# Variable effects of wind-energy development on seasonal habitat selection of pronghorn

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**Abstract.** In the face of climate change, wind energy represents an important alternative to oil and gas extraction to meet increasing energy demands, but it has the potential to disrupt wildlife populations. Because behavioral adjustments, such as altered habitat selection, are a primary way that long-lived species respond to novel disturbances, we evaluated effects of wind energy development on pronghorn (*Antilocapra americana*) space use and habitat selection. Using data from GPS-collared female pronghorn in the Shirley Basin of south-central Wyoming, USA, we tested four potential effects of wind turbines on pronghorn space use during the summer and winter: (1) displacement away from wind turbines, (2) increase in size of home ranges, (3) short-term avoidance behavior within home ranges, and (4) changes in avoidance behavior within home ranges over time. We monitored 166 individuals over five summers (2010, 2011, 2018, 2019, and 2020) and 142 individuals over five winters (2009/2010, 2010/2011, 2011/2012, 2018/2019, and 2019/2020) and used resource selection functions to evaluate selection relative to turbines after controlling for other habitat factors, such as snow depth. Although a lack of consistent negative effects of wind turbines on pronghorn across years suggested that wind energy development may have less severe and more intermittent effects on pronghorn than oil and gas development has had on other ungulates, there was a trend toward increased displacement during the study and behavioral avoidance was apparent for individuals in close proximity to turbines. However, pronghorn were highly variable in their fine-scale habitat selection, across both individuals and years, which could make effects of wind energy development difficult to detect. Nevertheless, some individuals, particularly those close to wind-energy facilities, did avoid turbines, which could translate to population-level behavioral or demographic changes over time and affect the resilience and stability of the population. Over time, the accumulation of development, including wind turbines, roads, and fences, can both limit movement and fragment habitat, potentially reaching a critical threshold beyond which populations are negatively impacted.

**Key words:** *Antilocapra americana;* energy development; habitat selection; pronghorn; resource selection; wind-energy development.

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## INTRODUCTION

In the face of climate change, wind energy represents an important alternative to oil and gas extraction to meet high and increasing energy demands, but it has the potential to disrupt wildlife populations (Allison et al. 2019). Across the globe, wind energy is a key component of strategies to reduce carbon emissions (Fargione et al. 2012, Allison et al. 2019) and has become the world's fastest growing source of electricity, with production increasing 23-fold in the last 20 yr (Jones and Pejchar 2013, Jones et al. 2015). Research on interactions of wildlife with wind-energy development has largely focused on bird and bat fatalities from collisions with wind turbines (Allison et al. 2019) and the effects on grouse (LeBeau et al. 2014, 2017, Winder et al. 2014*a*, *b*), but little is known about the effects on other terrestrial species, including ungulates (Lovich and Ennen 2013). Responses of ungulates to other forms of energy development, including oil and gas, have generally been overwhelmingly negative (Dyer et al. 2001, Beckmann et al. 2012, Northrup and Wittemyer 2013, Buchanan et al. 2014, Sawyer et al. 2017, 2019), but ungulates may respond differently to the unique disturbances caused by wind-energy development (Jones and Pejchar 2013). Given the high potential for future wind-energy development (Copeland et al. 2011, Fargione et al. 2012), understanding whether impacts to ungulates are similar to those increasingly documented from oil and gas development will help wildlife managers sustain robust herds amid large-scale energy development.

Energy development can affect wildlife in a variety of ways, including increased mortality, decreased reproductive success, or altered behavior and displacement due to habitat loss (Sheldon and Lindzey 2005, Lovich and Ennen 2013, Northrup and Wittemyer 2013, Sawyer et al. 2013). Demographic effects may be the most apparent but have not been widely documented for ungulates in relation to oil and gas development (Sawyer et al. 2017, Reinking et al. 2018).

Rather, ungulates primarily respond behaviorally and have exhibited strong and continued avoidance of oil and gas development (Sawyer et al. 2006, 2017, Northrup et al. 2015). Ungulates have displayed both short-term and sustained avoidance of infrastructure at a small scale (Sawyer et al. 2006, 2009, 2017, 2019, Buchanan et al. 2014) and large-scale abandonment of seasonal ranges (Sawyer et al. 2019). In addition, avoidance behavior can often drive reductions in population abundance near energy development (Christie et al. 2015, Sawyer et al. 2017) and can lead to the loss of high-use habitats for wildlife (Buchanan et al. 2014).

Although strong negative effects have been documented for oil and gas development, wind-energy development differs in both the type and amount of disturbance and could thus affect wildlife populations differently (Jones and Pejchar 2013, Jones et al. 2015). For both oil and gas and wind energy, road construction represents one of the largest land-use changes (Jones et al. 2015), and roads commonly alter resource use by ungulates (Kolar 2009, Sawyer et al. 2009, Buchanan et al. 2014, Seidler et al. 2015, Christie et al. 2017). However, a comparison of habitat loss based on existing development in Colorado and Wyoming suggested that wind-energy development resulted in fewer impacts per unit area compared with oil and gas (Jones and Pejchar 2013). In addition, ungulate avoidance of oil and gas developments is typically related to increased human activity (Dyer et al. 2001, Sawyer et al. 2009, Beckmann et al. 2012, Buchanan et al. 2014), which is often higher in oil and gas compared to wind-energy development (Jones and Pejchar 2013).

