1980–2019 from the Wyoming Oil and Gas Conservation Commission (Data) for each herd unit. We used spud date, the date when drilling activity began, to determine the year a new well was added to each herd unit. If spud date was not available, we used the date of the first completion report filing. We calculated the cumulative number of oil and gas wells added each year from 1980 onward to determine the increase in oil well development within each herd unit.

Wildfires are increasing across the western and central U.S. (Dennison et al., 2014; Donovan et al., 2017) linked to changing climate (Dennison et al., 2014; Westerling et al., 2006), shifting vegetation cover (Balch et al., 2013; Donovan et al., 2020c; Pilliod et al., 2017), and anthropogenic ignitions (Balch et al., 2017). Thus, we also assessed the impacts of fire on pronghorn by calculating the annual total area burned within each herd unit using burn perimeters from 1984–2019 from the Monitoring Trends in Burn Severity Database (MTBS Project, 2022).

Table 1

Environmental variables assessed across W	Vyoming and the	eir predicted im	pacts on pronghorn.
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Environmental Variable	Predicted Impact on Pronghorn	Rationale
Perennial forbs and grasses	Positive	Pronghorn select for perennial forbs and grasses found in native rangelands (Jakes et al., 2020; Milligan et al., 2021)
Shrubs	Positive	Pronghorn select for shrubs associated with sagebrush habitat (Christie et al., 2017; Smith et al., 2020).
Trees	Negative	Trees in rangeland systems are associated with woody encroachment and afforestation that can drive losses
		in forage and rangeland habitat, eventually leading to a regime shift to an alternative woodland state (Coates et al., 2017; Twidwell et al., 2013). In addition, trees decrease visibility, potentially increasing predation risk (Goldsmith, 1990).
Annual forbs and grasses	Negative	Recent increases in annual forbs and grasses are generally associated with the large-scale invasion of non- native species such as cheatgrass (<i>Bromus tectorum</i>), which are degrading sagebrush habitat across much of western North America (Balch et al., 2013; Mahood and Balch, 2019).
Winter precipitation	Negative	Winter precipitation is associated with snow cover and depth, which can decrease pronghorn mobility and increase foraging energy expenditure leading to higher mortality (Barrett, 1982; Reinking et al., 2019; Smith et al., 2020; Taylor et al., 2016).
Spring precipitation	Positive	Increased spring precipitation results in higher quality and quantity of forage and higher pronghorn densities (Brown et al., 2006; Gedir et al., 2015)
Roads	Negative	Roads fragment habitat and facilitate movement of predators and hunters (Gamo et al., 2017; Hebblewhite et al., 2009; Popp and Donovan, 2016; Seidler et al., 2015).
Oil and gas development	Negative	Oil and gas development is associated with habitat loss both directly and through fragmentation which can lead to habitat abandonment and lower pronghorn abundance (Christie et al., 2015; Sawyer et al., 2019)
Fire	Mixed	Fires can degrade sagebrush habitat (Balch et al., 2013; Mahood and Balch, 2019); however, they also reduce tree cover to restore rangeland habitat impacted by woody encroachment (Bielski et al., 2021; Donovan et al., 2020b). Pronghorn have been shown to utilize recently burned areas (Augustine and Derner, 2015; Courtney, 1980)

2.3. Analysis

We assessed long-term trends in pronghorn productivity through time within each herd unit using Mann Kendall monotonic trend tests (McLeod, 2011). Mann Kendall trend tests are non-parametric tests often used to detect significant upward or downward trends in long-term time series data. Numerous abiotic and biotic factors can influence population demographics and these factors vary from one population to the next, making it unlikely that there is a single unifying threshold in population productivity that can be used to indicate when populations will experience declines in size. Instead, we used Mann Kendall's test statistic Tau, which focuses on capturing patterning in data rather than specific threshold values (McLeod, 2011). Unlike slope, which is a measure of the magnitude of decline or increase through time, Tau represents the degree to which a trend is monotonic, i.e., the degree with which it consistently increases or decreases. Tau ranges from -1 to 1, where a greater positive Tau indicates a stronger positive monotonic trend (a value of 1 indicates a perfect positive monotonic trend), and a greater negative Tau indicates a stronger negative monotonic trend (a value of -1 indicates a perfect negative monotonic trend). We used Auto Correlation Function (ACF) plots to identify serial autocorrelation within time series data. When autocorrelation was indicated, we used a block bootstrapping procedure and modified Mann Kendall tests (modified to adjust of serial correlation) to improve significance tests (McLeod, 2011; Patakamuri and O'Brien, 2021). We similarly used Mann Kendall trend tests to assess long-term trends in vegetation (perennial forb and grass cover and biomass, annual forb and grass cover and biomass, tree cover, shrub cover), climate (spring precipitation, winter precipitation), and anthropogenic disturbances (oil and gas wells) through time.

We modelled the responses of pronghorn productivity to the environment using two modelling approaches. First, we used linear mixed effects models to determine the relationship between annual pronghorn productivity and annual variability in environmental variables (Table 1; excluding roads), using herd unit as a random intercept (Pinheiro et al., 2021). Following the top-down strategy recommended in Zuur et al., (2009), we used Akaike's Information Criterion adjusted for small sample sizes (AICc; Akaike, 1973) to select among random intercept versus random intercept and slope models that contained our global model structure within the fixed component. A random intercept model was preferred over a random intercept and slope model. Second, we used linear models to determine relationships between long-term trends in productivity in response to patterns in environmental variables over our study period. The Tau of productivity, calculated from Mann Kendall monotonic trend tests, was used to represent long-term trends in productivity for each herd unit (n=40). There were multiple instances where we had similar measures (e.g., perennial forb and grass cover versus biomass) or, in the case of our long-term models, multiple long-term summary statistics for the same variable (Tau of tree cover versus average tree cover of each herd unit). In such cases, we used AICc to determine which measure or summary statistic was better at predicting our dependent variable (Appendix 1: Section S2). Preferred forms of each variable as indicated by AICc were

Table 2

Candidate models used to predict (1) the change in annual pronghorn juveniles per 100 females and (2) long-term trends in
pronghorn juveniles per 100 females represented by Tau, calculated using Mann Kendall monotonic trend tests.