Pronghorn (*Antilocapra americana*) are endemic to western North America and both culturally and economically important in the state of Wyoming, which encompasses more than 50% of historic pronghorn habitat (O'Gara and Yoakum 2004). Pronghorn are also unique, particularly in North America, in that they are semi-nomadic and display highly variable movement patterns (Sawyer et al. 2005, 2019, Kolar et al. 2011). Wyoming has experienced large increases in

energy extraction and has one of the highest capacities for wind development in the United States (Copeland et al. 2011), with many existing and proposed developments for wind energy occurring in critical winter range for pronghorn. However, there is no clear consensus on how or if other energy development projects have affected pronghorn (Hebblewhite 2011, Christie et al. 2015, 2017, Taylor et al. 2016, Reinking et al. 2018, 2019, Sawyer et al. 2019, Smith et al. 2020). The high variability in movement displayed by pronghorn can make it harder to detect a directional behavioral response to disturbance than for species with more consistent movements (Sawyer et al. 2005, 2019, Kolar et al. 2011). Nevertheless, knowledge of behavioral changes such as displacement or avoidance is critical, because these behavioral adjustments are a primary way that long-lived species are impacted by novel disturbances and could have important effects on individual and population-level fitness (Creel and Christianson 2008, Sawyer et al. 2017).

To better understand how ungulates respond to novel disturbances, we evaluated the effects of wind-energy development on female pronghorn space use and habitat selection during winter and summer seasons. Using data from GPS-collared female pronghorn monitored 2010–2012 and 2018–2020 in a landscape with multiple wind-energy facilities in various stages of development and operation in the Shirley Basin of south-central Wyoming, USA, we tested four predictions regarding the effects of wind energy on pronghorn space use. If wind-energy development decreased habitat suitability, we predicted that (1) pronghorn would select home ranges farther from turbines during and after construction and (2) pronghorn closer to wind turbines would have larger home ranges. If wind-energy development resulted in behavioral avoidance, we predicted (3) that individuals would select areas within their home ranges that were farther from existing and under-construction wind turbines and (4) that the avoidance behavior would persist or increase within 10 yr of construction.

## Study Area

We evaluated habitat selection by female pronghorn in the Shirley Basin near Medicine Bow in Carbon and Albany Counties, Wyoming, USA (Fig. 1). Wyoming contains over 50% of historic pronghorn habitat (O'Gara and Yoakum 2004) and the Medicine Bow pronghorn herd is the largest in Wyoming and likely North America. Our study area included areas identified as crucial winter range by the Wyoming Game and Fish Department and was dominated by arid shrublands and grasslands, with the most prevalent cover type being Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). Elevation ranged from 1320 m to 3350 m. Temperatures ranged from 0.0 to 36.7°C in the summer (June–August) and from −42.2 to 8.9°C in the winter (December–February).

Our study focused on two existing wind-energy facilities and two wind-energy projects under construction. The Seven Mile Hill (hereafter, Seven Mile) wind-energy project, located between Hanna and Medicine Bow, in Carbon County, WY, consisted of 79, 1.5-megawatt (MW) wind turbines and became operational in December 2008. The Dunlap Ranch (hereafter Dunlap) wind-energy facility, located north of Medicine Bow, WY, consisted of 74, 1.5-MW wind turbines and was constructed from September 2009 to September 2010. Construction of two new wind-energy facilities, Ekola Flats and TB Flats, began in April 2019, with completion planned for fall 2020. Ekola Flats was located just west of Medicine Bow, WY, and will include 67, 4.2-MW and 14, 2.3-MW turbines. TB Flats was located approximately 18.2 miles north of Medicine Bow, WY, and will consist of 94, 4.2-MW and 55, 2.0-MW turbines. Wind-energy facility development began with the construction of roads, substations, and turbine foundations in September 2010 for Dunlap and April 2019 for Ekola Flats and TB Flats (Energy 2009, Ekola Flats Wind Energy LLC, 2018, TB Flats Wind Energy LLC, 2018). Construction in both time periods was stopped in late December due to winter weather and restarted in the spring. Turbines were erected from May–September 2010 at Dunlap and May–September 2020 at Ekola Flats and TB Flats. There were four additional wind-energy facilities on the periphery of the study area: Little Medicine Bow (10, 0.6-MW turbines, completed by 2000), Foote Creek Rim (100, 0.6-MW and 33, 0.75-MW turbines, completed by 2000), Rock River (50, 1.0-MW turbines, completed in 2001), and High Plains (85, 1.5-MW turbines, completed by 2009).
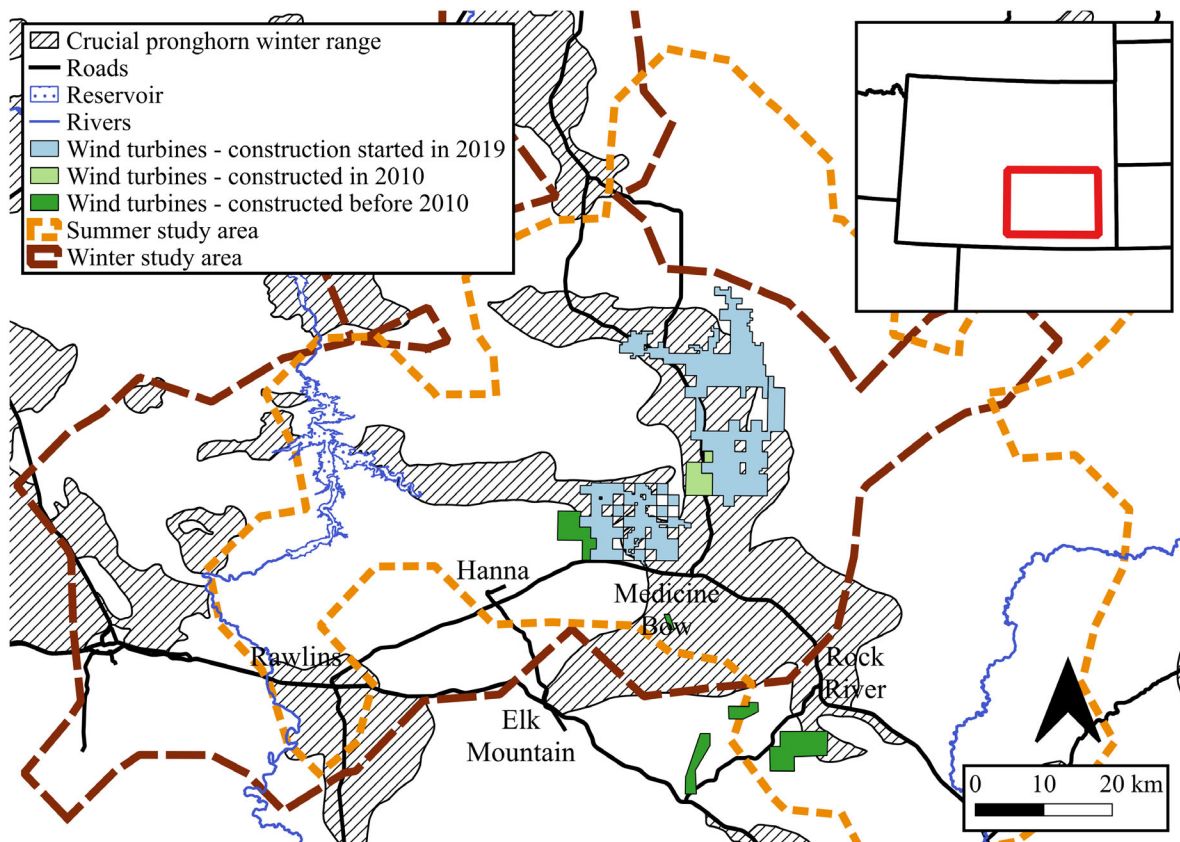
Fig. 1. Area in south-central Wyoming, USA, where collared pronghorn were monitored to document space use and habitat selection, 2010–2020. The area included two wind energy projects that were started in 2019 (Ekola Flats and TB Flats; light blue) and one wind energy project that was constructed from 2009 to 2010 (Dunlap; light green). All other wind energy projects (dark green) were in operation by 2009 and included Seven Mile in the core of the study area and Little Medicine Bow, Rock River, Foote Creek Rim, and High Plains on the periphery. The study areas, calculated as the 99% utilization distributions from all pronghorn locations in a season, for both summer and winter are shown in brown.

## METHODS

We monitored female pronghorn with GPS collars from 2010–2012 and 2018–2020. Only female pronghorn were monitored because of their importance for population dynamics. Initially, 35 and 17 adult female pronghorn were captured using helicopter net gunning (Leading Edge Aviation, Lewiston, Idaho, USA) in January 2010 and December 2011, respectively, and animals were monitored through 2012. Subsequently, 80 adult female pronghorn were captured in March 2018 (Native Range Capture Services, Elko, Nevada, USA), with additional captures of 20, 13, 16, and 37 females in December 2018, March

2019, November 2019, and March 2020, respectively. Animals were monitored through August 2020, with a goal of 80 active collars throughout the study period. Capture and handling protocols were approved by University of Wyoming Institutional Animal Care and Use Committee (protocols 01012010 and 20180306MK00297-03) and Wyoming Game and Fish Department (Chapter 33 Permit IDs 742 and 1162). Captured animals were fitted with store-on-board GPS neck collars (model G2110B; Advanced Telemetry System, Isanti, Minnesota, USA and RECON-4560-4; Telonics, Mesa, Arizona, USA). Collars from the first study period (2010–2012) recorded locations every 11 h during the summer and

every 7 h during the winter. Collars were programmed to fall off in April 2012 and all collars were recovered by May 2012. Collars from the second study period (2018–2020) transmitted locations every 8 h via satellite.

We manually screened location data to remove any erroneous locations. Because we were interested in seasonal habitat selection, we manually excluded migration locations defined by long-distance linear movements from the remaining cluster of points, so that all locations included in analyses were from an individual's seasonal range. We designated summer (June–August) and winter (December–February) seasons based on the timing of both spring (March–May) and fall (September–November) migration so that the seasons represented the time during which pronghorn were on seasonal ranges (M. Milligan, *unpublished data*). Based on these criteria, winter locations from the first 1–2 weeks of December and the last 2 weeks of February were excluded from 41 and 12 individuals, respectively, that had either not yet established or already left a seasonal range. To address any issues of autocorrelation among individuals found in the same group, we calculated a point-proximity metric for all pairwise combinations of individuals monitored in the same year (Cardillo and Warren 2016). The median overlap for all years and seasons was zero and we excluded all individuals ($n = 1$) that had high spatial overlap greater than that assumed to be random (>0.6).