Model	Dependent Variables
Annual candidate models	
1	~1
2	~Year
3	~Year + Shrub cover
4	~Year + Perennial forb and grass cover
5	~Year + Herbaceous biomass + Spring precipitation
6	~Year + Herbaceous biomass + Area burned + Spring precipitation
7	~Year + Shrub cover + Annual forb and grass cover + Area burned
8	~Year + Tree cover
9	~Year + Oil and gas wells
10	~Year + Winter precipitation
11	~Year + Tree cover + Oil and gas wells
12	~Year + Tree cover + Oil and gas wells + Winter precipitation
13	~Year + Annual forb and grass cover + Tree cover + Oil and gas wells
14	~Year + Shrub cover + Tree cover + Oil and gas wells
15	~Year + Herbaceous biomass + Tree cover + Oil and gas wells
Long-term trend candidate models	
1	~1
2	Tau of shrub cover
3	Tau of perennial forb and grass biomass
4	Tau of herbaceous biomass + Average spring precipitation
5	Tau of herbaceous biomass + Tau of burned area + Average spring precipitation
6	Tau of shrub cover + Tau of annual forb and grass biomass + Tau of burned area
7	Tau of tree cover
8	Total oil and gas wells
9	Tau of winter precipitation
10	Tau of tree cover + Total oil and gas wells
11	Tau of tree cover + Total oil and gas wells + Road Density + Tau of winter precipitation
12	Tau of annual forb and grass biomass + Tau of tree cover + Total oil and gas wells + Road Density
13	Tau of shrub cover + Tau of tree cover + Total oil and gas wells
14	Tau of herbaceous biomass + Tau of tree cover + Total oil and gas wells

included within our models (Table 2). Because biomass data started in 1986, modeled data spanned 1986–2019.

Using a multi-model inference approach, we generated candidate model sets composed of variables that we predicted would positively impact pronghorn productivity (e.g., shrubs, spring precipitation), variables we predicted would negatively impact pronghorn productivity (e.g., trees, oil and gas well development), and a combination of the two (Tables 1, 2). Year was also included in models as a discrete numeric variable. We screened independent variables for collinearity by using pairwise correlations. When variables had a Pearson's correlation coefficient >0.65, we did not include them within the same candidate model. We used global models to test for violation of model assumptions before candidate model sets were input into AICc to determine the most parsimonious model (Burnham and Anderson, 2002). Burnham and Anderson, (2002) suggest that models with a Δ AICc < 2 have substantial support. When multiple models fell within this range, we classified them as our confidence set, and applied model averaging using the zero average method to determine model averaged coefficients that could be used to predict the relationships between pronghorn productivity and patterns in environmental change (Barton, 2020; Burnham and Anderson, 2002; Grueber et al., 2011). We completed all analyses using R software v. 4.0.4 (R Core Team, 2021).

3. Results

3.1. Patterns in pronghorn productivity

Pronghorn productivity declined significantly across 43% (17 of 40) of pronghorn herds in Wyoming between 1984 and 2019 (Fig. 1b; Appendix 1: Tables S1–1; Appendix 1: Figs. S3–1). Average juveniles per 100 females ranged from 40 \pm 12 SD (Badger Basin Herd Unit 207) to 83 \pm 11 SD (Crazy Woman Herd Unit 318; Fig. 1a). Declines in productivity were not limited to populations with low overall productivity numbers. Populations with some of the greatest average productivity over our study period also experienced strong declines in productivity (Fig. 1).

3.2. Patterns in global change drivers

All herd units experienced significant increases in one or more drivers of global change identified as threats to pronghorn populations during our study period. Woody encroachment, annual forb and grass invasion, and oil and gas wells all significantly increased across the majority of herd units in Wyoming (Table 3; Fig. 2; Appendix 1: Tables S1–2). Seventy percent (28 of 40) of herd units had significant positive monotonic trends in tree cover (Fig. 2; Appendix 1: Tables S1–2), though there was high variation in tree cover across herds, ranging from an average of less than 1% in Pumpkin Buttes (Herd Unit 309) to $18\% \pm 4$ SD in Elk Mountain (Herd Unit 528). Annual forb and grass cover (ranging from an average of $3\% \pm 0.7$ SD in the Red Desert [Herd Unit 615] to $15\% \pm 5$ SD cover in Leiter [Herd Unit 321]) significantly increased across 58% of herd units, while annual forb and grass biomass (ranging from an average



Fig. 1. Maps of Wyoming, USA pronghorn herd units colour coded to represent (a) the average number of juveniles per 100 females and (b) significant monotonic trends in juveniles per 100 females, from 1984–2019. Monotonic trends are represented by a Tau value (ranging from -1 to 1), calculated using Mann-Kendall monotonic trend tests. Numbers in each polygon represent herd unit number used by the Wyoming Game and Fish Department.

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Table 3

A summary of trends in productivity (juveniles per 100 females), environmental variables predicted to have positive or negative outcomes for pronghorn across 40 herd units in Wyoming, USA, as indicated by Mann Kendall monotonic trend tests.

Variable	Percent increasing	Percent decreasing	Percent significantly increasing	Percent significantly decreasing	
Productivity	20	80	0	42.5	
Variables predicted to have negative outcomes					
Annual forb and grass cover	92.5	7.5	57.5	0	
Annual forb and grass biomass	100	0	90	0	
Tree cover	90	10	70	2.5	
Winter precipitation	82.5	17.5	7.5	0	
Oil and gas wells	95	NA	95	NA	
Variables predicted to have positive outcomes					
Perennial forb and grass cover	60	40	7.5	12.5	
Perennial forb and grass biomass	90	10	27.5	0	
Shrub cover	52.5	47.5	5	2.5	
Herbaceous biomass	95	5	25	0	
Spring precipitation	100	0	10	0	

of 11 kg/ha \pm 3 SD Wind River to 206 kg/ha \pm 121 SD in Leiter) significantly increased across 90% of herd units (Fig. 2; Appendix 1: Tables S1–2). Oil and gas well numbers increased across all herd units except two, where no oil and gas wells were recorded (Big Creek [Herd Unit 529] and North Ferris [Herd Unit 636]; Fig. 2). The greatest average.

number of wells was in the Pumpkin Buttes Herd Unit (6283 ± 5186 SD wells). Annual total winter precipitation also increased to a small extent over our study period, but only in 3 herd units at the center of the state (averages ranging from 3667 mm \pm 1316 SD in Chalk Bluffs [Herd Unit 520] to 309,387 mm \pm 84,508 SD in Sublette [Herd Unit 401]; Fig. 2).

Although global change threats to pronghorn were increasing across the majority of herd units, perennial forb and grass cover (averages ranging from $19\% \pm 3$ SD in Bitter Creek [Herd Unit 414] to $61\% \pm 6$ SD in Chalk Bluffs) and shrub cover (averages ranging from $6\% \pm 2$ SD in Chalk Bluffs to $24\% \pm 2$ SD in Carter Lease [Herd Unit 419]), important components of pronghorn habitat, remained relatively stable and only declined in a few herd units (5 and 1 herd unit respectively; Fig. 2). Perennial forb and grass biomass significantly increased in 3 herd units (averages ranging from 218 kg/ha ± 46 SD in Bitter Creek to 1254 kg/ha ± 180 SD in Beckton [Herd Unit 355]) and herbaceous biomass significantly increased across 63% of herd units (averages ranging from 218 kg/ha ± 59 SD in Bitter Creek to 1311 kg/ha ± 131 SD in Beckton; Fig. 2). No herd units demonstrated declines in herbaceous biomass or perennial forb and grass biomass and only significantly increased in 4 herd units (averages ranging from 6857 mm ± 2429 SD in Bit Creek to 211,564 mm $\pm 71,047$ SD in Sublette; Fig. 2).