*Habitat variables*

We identified nine habitat factors *a priori* that could influence pronghorn space use: sagebrush cover, herbaceous cover, tree canopy cover, terrain ruggedness, snow depth in winter, roads, fences, and wind turbines. Sagebrush is an important source of both cover and food for pronghorn (O'Gara and Yoakum 2004), but is low across a large portion of the study area. Therefore, we included both sagebrush and herbaceous cover as important land cover types. We used the 30 m resolution shrubland fractional components spatial layer derived from the National Land Cover Database (NLCD) describing the proportion of sagebrush (*Artemisia* spp.) and herbaceous canopy cover (Xian et al. 2015). Pronghorn prefer open landscapes (O'Gara and Yoakum 2004) and forested

landscapes are masked from the shrubland fractional components datasets (Xian et al. 2015), so we included an NLCD tree canopy cover layer (Coulston et al. 2012) to account for the primarily mountainous forested portions of the study area. We assumed that pronghorn could base home range selection on tree canopy cover but that it would not influence habitat selection behavior after an individual selected a seasonal range and so only included tree canopy cover in analyses evaluating the selection and size of seasonal home ranges. Because pronghorn typically prefer less rugged landscapes (O'Gara and Yoakum 2004, Kolar 2009), we calculated a terrain ruggedness index using a 10-m DEM (Wilson et al. 2007). The terrain ruggedness index represents the relative change in elevation between adjacent cells of a digital elevation model (DEM) and provides a quantitative measure of topographic heterogeneity (Riley et al. 1999). Deep snow can inhibit pronghorn movements and make it more difficult to find forage (O'Gara and Yoakum 2004, Beckmann et al. 2012), so we included daily estimates of snow depth for each year for the entire study area on a 1 km × 1 km grid (National Operational Hydrologic Remote Sensing Center 2004). Both roads and fences represent forms of anthropogenic disturbance and can act as barriers to animal movement, particularly for pronghorn (O'Gara and Yoakum 2004, Gates et al. 2012, Reinking et al. 2019, Xu et al. 2021). We calculated the distance to all roads, excluding ranch two-tracks because they are used less frequently. We digitized fences based on National Agricultural Imagery Program (NAIP) aerial imagery data and calculated distance to the nearest road or fence for the entire study area. To evaluate the effect of wind energy development, we calculated as separate variables the distance to existing wind turbines, distance to turbines under construction, and distance to future turbine sites. We had 4 yr of data preconstruction from two wind-energy facilities (Ekola Flats and TB Flats), 1 yr of data during construction for each of three wind-energy facilities (Dunlap, Ekola Flats, and TB Flats), and 4 and 5 yr of data post-construction from two wind-energy facilities (Dunlap and Seven Mile, respectively). Individual animals were monitored both within the wind-energy facilities and

in surrounding areas (up to 100 km from nearest turbine). Existing turbines were present in all study years, whereas turbines under construction were only present in three summers (2010, 2019, and 2020) and two winters (2010 and 2019/2020), and future turbine sites were only present in three summers (2010, 2011, and 2018) and 4 winters (2010, 2010/2011, 2011/2012, and 2018/2019). While construction activity peaked in the summer, we classified the two winters (2010 and 2019/2020) as construction periods because road construction had already started and was not stopped until late December due to winter weather (Energy 2009, Ekola Flats Wind Energy LLC, 2018, TB Flats Wind Energy LLC, 2018). Therefore, although turbines were not yet present, construction and the related increase in activity were occurring during December when pronghorn were selecting seasonal home ranges and would be expected to influence habitat selection. Because turbines were built in high-quality habitat, we included distance to future turbines to control for other habitat factors that were present at turbine locations prior to construction and we included the pre-construction period as a comparison with the during and post-construction phases. We log-transformed all distance measures to allow the effect to decrease at larger distances.

*Home range estimation*

We analyzed pronghorn space use data for summer (June–August) and winter (December–February) separately and evaluated space use at the landscape and home range scale, which corresponds to the second and third orders of selection, respectively (Johnson 1980). Because too few relocations can bias home range estimates (Seaman et al. 1999), we restricted analyses to individuals with ≥100 locations who were monitored for ≥30 d ($n = 166$); home range size was not dependent on the number of locations (summer: $P = 0.64$; winter: $P = 0.12$). Due to the autocorrelated nature of GPS data, we used the ctmm package (Calabrese et al. 2016) in Program R (version 3.5.0) to calculate 95% kernel home ranges for each individual for each season using an autocorrelated kernel density estimator (Fleming et al. 2015). Individuals that were monitored in multiple years typically did not have a consistent seasonal range from year to year, so we

calculated separate seasonal home ranges for each year of monitoring and treated them as independent samples.

*Home range selection*

To test our first prediction, that pronghorn would select home ranges farther from turbines during and after construction, we assessed second-order selection, or an individual's selection of a home range within the larger study area. We characterized pronghorn habitat use with estimated home ranges for each individual, in each season, for each year. To sample availability, we randomly allocated 1000 circular home ranges across the study area that were equal in area to the median pronghorn home range (summer: 32 km$^2$; winter: 360 km$^2$). The study area was defined as the 99% kernel home range estimated using locations from all collared individuals (summer: 8867 km$^2$; winter: 9276 km$^2$). Using the spatial layers described above, we characterized the following resources within each used and available home range: average percent sagebrush cover, average percent herbaceous cover, average tree canopy cover, average terrain ruggedness, average snow depth (for winter home ranges), density of roads, density of fences, and average distance to wind turbine using QGIS 3.10. For snow depth, we averaged each daily measurement to calculate an average value for each pixel for the winter period (December–February) each year and then calculated an average snow depth within each home range for the year the individual was monitored. We evaluated multicollinearity between predictors by computing variance inflation factors (VIFs) and only included models where all variables had a VIF < 10 (James et al. 2013). Due to multicollinearity, multiple wind energy variables (e.g., distance to existing turbine + distance to turbine under construction) could not be evaluated for winter models in all years.

We used logistic regression to compare used and available home ranges, with available home ranges weighted ($w = 1000$) to improve convergence (Northrup et al. 2013). We first selected a top habitat model using backward stepwise variable selection ($P < 0.05$; Bruce and Bruce 2017), because we had no *a priori* hypotheses about combinations of individual habitat variables and we were primarily interested in building a top

habitat model to test our hypothesis regarding wind turbine effects. We then evaluated the top habitat variables in combination with the anthropogenic variables of road density and fence density, thus selecting a top model containing both habitat and anthropogenic variables but not wind energy variables using the full dataset. We were not able to test effects of wind energy using the full dataset, because future turbine sites and turbines under construction were not present in every year. In 2010, existing turbines, turbines under construction, and future turbines were all present; from December 2010–February 2019, only existing turbines and future turbines were present; and from June 2019–August 2020, only existing turbines and turbines under construction were present. Therefore, we evaluated models with the top habitat and anthropogenic variables in combination with the relevant wind energy variables during each year separately. We compared models based on Akaike's information criterion for small sample sizes ($AIC_c$) and based inferences on the top model representing the majority of model weight ($w_i$; Burnham and Anderson 2002) rather than model averaging (Cade 2015, Banner and Higgs 2017). In cases with model uncertainty, we based inferences on the most parsimonious model and only retained additional parameters whose 85% confidence intervals did not overlap zero, which were considered to be significant because that interval is compatible with an information-theoretic approach (Arnold 2010). Pronghorn migrated away from wind-energy facilities in 3 harsh winters (2010/2011, 2018/2019, and 2019/2020), but inferences regarding the effects of wind turbines on home range selection did not change regardless of whether these individuals were included (Appendix S1:Table S1). Therefore, we used data from all individuals in our analyses.

### Home range size

To test our second prediction that pronghorn closer to wind turbines would have larger home ranges, we used linear models to evaluate the effects of each metric described above on home range size. Model errors were not normally distributed, so we log-transformed home range size. Analyses proceeded from variable to model selection as described above for home range selection. A similar sensitivity analysis suggested that the effect of wind turbines on home range size did not change with the inclusion of individuals that migrated away from the wind-energy facilities in some winters (Appendix S1:Table S2), so we included data from all individuals in our analyses.

### Within-home range selection

To test our third prediction that individuals would select areas within their home ranges that were farther from existing and under-construction wind turbines, we assessed third-order habitat selection, or the selection of habitat within an individual's home range, using resource selection functions to compare used and available points following Design 3 of Manly et al. (2002). We conducted 1000 simulations for each individual to determine the number of available points required for coefficient estimates to converge (Northrup et al. 2013). We sampled available points at a 5:1 available: used ratio within each individual animal's home range and we weighted available points ($w = 1000$) to balance both coefficient convergence and computational efficiency (Fithian and Hastie 2013, Northrup et al. 2013). We estimated separate resource selection models for each individual in each season for each year to allow for the estimation of individual-specific regression coefficients (Davidian and Giltinan 1995, Fieberg et al. 2010). We evaluated three variable categories: habitat, anthropogenic features, and wind energy. Habitat covariates included proportion sagebrush cover, proportion herbaceous cover, terrain ruggedness, and snow depth (for winter models). Because pronghorn select habitat based on cues from outside their immediate vicinity (Einarsen 1948, Seidler et al. 2015), we used a moving window analysis to calculate values for each habitat variable at each pixel averaged within a buffer of 1600 m (summer models) and 775 m (winter models), which represented the median distance between consecutive locations of individual pronghorn in each season. Covariates representing anthropogenic disturbance included distance to road and distance to fence. Finally, wind energy variables included distance to existing turbine, distance to future turbine, and distance to turbines under construction. We used the full model containing habitat, anthropogenic, and all relevant wind variables for each individual to

calculate individual selection coefficients, because we were primarily interested in the effects of wind energy after controlling for other factors (Cade 2015, Banner and Higgs 2017).

We evaluated population-level habitat selection by averaging individual coefficients for each variable. We removed all outliers that were >3 or < −3 standard deviations from the mean for each variable because, given the data were scaled, the outliers were not biologically reasonable and not driving population-level trends. Coefficients were removed for 10, 5, and 7 individual/seasons for distance to existing turbine, distance to turbine under construction, and distance to future turbine, respectively. We calculated population-level selection coefficients $(\widehat{\overline{\beta}}_j)$ by averaging the individual selection coefficients across the population and calculated the variance as:

$$\mathrm{var}\left(\widehat{\overline{\beta}}_j\right) = \frac{1}{n-1}\sum_{i=1}^{n}\left(\widehat{\beta}_{ij} - \widehat{\overline{\beta}}_j\right)^2$$

where $\widehat{\beta}_{ij}$ are the individual selection coefficients, which accounts for inter-animal variation (Marzluff et al. 2004, Sawyer et al. 2006). We then assessed whether selection was significant based on whether 95% confidence intervals overlapped zero because no model selection was performed at the population level (Arnold 2010).