The annual total area burned by fire, which was predicted to have both positive (reduce trees, increase perennial forb and grass cover and biomass) and negative (reduce shrubs, increase annual forb and grass cover and biomass) impacts on pronghorn, significantly increased in 4 herd units (Appendix 1: Figure S2-13). A significant increase in burned area in the Wind River herd unit aligned with the only herd unit that demonstrated a significant decline in tree cover (Fig. 2). There were several herd units that did not experience any fire over our study period, while the Sublette herd unit had the greatest average annual burned area at 3623.42 ha \pm 6097 SD.

3.3. Drivers of global change impact on pronghorn productivity

The most parsimonious model for annual changes in productivity was the model containing shrub cover and year (Tables 2 and 4). Model coefficients indicated that approximately every 4 years, the number of juveniles per 100 females decreased by 1 over our study period (estimate = -0.28, SE = 0.04, p <0.01; Fig. 3; Appendix 1: S4–1). There was a positive relationship between productivity and shrub cover, where with every 1% increase in shrub cover within a herd unit, the number of juveniles per 100 females increased by 1 (estimate = 1.05, SE = 0.21, p <0.01; Fig. 3). Shrub cover did not change drastically across most herd units (Fig. 2), and thus, could not explain long-term trends in declining pronghorn productivity we observed.

Model selection among candidate models tracking long-term productivity trends across herds indicated that the cumulative number of oil and gas wells within herd units was the best predictor of declining productivity. However, two additional models fell within 2 AIC of the top model: one including the cumulative number of oil and gas wells and the Tau of tree cover, and the other containing the cumulative number of oil and gas wells, the Tau of tree cover, and the Tau of total herbaceous biomass (Table 4). More consistent declines in productivity through time were associated with a greater cumulative number of oil and gas wells within a herd unit (estimate = -1.83×10^{-5} , SE = 8.28×10^{-6} , p = 0.03) and greater tree cover (estimate = -0.08, SE = 0.09, p = 0.40; Fig. 4). This aligns with increases in oil and gas development and tree cover recorded across several herds in the Wyoming Basin Steppe (Fig. 2). In contrast, more consistent increases in productivity through time were associated with increased herbaceous.

biomass within herd units (estimate = 0.08, SE = 0.19, p = 0.68; Fig. 4), again aligned with increases in herbaceous biomass identified across herd units (Fig. 2).



Fig. 2. The strength of significant temporal trends in climate, vegetation, and anthropogenic change variables within pronghorn herd units in Wyoming, USA between 1984 and 2019 (1986–2019 for biomass data) as indicated by Tau (ranging from -1 to 1) from Mann Kendall monotonic trend tests. Significant trends in environmental variables that were predicted to positively impact pronghorn within each herd unit are coloured in blue, while significant trends predicted to negatively impact pronghorn within each herd unit are colour indicates a greater positive or negative Tau value. Herd units with non-significant trends are coloured grey.

4. Discussion

Pronghorn productivity is declining in the center of their distribution in response to large-scale drivers of global change. While the Wyoming Basin is viewed as a stronghold for pronghorn populations, increasing oil and gas development and tree encroachment may

Table 4

The top 5 AIC model rankings for annual models, used to assess relationships between annual pronghorn herd unit productivity (juveniles per 100 females) and annual variability in environmental variables, and for long-term trend models, used to assess the relationship between the Tau of productivity through time and patterns in environmental variables in Wyoming, USA. Annual models were linear mixed effects models with herd unit as the random effect while long-term models were linear models. Tau values used in long-term models ranged from -1 to 1 and are calculated using Mann Kendall monotonic trend tests.

Model	Df	LogL	AICc	ΔAICc	Weight
Annual models					
\sim Year + Shrub cover	5	-4867.99	9746.03	0.00	0.93
~Year + Shrub cover + Annual forb and grass cover + Area burned	8	-4868.56	9751.22	5.19	0.07
\sim Year + Shrub cover + Tree cover + Oil and gas wells	7	-4871.37	9756.84	10.80	0.00
\sim Year + Tree cover	7	-4871.37	9763.20	17.17	0.00
~Year	5	-4876.58	9766.32	20.29	0.00
Long-term trend models					
~Total oil and gas wells	3	16.40	-26.14	0	0.21
\sim Tau of tree cover + Total oil and gas wells	4	17.61	-26.07	0.07	0.20
\sim Tau of herbaceous biomass + Tau of tree cover + Total oil and gas wells	5	18.47	-25.18	0.96	0.13
\sim Tau of shrub cover $+$ Tau of annual forb and grass biomass $+$ Tau of burned area	4	16.54	-23.93	2.21	0.07
$\sim\!\!\text{Tau}$ of shrub cover $+$ Tau of tree cover $+$ Total oil and gas wells	5	17.74	-23.71	2.43	0.06



Fig. 3. Predicted relationships in annual changes in productivity (juveniles per 100 females) relative to (a) shrub cover and (b) year in Wyoming, USA. Shaded area represents 95% confidence intervals. Grey points represent raw data.

be increasing pronghorn population susceptibility to decline. Increases in pronghorn productivity are associated with higher shrub cover and long-term increases in herbaceous biomass, suggesting that declines in rangeland habitat quality associated with oil and gas development and tree encroachment (e.g., Avirmed et al., 2015; Miller et al., 2000) are helping to drive long-term losses in pronghorn productivity. This follows trends of declining pronghorn productivity found across a number of jurisdictions in past research, suggested to be in part, due to density-dependent responses related to decreased forage conditions and habitat fragmentation in pronghorn habitat (Jones and Yoakum, 2010).