To evaluate turbine effects and account for pronghorn far from wind-energy facilities, we tested for interactive effects between turbine status (existing, future, or under construction) and proximity of an individual's home range to turbine on the individual selection coefficients for distance to turbines. If wind-energy development had negative effects, the interaction term should be significant, with no relationship between selection and distance to turbine during the pre-construction period, but a negative relationship during and post-construction, with pronghorn occupying home ranges closer to turbines exhibiting greater avoidance within the home range. We used linear models to evaluate whether individual selection coefficients for wind turbine were related to all combinations of disturbance period (pre-construction, during construction, post-construction) and the average proximity of an individual's home range to wind turbines. For the pre-disturbance period, we used individual selection coefficients for distance to future

turbine site from individuals monitored from December 2010–February 2012 and from June 2018–February 2019. For the construction period, we used individual selection coefficients for distance to turbine under construction for individuals monitored in 2010 and from June 2019–August 2020. For the post-construction period, we used individual selection coefficients for distance to existing turbine for all monitoring years. An individual's proximity to turbine was calculated as the average distance across that individual's entire home range to future turbine sites for the pre-construction period, to turbines under construction for the construction period, and to existing turbines for the post-construction period. We compared models based on Akaike's information criterion for small sample sizes ($\mathrm{AIC}_c$) following the criteria described above.

*Changes in selection over time*

Finally, to test our fourth prediction that avoidance behavior would persist or increase within 10 yr of construction, we tested whether habitat selection of an existing wind-energy facility (Dunlap) had changed >5 yr following construction. We only included individuals with home ranges that overlapped a 10 km buffer of the Dunlap wind-energy facility and we conducted a two-tailed *t*-test ($a = 0.05$) comparing individual selection coefficients for distance to turbine for individuals that used Dunlap in the short-term (2011–2012) and in the long-term (2018–2020) after construction. Using the same subset of data, we used linear models to evaluate an interaction model set similar to that described for the within-home range selection analysis, where the selection coefficient for each individual for distance to existing turbine (Dunlap for this subset of individuals) was the response variable. The predictor variables were all possible combinations of time period (short-term vs. long-term) and average proximity of an individual's home range to wind turbines. If wind-energy development had negative effects only in the short-term, the interaction terms should be significant, with no relationship between selection and distance to turbine during the second period, but a negative relationship during the short-term period, with pronghorn occupying home ranges closer to turbines exhibiting greater avoidance within the home range.

## RESULTS

We monitored 166 individuals during the summer (30 in 2010, 11 in 2011, 72 in 2018, 70 in 2019, 70 in 2020) and 142 individuals in winter (31 in 2010, 24 in 2010/2011, 23 in 2011/2012, 75 in 2018/2019, 72 in 2019/2020). Eighty-seven individuals were monitored in multiple summers and 83 individuals were monitored in multiple winters, so we had a total of 253 individual home ranges in summer and 225 individual home ranges in winter. For pronghorn included in analyses, the number of locations per individual ranged from 100 to 276 during the summer and 109 to 311 in the winter.

### Home range selection

We found evidence that pronghorn were displaced when selecting home ranges relative to existing turbines in three summers and one winter, but that the effects of turbines under construction were negligible. Summer home ranges of pronghorn had lower terrain ruggedness, lower herbaceous cover, and lower fence densities than available areas (Appendix S1: Tables S3–S4, Fig. S1). Winter home ranges had lower terrain ruggedness, higher sagebrush cover, higher herbaceous cover, and lower tree canopy cover (Appendix S1: Tables S4-S5, Fig. S2). In the 3 most recent summers (2018–2020), pronghorn selected home ranges farther from existing turbines, although the strength of the effect varied by year (Fig. 2). In the winter, pronghorn selected home ranges farther from existing turbines in 2019/2020 (Fig. 2). In the construction years, pronghorn selected summer home ranges closer to turbines under construction, but winter home range selection was not related to turbines under construction (Fig. 2). Pronghorn selected home ranges closer to future turbine sites in summer 2018 and farther from future turbine sites in winter 2010/2011, but the effect was not significant in other years (Appendix S1: Tables S3–S5).