We found that both tree cover and oil and gas development have increased substantially across most herd units in Wyoming over the last ~40 years. Wyoming ranked eighth nationally in crude oil production in the U.S. in 2020 and saw natural gas production increase 7-fold from 1978 to its peak in 2010 (Wyoming State Geological Survey, 2021). Expansive increases in oil and gas development are a well-known threat to rangeland ecosystems in Wyoming, driving declines in iconic rangeland species like the greater sage-grouse (*Centrocercus urophasianus*; Gregory and Beck, 2014; Hess and Beck, 2012). For pronghorn, fragmentation caused by oil and gas development has been suggested to drive declines in population productivity by increasing pronghorn numbers within smaller, more isolated patches of habitat (Jones and Yoakum, 2010). In contrast, tree encroachment is not a widely recognised threat to Wyoming sagebrush ecosystems. This may be tied to relatively low levels of tree encroachment in the state; we identified a maximum average tree cover of 18% within herd units. However, low levels of tree encroachment have been shown to have drastic impacts on sagebrush-dependent wildlife. For instance, pinyon-juniper cover as low as 2–5 trees per ha has been shown to cause greater



Fig. 4. Predicted relationships for the top three models predicting long-term trends in productivity (juveniles per 100 females) relative to (a) the number of oil and gas wells, (b) change in tree cover (Tau), and (c) the change in herbaceous biomass (Tau) from model averaged coefficients (black solid line). Grey shaded area represents a 95% confidence interval. Grey points represent the raw data distribution.

sage-grouse to abandon otherwise suitable habitat (Baruch-Mordo et al., 2013; Coates et al., 2017). Low levels of tree cover may drive declines in pronghorn productivity through increased predation rates by providing cover for predators (Goldsmith, 1990). Moreover, tree cover can drive loss of forage associated with sagebrush and grassland cover (Bielski et al., 2021; Miller et al., 2000) and drive behavioural avoidance (Milligan et al., 2021; Reinking et al., 2018; Sawyer et al., 2019).

Our results contribute to the overwhelming evidence that early management of invading trees within sagebrush habitat will help to protect iconic rangeland species like pronghorn. Conifer encroachment has already been recognised as a threat within sagebrush ecosystems (Maestas et al., 2021; NRCS, 2021). The impacts of conifer encroachment rapidly increase as tree cover increases (Roberts et al., 2018). Preventative management and management applied in the early phases of encroachment is thus the most impactful and cost-effective approach. Manual removal of trees in early stages of invasion along with infrequent moderate intensity fires have been recommended in recent management frameworks for controlling conifer encroachment (Maestas et al., 2021; NRCS, 2021).

Other drivers of global change viewed as threats to pronghorn, including non-native annual grass invasions, wildfire, roads, and increased winter precipitation, were not prominent drivers of long-term declines in pronghorn productivity. Annual forb and grass biomass and cover were relatively low across herd units. Wildfires were similarly only increasing in a few herd units. It is possible that cheatgrass is not yet well enough established across the region for the fire-annual invasion cycle to have strong impacts on pronghorn's sagebrush habitat (Balch et al., 2013; D'Antonio and Vitousek, 1992). However, the fire-invasive annual grass cycle prominent in the Great Basin where perennial grasses are less adapted to fire has not been shown to occur in the western Great Plains (Archer et al., 2023; Porensky and Blumenthal, 2016). Roads were also not found to have a significant impact on pronghorn productivity. This may be an artifact of our data set, as time-series data for road cover were not available at the time of our study. However, the impacts of oil and gas development likely indirectly represent road development impacts on pronghorn. In addition to fencing, each well pad is associated with on average 2 km of roads (BLM, 2003) which can fragment pronghorn habitat and increase access for hunters and predators (Gamo et al., 2017; Jakes et al., 2020). Predation was not directly included in our assessment due to data limitations associated with large spatial and temporal scales of our analysis, but likely plays an important role in population dynamics through both direct and indirect effects on adult and juvenile survival (Gosselin et al., 2015; Hatter and Janz, 1994). Predators are often a leading proximate cause of fawn mortality in pronghorn (Barrett, 1982; Beale and Smith, 1973; Linnell et al., 1995; Panting et al., 2021). However, because maternal nutritional status and body mass index for fawns typically determine the fate of a fawn regardless of proximate cause of mortality (Panting et al., 2021), links to predation and fawn mortality are likely partially captured by the large-scale changes in habitat quality we assessed. We did not assess hunting pressure in our models. In Wyoming, over 15,000 adult female pronghorn were harvested in 2018 alone (Wyoming Game and Fish Department, 2022). However, annual harvest quotas are dictated by annual fawn:doe ratios from the previous year and thus are not independent from pronghorn productivity (Christie et al., 2015).

Because roads, along with drivers of global change like winter precipitation (associated with snow cover) commonly impact pronghorn movement and migration patterns (Jacques et al., 2009; White et al., 2007), it is possible that these factors are more likely to directly impact immigration patterns among populations than population productivity. Assessing combined patterns in immigration and productivity would likely better indicate the impacts of drivers of global change on pronghorn populations. However, assessments of immigration are notoriously difficult. Assessing immigration requires exhaustive population monitoring to quantify movements to and from a population, which are rare (Millon et al., 2019; Williams et al., 2002). While dispersal can be tracked using telemetry movement data, large-mammal movement data are often collected over 2–3-year time scales and on a small subset of a population (e.g. Reinking et al., 2019; Taylor et al., 2016). Low fidelity to winter seasonal ranges also makes immigration challenging to track for pronghorn (Morrison et al., 2021). Increases in the number of collared individuals and the longevity of movement studies may allow for better assessments of changing immigration patterns to determine the cumulative impacts of drivers of global change on population resilience. Alternatively, genetic assessments of gene flow, which have been used to assess connectivity among pronghorn populations, could be used to determine relationships between drivers of global change and pronghorn immigration (LaCava et al., 2020). This becomes increasingly important as large declines in habitat connectivity are predicted for pronghorn over the next century (Zeller et al., 2021). Our assessment should assist managers in identifying where these more detailed assessments are needed in Wyoming.

Focusing research on assessing changing population demographics in species experiencing shifting conditions from drivers of global change may help support preventative conservation for more effective long-term conservation outcomes and decrease the need for short-term reactive approaches (Wilson et al., 2011). Population monitoring efforts in recent decades have generated large amounts of population-level data that span multiple jurisdictions, providing readily available information that can be used to help identify the impacts of drivers of global change on populations across regions. Our results can be used to target populations for smaller-scale population modelling to generate population-level management approaches. Because of the larger ranges associated with big game species, management focused on these species may help apportion protection to other smaller ranging species at risk (Branton and Richardson, 2011; Caro, 2003; Tack et al., 2019), though outcomes can be species- and scale-dependent (e.g., Carlisle et al., 2018). Large-scale population data sets that occur across multiple jurisdictions like those utilised in this study allow us to track trends that may not be detectable from a more local perspective (e.g., Donovan, Roberts, et al., 2020a) and assess the impacts of drivers of global change that function well beyond the local scale (e.g. Johnson et al., 2017). Such research is fundamental for keeping common species common.

CRediT authorship contribution statement

Twidwell Dirac: Writing – review & editing, Conceptualization. Allen Craig R.: Writing – review & editing, Writing – original draft, Conceptualization. Roberts Caleb P.: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. Wonkka Carissa L.: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. Beck Jeffrey L.: Writing – review & editing, Writing – original draft, Conceptualization. Donovan Victoria M.: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization.

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.

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Open research statement

Data will be provided upon acceptance of the manuscript. The authors need to confirm data sharing policies for the data provided by the Wyoming Game and Fish Department. Data will be permanently archived with Dryad.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02848.

References

Akaike, H., 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika 60, 255-265.

Allred, B.W., Smith, W.K., Twidwell, D., Haggerty, J.H., Running, S.W., Naugle, D.E., Fuhlendorf, S.D., 2015. Ecosystem services lost to oil and gas in North America. Science 348, 401–402. https://doi.org/10.1126/science.aaa4785.

- Archer, D., Toledo, D., Blumenthal, D.M., Derner, J., Boyd, C., Davies, K., Hamerlynck, E., Sheley, R., Clark, P., Hardegree, S., Pierson, F., Clements, C., Newingham, B., Rector, B., Gaskin, J., Wonkka, C.L., Jensen, K., Monaco, T., Vermeire, L.T., Young, S.L., 2023. Invasive annual grasses—Reenvisioning approaches in a changing climate. J. Soil Water Conserv. https://doi.org/10.2489/jswc.2023.00074.
- Augustine, D.J., Derner, J.D., 2015. Patch burn grazing management in a semiarid grassland: consequences for pronghorn, plains pricklypear, and wind erosion. Rangel. Ecol. Manag. 68, 40–47. https://doi.org/10.1016/j.rama.2014.12.010.
- Avirmed, O., Lauenroth, W.K., Burke, I.C., Mobley, M.L., 2015. Sagebrush steppe recovery on 30–90-year-old abandoned oil and gas wells. Ecosphere 6. https://doi. org/10.1890/ES14-00175.1.
- Balch, J.K., Bradley, B.A., D'Antonio, C.M., Gómez-Dans, J., 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob. Change Biol. 19, 173–183. https://doi.org/10.1111/gcb.12046.
- Balch, J.K., Bradley, B.A., Abatzoglou, J.T., Nagy, R.C., Fusco, E.J., Mahood, A.L., 2017. Human-started wildfires expand the fire niche across the United States. PNAS 114, 2946–2951. https://doi.org/10.1073/pnas.1617394114.
- Barnowe-Meyer, K.K., White, P.J., Byers, J.A., 2011. Maternal Investment by Yellowstone Pronghorn Following Winter Habitat Deterioration. West. North Am. Nat. 71, 222–233. https://doi.org/10.3398/064.071.0209.
- Barrett, M.W., 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. J. Wildl. Manag. 46, 991–1002. https://doi.org/10.2307/3808232.

Barton, K. MuMIn: Multi-Model Inference.R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn.

- Baruch-Mordo, S., Evans, J.S., Severson, J.P., Naugle, D.E., Maestas, J.D., Kiesecker, J.M., Falkowski, M.J., Hagen, C.A., Reese, K.P., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biol. Conserv. 167, 233–241. https://doi.org/10.1016/j.biocon.2013.08.017.
- Beale, D.M., Smith, A.D., 1973. Mortality of pronghorn antelope fawns in western Utah. J. Wildl. Manag. 37, 343–352. https://doi.org/10.2307/3800125. Bender, L.C., Boren, J.C., Halbritter, H., Cox, S., 2013. Factors influencing survival and productivity of pronghorn in a semiarid grass-woodland in east-central New
- Mexico. Hum. -Wildl. Interact. 7, 313–324. Bielski, C.H., Scholtz, R., Donovan, V.M., Allen, C.R., Twidwell, D., 2021. Overcoming an "irreversible" threshold: a 15-year fire experiment. J. Environ. Manag. 291,
- bleiski, C.H., Scholdz, R., Dohovan, V.M., Ahen, C.K., Twhwen, D., 2021. Overcoming an irreversible threshold: a 15-year fire experiment. J. Environ. Manag. 291, 112550 https://doi.org/10.1016/j.jenvman.2021.112550.
- Bishop, C.J., Unsworth, J.W., Garton, E.O., 2005. Mule deer survival among adjacent populations in Southwest Idaho. J. Wildl. Manag. 69, 311–321. https://doi.org/ 10.2193/0022-541X(2005)069<0311:MDSAAP>2.0.CO;2.
- Bonnot, T.W., Thompson, F.R., Millspaugh, J.J., 2017. Dynamic-landscape metapopulation models predict complex response of wildlife populations to climate and landscape change. Ecosphere 8, e01890. https://doi.org/10.1002/ecs2.1890.
- Bottrill, M.C., Joseph, L.N., Carwardine, J., Bode, M., Cook, C., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R.L., Walker, S., Wilson, K.A., Possingham, H.P., 2008. Is conservation triage just smart decision making? Trends Ecol. Evol. 23, 649–654. https://doi.org/10.1016/j. tree.2008.07.007.
- Bradley, B.A., 2010. Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33, 198–208. https://doi.org/10.1111/j.1600-0587.2009.05684.x.

Branton, M., Richardson, J.S., 2011. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. Conserv. Biol. 25, 9–20. https://doi.org/10.1111/j.1523-1739.2010.01606.x.

Britten, G.L., Dowd, M., Worm, B., 2016. Changing recruitment capacity in global fish stocks. PNAS 113, 134–139. https://doi.org/10.1073/pnas.1504709112.

Brown, D.E., Conover, M.R., 2011. Effects of large-scale removal of coyotes on pronghorn and mule deer productivity and abundance. J. Wildl. Manag. 75, 876–882. https://doi.org/10.1002/jwmg.126.

Brown, D.E., Warnecke, D., McKinney, T., 2006. Effects of midsummer drought on mortality of doe pronghorn (Antilocapra americana). Southwest. Nat. 51, 220–225.

- Bureau of Land Management (BLM), 2003. Final environmental impact statement and proposed plan amendment for the Powder River Basin oil and gas project. U.S. Department of Interior, Buffalo, Wyoming, U.S.A.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- Butchart, S.H.M., Walpole, M., Collen, B., Strien, A., van, Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168. https://doi.org/10.1126/science.1187512.

Canon, S.K., Bryant, F.C., 1997. Bed-site characteristics of pronghorn fawns. J. Wildl. Manag. 61, 1134–1141. https://doi.org/10.2307/3802111.

- Capdevila, P., Stott, I., Beger, M., Salguero-Gómez, R., 2020. Towards a comparative framework of demographic resilience. Trends Ecol. Evol. 35, 776–786. https:// doi.org/10.1016/j.tree.2020.05.001.
- Capdevila, P., Noviello, N., McRae, L., Freeman, R., Clements, C.F., 2021. Global patterns of resilience decline in vertebrate populations. Ecol. Lett. https://doi.org/ 10.1111/ele.13927.
- Carlisle, J.D., Chalfoun, A.D., Smith, K.T., Beck, J.L., 2018. Nontarget effects on songbirds from habitat manipulation for greater sage-grouse: implications for the umbrella species concept. Condor: Ornithol. Appl. 120, 439–455. https://doi.org/10.1650/CONDOR-17-200.1.
- Caro, T.M., 2003. Umbrella species: critique and lessons from East Africa. Anim. Conserv. Forum 6, 171-181. https://doi.org/10.1017/S1367943003003214.
- Christie, K.S., Jensen, W.F., Boyce, M.S., 2017. Pronghorn resource selection and habitat fragmentation in North Dakota. J. Wildl. Manag. 81, 154–162. https://doi. org/10.1002/jwmg.21147.
- Christie, K.S., Jensen, W.F., Schmidt, J.H., Boyce, M.S., 2015. Long-term changes in pronghorn abundance index linked to climate and oil development in North Dakota. Biol. Conserv. 192, 445–453. https://doi.org/10.1016/j.biocon.2015.11.007.