### Home range size

We found no evidence that proximity to turbines was correlated with larger home ranges in either summer or winter. Median home range size in summer was 32.46 km$^2$, but ranged from 2.52 to 1890.21 km$^2$, with similar variation seen across years (Fig. 3). In contrast, median home
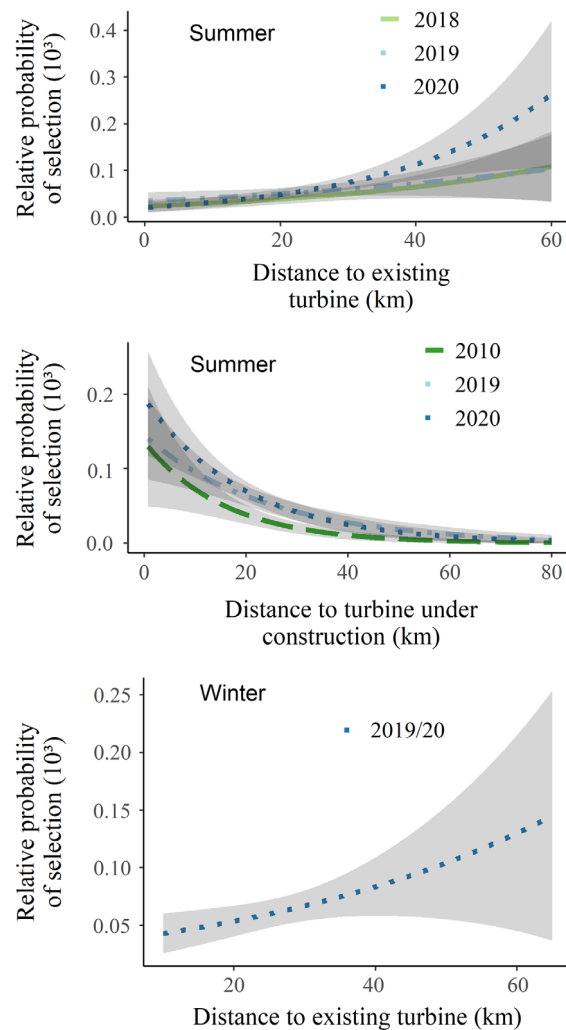


Fig. 2. Estimated relative probability of home range selection relative to distance to existing turbine (left panels) and turbine under construction (right panels) in summer (top) and winter (bottom), with 85% confidence intervals shown in gray, south-central Wyoming, USA, 2010–2020. Only years for which variables were significant are shown. Turbine construction only occurred during 2010 and 2019-2020.

range size in winter was 360.44 km$^2$ and ranged from 10.05 to 5940.80 km$^2$, with pronghorn having larger home ranges in 2010/2011, 2018/2019, and 2019/2020, which were all harsh winters (Fig. 3). Size of home ranges in summer was not related to habitat variables, but in winter increased with sagebrush cover, tree canopy cover, and snow depth, but decreased with

increasing fence density (Appendix S1: Tables S4, S6 and S7, Fig. S3). In both summer and winter, wind turbines had little to no effect on home range size, with only distance to turbines under construction being important in 2010, when predicted home range size was smaller near turbines (Fig. 4, Appendix S1: Table S6–S7).

*Within-home range selection*

We found little evidence that wind turbines caused avoidance behavior within home ranges at the population level. There was significant individual variation in the direction of selection across all variables evaluated, which translated to no population-level selection for any variable in either season in all years (Fig. 5) with the exception of distance to future turbine in summer 2011, although sample sizes were low during that season ($n = 11$). Across all individuals, population-level selection based on distance to either existing or under construction turbines was not significant in either summer or winter, with confidence intervals overlapping zero (Fig. 5). An interaction between disturbance period and proximity of an individual's home range to wind turbines best predicted individual selection coefficients in both summer and winter, although the relationships differed by season (Table 1; Fig. 6). Pronghorn nearest wind-energy facilities avoided turbines under construction in the summer and existing turbines in the winter (Fig. 6).



Fig. 4. Predicted pronghorn summer home range size relative to distance to turbine under construction, with 85% confidence intervals shown in gray, south-central Wyoming, USA, 2010–2020. Only years for which distance to turbine was significant are shown.