Clements, C.F., Ozgul, A., 2018. Indicators of transitions in biological systems. Ecol. Lett. 21, 905-919. https://doi.org/10.1111/ele.12948.

Coates, P.S., Prochazka, B.G., Ricca, M.A., Gustafson, K.B., Ziegler, P., Casazza, M.L., 2017. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. Rangel. Ecol. Manag., Woody Invasion West. Rangel.: Using grouse focal Species Ecosyst. Restor. 70, 25–38. https://doi.org/10.1016/j.rama.2016.09.001.

Collins, G.H., 2016. Seasonal distribution and routes of pronghorn in the northern Great Basin. West. North Am. Nat. 76, 101–112.

Courtney, R.F., 1989. Pronghorn use of recently burned mixed prairie in Alberta. J. Wildl. Manag. 53, 302–305. https://doi.org/10.2307/3801127.

- D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63–87.
- Dennison, P.E., Brewer, S.C., Arnold, J.D., Moritz, M.A., 2014. Large wildfire trends in the western United States, 1984–2011. Geophys. Res. Lett. 41, 2014GL059576 https://doi.org/10.1002/2014GL059576.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. BioScience 67, 534–545. https://doi.org/10.1093/biosci/bix014.

- Donovan, V.M., Wonkka, C.L., Wedin, D.A., Twidwell, D., 2020c. Land-use type as a driver of large wildfire occurrence in the U.S. Great Plains. Remote Sens. 12, 1869. https://doi.org/10.3390/rs12111869.
- Donovan, V.M., Roberts, C.P., Wonkka, C.L., Beck, J.L., Popp, J.N., Allen, C.R., Twidwell, D., 2020a. Range-wide monitoring of population trends for Rocky Mountain bighorn sheep. Biol. Conserv. 248, 108639 https://doi.org/10.1016/j.biocon.2020.108639.

Donovan, V.M., Wonkka, C.L., Twidwell, D., 2017. Surging wildfire activity in a grassland biome. Geophys. Res. Lett. 44, 2017GL072901 https://doi.org/10.1002/2017GL072901.

Donovan, V.M., Twidwell, D., Uden, D.R., Tadesse, T., Wardlow, B.D., Bielski, C.H., Jones, M.O., Allred, B.W., Naugle, D.E., Allen, C.R., 2020b. Resilience to large, "Catastrophic" wildfires in North America's grassland biome. Earth'S.Future 8, e2020EF001487. https://doi.org/10.1029/2020EF001487.

Drake, J.M., Griffen, B.D., 2010. Early warning signals of extinction in deteriorating environments. Nature 467, 456–459. https://doi.org/10.1038/nature09389. Eberhardt, L.L., 1977. "Optimal" management policies for marine mammals. Wildl. Soc. Bull. (1973-2006) 5 162–169.

Emmerich, J., Guenzel, R., Jahnke, L., Kroger, B., Nemick, J., Rudd, B., Woolley, T., 2007. Pronghorn Antelope (Antilocapra americana). In: Tessmann, S.A., Bohne, J. R. (Eds.), Handbook of Biological Techniques. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA, pp. 1–59.

Finn, S.P., Knick, S.T., 2011. Changes to the Wyoming Basins landscape from oil and natural gas development. Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, Kansas, USA, pp. 69–87.

Fogarty, D.T., Roberts, C.P., Uden, D.R., Donovan, V.M., Allen, C.R., Naugle, D.E., Jones, M.O., Allred, B.W., Twidwell, D., 2020. Woody plant encroachment and the sustainability of priority conservation areas. Sustainability 12, 8321. https://doi.org/10.3390/su12208321.

Frankson, R., Kunkel, K., Stevens, L.E., Easterling, D., Stewart, B.C., 2017. Wyoming State Climate Summary. NOAA Technical Report NESDIS 149-WY.

Fujiwara, M., Mohr, M.S., Greenberg, A., 2014. The effects of disease-induced juvenile mortality on the transient and asymptotic population dynamics of Chinook salmon (Oncorhynchus tshawytscha). PLoS One 9, e85464. https://doi.org/10.1371/journal.pone.0085464.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol. Evol. 13, 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8.

Gamo, R.S., Smith, K.T., Beck, J.L., 2017. Energy development and hunter success for mule deer and pronghorn in Wyoming. Wildl. Soc. Bull. 41, 62–69. https://doi.org/10.1002/wsb.728.

Gasaway, W.C., Stephenson, R.O., Davis, J.L., Shepherd, P.E.K., Burris, O.E., 1983. Interrelationships of Wolves, Prey, and Man in Interior Alaska. Wildl. Monogr. 1–50.

Gedir, J.V., Cain, I.I.I., Harris, J.W., Turnbull, T.T, G., 2015. Effects of climate change on long-term population growth of pronghorn in an arid environment. Ecosphere 6. https://doi.org/10.1890/ES15-00266.1.

Gerber, L.R., 2016. Conservation triage or injurious neglect in endangered species recovery. PNAS 113, 3563–3566. https://doi.org/10.1073/pnas.1525085113. Goldsmith, A.E., 1990. Vigilance behavior of pronghorns in different habitats. J. Mammal. 71, 460–462. https://doi.org/10.2307/1381961.

Gosselin, J., Zedrosser, A., Swenson, J.E., Pelletier, F., 2015. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. Proc. R. Soc. B: Biol. Sci. 282, 20141840. https://doi.org/10.1098/rspb.2014.1840.

Graham, N. a J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Robinson, J., Bijoux, J.P., Daw, T.M., 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conserv. Biol. 21, 1291–1300. https://doi.org/10.1111/j.1523-1739.2007.00754.x.

Gregory, A.J., Beck, J.L., 2014. Spatial heterogeneity in response of male greater sage-grouse lek attendance to energy development. PLoS One 9, e97132. https://doi.org/10.1371/journal.pone.0097132.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evolut. Biol. 24, 699–711.

Hatter, I.W., Janz, D.W., 1994. Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. Can. J. Zool. 72, 878–884. https://doi.org/10.1139/z94-119.

Hebblewhite, M., Munro, R.H., Merrill, E.H., 2009. Trophic consequences of postfire logging in a wolf-ungulate system. For. Ecol. Manag. 257, 1053–1062. https://doi.org/10.1016/j.foreco.2008.11.009.

Hess, J.E., Beck, J.L., 2012. Disturbance factors influencing greater sage-grouse lek abandonment in north-central Wyoming. J. Wildl. Manag. 76, 1625–1634. https://doi.org/10.1002/jwmg.417.

Jacques, C.N., Jenks, J.A., Klaver, R.W., 2009. Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. J. Mammal. 90, 433–441. https://doi.org/10.1644/07-MAMM-A-395.1.

Jakes, A.F., DeCesare, N.J., Jones, P.F., Gates, C.C., Story, S.J., Olimb, S.K., Kunkel, K.E., Hebblewhite, M., 2020. Multi-scale habitat assessment of pronghorn migration routes. PloS One 15, e0241042.

Johnson, H.E., Sushinsky, J.R., Holland, A., Bergman, E.J., Balzer, T., Garner, J., Reed, S.E., 2017. Increases in residential and energy development are associated with reductions in recruitment for a large ungulate. Glob. Change Biol. 23, 578–591. https://doi.org/10.1111/gcb.13385.

Jones, M.O., Allred, B.W., Naugle, D.E., Maestas, J.D., Donnelly, P., Metz, L.J., Karl, J., Smith, R., Bestelmeyer, B., Boyd, C., Kerby, J.D., McIver, J.D., 2018. Innovation in rangeland monitoring: annual, 30 m, plant functional type percent cover maps for U.S. rangelands, 1984–2017. Ecosphere 9, e02430. https://doi. org/10.1002/ecs2.2430.

Jones, P.F., Yoakum, J.D., 2010. Where are all the pronghorn fawns: is low fawn recruitment an issue revisited. Proc. 24th Bienn. Pronghorn Workshop.: Partn. Pronghorn 24, 65–78.

- Joseph, L.N., Maloney, R.F., Possingham, H.P., 2009. Optimal allocation of resources among threatened species: a project prioritization protocol. Conserv. Biol. 23, 328–338. https://doi.org/10.1111/j.1523-1739.2008.01124.x.
- Knapp, P.A., 1996. Cheatgrass (Bromus tectorum L) dominance in the Great Basin Desert: History, persistence, and influences to human activities. Glob. Environ. Change 6, 37–52. https://doi.org/10.1016/0959-3780(95)00112-3.

Kruszynski, C., Bailey, L.D., Bach, L., Bach, P., Fritze, M., Lindecke, O., Teige, T., Voigt, C.C., 2021. High vulnerability of juvenile Nathusius' pipistrelle bats (Pipistrellus nathusii) at wind turbines. Ecol. Appl. N./a, e2513. https://doi.org/10.1002/eap.2513.

LaCava, M.E.F., Gagne, R.B., Stowell, S.M.L., Gustafson, K.D., Buerkle, C.A., Knox, L., Ernest, H.B., 2020. Pronghorn population genomics show connectivity in the core of their range. J. Mammal. 101, 1061–1071. https://doi.org/10.1093/jmammal/gyaa054.

Linnell, J.D.C., Aanes, R., Andersen, R., 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildl. Biol. 1, 209–223. https://doi.org/10.2981/wlb.1995.0026.

- Maestas, J.D., Naugle, D.E., Chambers, J.C., Tack, J.D., Boyd, C.S., Tague, J.M., 2021. Chapter M. Conifer Expansion. In: Remington, T.E., Deibert, P.A., Hanser, S.E., Davis, D.M., Robb, L.A., Welty, J.L. (Eds.), Sagebrush Conservation Strategy— Challenges to Sagebrush Conservation. U.S. Geological Survey Open-File Report 2020-1125. Reston, VA, pp. 139–152.
- Mahood, A.L., Balch, J.K., 2019. Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984–2014). Ecosphere 10, e02591. https://doi.org/10.1002/ecs2.2591.
- McCarthy, M.A., Thompson, C.J., Garnett, S.T., 2008. Optimal investment in conservation of species. J. Appl. Ecol. 45, 1428–1435. https://doi.org/10.1111/j.1365-2664.2008.01521.x.

McLeod, A.I. Kendall: Kendall rank correlation and Mann-Kendall trend test.R package version 2.2. https://CRAN.R-project.org/package=Kendall.

Miller, R.F., Svejcar, T.J., Rose, J.A., 2000. Impacts of western juniper on plant community composition and structure. J. Range Manag. 53, 574–585. https://doi.org/ 10.2307/4003150.

Milligan, M.C., Johnston, A.N., Beck, J.L., Smith, K.T., Taylor, K.L., Hall, E., Knox, L., Cufaude, T., Wallace, C., Chong, G., Kauffman, M.J., 2021. Variable effects of wind-energy development on seasonal habitat selection of pronghorn. Ecosphere 12, e03850. https://doi.org/10.1002/ecs2.3850.

Millon, A., Lambin, X., Devillard, S., Schaub, M., 2019. Quantifying the contribution of immigration to population dynamics: a review of methods, evidence and perspectives in birds and mammals. Biol. Rev. 94, 2049–2067. https://doi.org/10.1111/brv.12549.

Morrison, T.A., Merkle, J.A., Hopcraft, J.G.C., Aikens, E.O., Beck, J.L., Boone, R.B., Courtemanch, A.B., Dwinnell, S.P., Fairbanks, W.S., Griffith, B., Middleton, A.D., Monteith, K.L., Oates, B., Riotte-Lambert, L., Sawyer, H., Smith, K.T., Stabach, J.A., Taylor, K.L., Kauffman, M.J., 2021. Drivers of site fidelity in ungulates. J. Anim. Ecol. 90, 955–966. https://doi.org/10.1111/1365-2656.13425.

MTBS Project, 2022. MTBS Burned Areas Boundaries Dataset [Dataset]. URL (https://www.mtbs.gov/direct-download).

Natural Resource Conservation Service (NRCS), 2021. A framework for conservation action in the Sagebrush Biome. Working Lands for Wildlife, USDA-NRC. Washington, DC.

O'Donnell, M.S., Fancher, T.S., Freeman, A.T., Ziegler, A.E., Bowen, Z.H., Aldridge, C.L., 2014. Wyoming Roads (2009). U.S. Geological Survey Data Series 821.

- Panting, B.R., Gese, E.M., Conner, M.M., Bergen, S., 2021. Factors Influencing Survival Rates of Pronghorn Fawns in Idaho. J. Wildl. Manag. 85, 97–108. https://doi.org/10.1002/jwmg.21956.
- Parker, K.L., Barboza, P.S., Gillingham, M.P., 2009. Nutrition integrates environmental responses of ungulates. Funct. Ecol. 23, 57–69. https://doi.org/10.1111/ j.1365-2435.2009.01528.x.

Patakamuri, S.K., O'Brien, N. modifiedmk: Modified Versions of Mann Kendall and Spearman's Rho Trend Tests.R package version 1.6. https://CRAN.R-project.org/ package=modifiedmk.

Pilliod, D.S., Welty, J.L., Arkle, R.S., 2017. Refining the cheatgrass-fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. Ecol. Evol. 7, 8126–8151. https://doi.org/10.1002/ece3.3414.

Pimm, S.L., Raven, P., 2000. Biodiversity: Extinction by numbers. Nature 403, 843-845. https://doi.org/10.1038/35002708.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344. https://doi.org/10.1126/science.1246752.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2021. nlme: Linear and Nonlinear Mixed Effects Models.R package version 3.1-152. https://CRAN.R-project.org/ package=nlme.

Popp, J.N., Donovan, V.M., 2016. Fine-scale tertiary-road features influence wildlife use: a case study of two major North American predators. Anim. Biol. 66, 229–238. https://doi.org/10.1163/15707563-00002500.

- Porensky, L.M., Blumenthal, D.M., 2016. Historical wildfires do not promote cheatgrass invasion in a western Great Plains steppe. Biol. Invasions 18, 3333–3349. https://doi.org/10.1007/s10530-016-1225-z.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/. Reinking, A.K., Smith, K.T., Mong, T.W., Read, M.J., Beck, J.L., 2019. Across scales, pronghorn select sagebrush, avoid fences, and show negative responses to anthropogenic features in winter. Ecosphere 10, e02722. https://doi.org/10.1002/ecs2.2722.
- Reinking, A.K., Smith, K.T., Monteith, K.L., Mong, T.W., Read, M.J., Beck, J.L., 2018. Intrinsic, environmental, and anthropogenic factors related to pronghorn summer mortality. J. Wildl. Manag. 82, 608–617. https://doi.org/10.1002/jwmg.21414.
- Roberts, C.P., Uden, D.R., Allen, C.R., Twidwell, D., 2018. Doublethink and scale mismatch polarize policies for an invasive tree. PLoS One 13, e0189733. https://doi.org/10.1371/journal.pone.0189733.
- Roberts, C.P., Uden, D.R., Cady, S.M., Allred, B., Fuhlendorf, S., Jones, M.O., Maestas, J.D., Naugle, D., Olsen, A.C., Smith, J., Tack, J., Twidwell, D., 2021. Tracking spatial regimes as an early warning for a species of conservation concern. Ecol. Appl., e02480 https://doi.org/10.1002/eap.2480.
- Sawyer, H., Beckmann, J.P., Seidler, R.G., Berger, J., 2019. Long-term effects of energy development on winter distribution and residency of pronghorn in the Greater Yellowstone Ecosystem. Conserv. Sci. Pract. 1, e83 https://doi.org/10.1111/csp2.83.
- Schneider, R.R., Hauer, G., Adamowicz, W.L. (Vic, Boutin, S., 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. Biol. Conserv., Conserv. Plan. Emerg. Glob. Clim. Econ. realities 143, 1603–1611. https://doi.org/10.1016/j.biocon.2010.04.002.
- Scholtz, R., Twidwell, D., 2022. The last continuous grasslands on Earth: identification and conservation importance. Conserv. Sci. Pract. 4, e626 https://doi.org/ 10.1111/csp2.626.
- Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conserv. Lett. 3, 91–97. https://doi.org/10.1111/j.1755-263X.2010.00096.x.
- Seidler, R.G., Long, R.A., Berger, J., Bergen, S., Beckmann, J.P., 2015. Identifying impediments to long-distance mammal migrations. Conserv. Biol. 29, 99–109. https://doi.org/10.1111/cobi.12376.
- Smith, K.T., Taylor, K.L., Albeke, S.E., Beck, J.L., 2020. Pronghorn winter resource selection before and after wind energy development in South-Central Wyoming. Rangel. Ecol. Manag. 73, 227–233. https://doi.org/10.1016/j.rama.2019.12.004.
- Tack, J.D., Jakes, A.F., Jones, P.F., Smith, J.T., Newton, R.E., Martin, B.H., Hebblewhite, M., Naugle, D.E., 2019. Beyond protected areas: private lands and public policy anchor intact pathways for multi-species wildlife migration. Biol. Conserv. 234, 18–27. https://doi.org/10.1016/j.biocon.2019.03.017.
- Taylor, K.L., Beck, J.L., Huzurbazar, S.V., 2016. Factors influencing winter mortality risk for pronghorn exposed to wind energy development. Rangel. Ecol. Manag. 69, 108–116. https://doi.org/10.1016/j.rama.2015.12.003.
- Twidwell, D., Rogers, W.E., Fuhlendorf, S.D., Wonkka, C.L., Engle, D.M., Weir, J.R., Kreuter, U.P., Taylor, C.A., 2013. The rising Great Plains fire campaign: citizens' response to woody plant encroachment. Front. Ecol. Environ. 11, e64–e71. https://doi.org/10.1890/130015.
- Walston, L.J., Cantwell, B.L., Krummel, J.R., 2009. Quantifying spatiotemporal changes in a sagebrush ecosystem in relation to energy development. Ecography 32, 943–952.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834.

White, P.J., Davis, T.L., Barnowe-Meyer, K.K., Crabtree, R.L., Garrott, R.A., 2007. Partial migration and philopatry of Yellowstone pronghorn. Biol. Conserv. 135, 502–510. https://doi.org/10.1016/j.biocon.2006.10.041.

Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press.

Wilson, H.B., Joseph, L.N., Moore, A.L., Possingham, H.P., 2011. When should we save the most endangered species? Ecol. Lett. 14, 886–890. https://doi.org/

10.1111/j.1461-0248.2011.01652.x. WOGCC (Wyoming Oil and Gas Conservation Commission). WOGCC Data 2020. URL http://pipeline.wyo.gov/legacywogcce.cfm.

Wyoming Game and Fish Department, 2022. 2018 Annual Reports of Big and Trophy Game Harvest [WWW Document]. Wyoming Game and Fish Department. URL (https://wgfd.wyo.gov/Hunting/Harvest-Reports) (accessed 3.22.22).

Wyoming State Geological Survey, 2021. Wyoming's Oil and Gas Facts. Wyoming State Geological Survey, Laramie, Wyoming.

Yoakum, J.D., O'Gara, B.W., 2000. Pronghorn. In: Demarais, S., Krausman, P.R. (Eds.), Ecology and Management of Large Mammals in North America. Precntic Hall. Upper Saddle River, New Jersey, pp. 559–588.

Zeller, K.A., Schroeder, C.A., Wan, H.Y., Collins, G., Denryter, K., Jakes, A.F., Cushman, S.A., 2021. Forecasting habitat and connectivity for pronghorn across the Great Basin ecoregion. Divers. Distrib. 27, 2315–2329. https://doi.org/10.1111/ddi.13402.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, Statistics for Biology and Health. Springer-Verlag, New York.