*Changes in selection over time*

Our results suggest that pronghorn did not change selection behavior relative to wind turbines in the long-term post-construction. For individuals using the area around Dunlap, selection relative to distance to existing turbine did not change significantly from the period directly
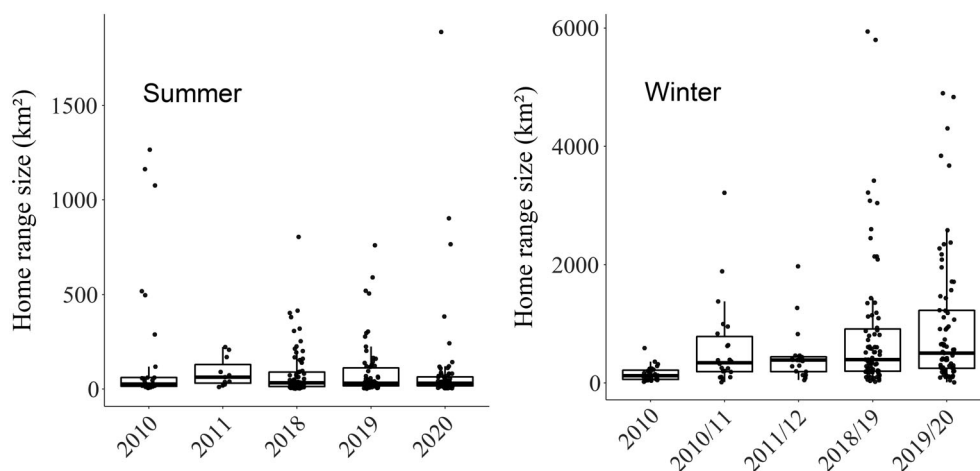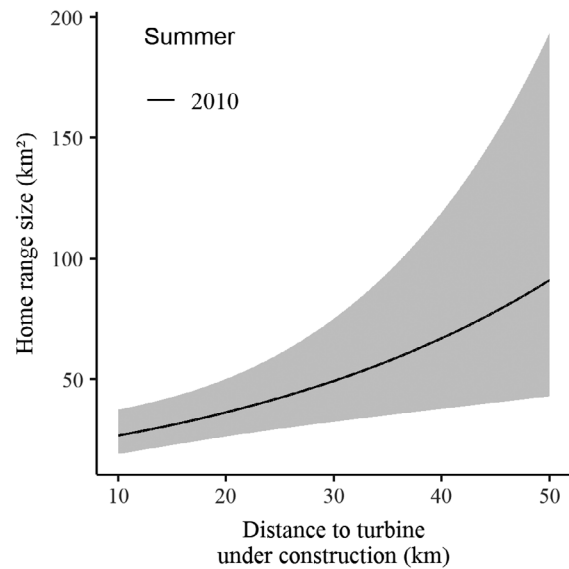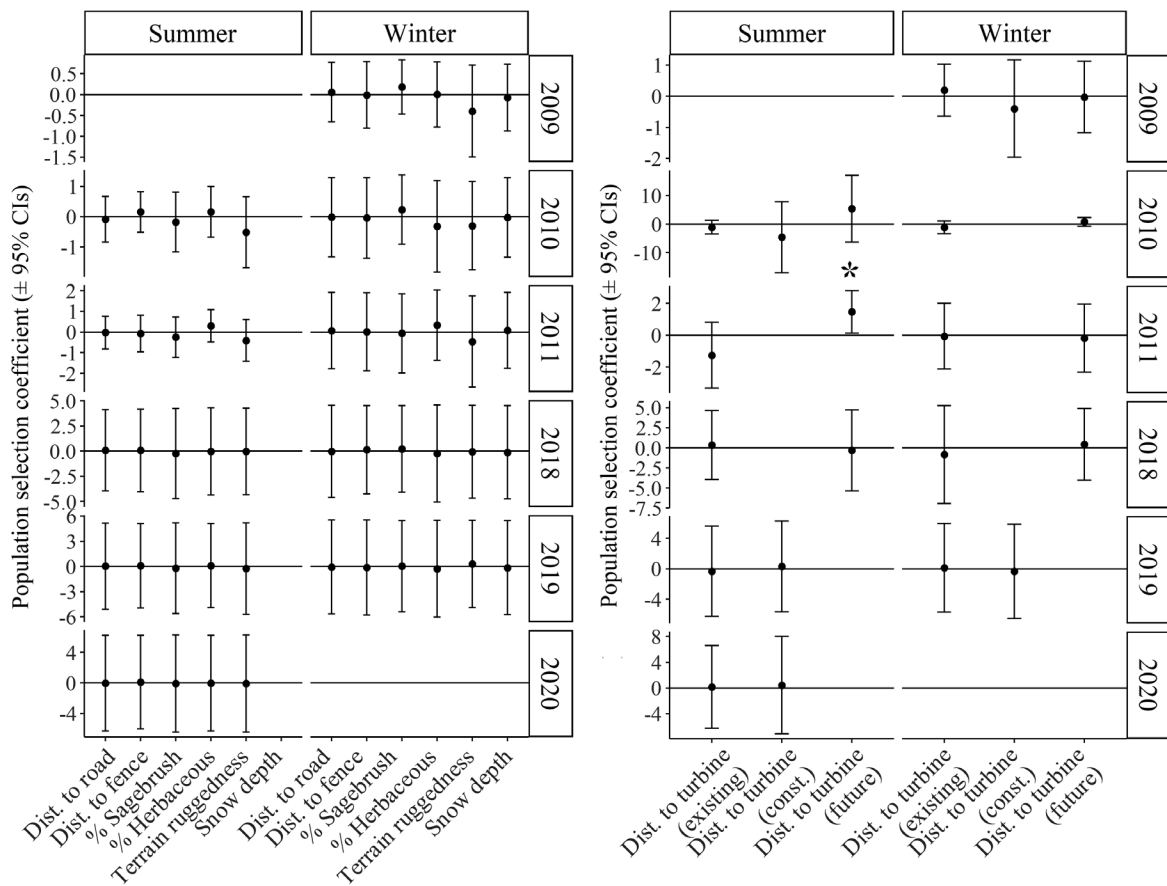


Fig. 3. Distribution of home range sizes for female pronghorn monitored in summer (left) and winter (right) in each year, south-central Wyoming, USA, 2010–2020.

Fig. 5. Population-level selection coefficients (±95% confidence intervals) for habitat, anthropogenic, and wind variables predicting individual pronghorn resource selection within the home range in the summer and winter for each year, south-central Wyoming, USA, 2010–2020. Individual-level selection coefficients were calculated using individual logistic regression models and averaged to calculate population-level coefficients following Marzluff et al. (2004). Outliers that were >3 or <−3 standard deviations from the mean were removed. Wind variables are shown separately because of the much larger scale and variation among individuals. Winters are labeled based on the year in December (i.e., winter 2010/2011 is labeled as 2010).

following construction (2011–2012) compared to the long-term (2018–2020) after construction in either season (summer: $P = 0.23$; winter: $P = 0.67$), although sample sizes were small (summer: seven individuals in 2011, 66 individuals in 2018–2020; winter: 30 individuals in 2011–2012 and 31 individuals in 2018–2020). Individual selection coefficients were only related to distance to turbine in the summer, with no evidence for a change between time periods, but an interaction between time period and proximity of an individual's home range to wind turbines best predicted individual selection coefficients in the

winter (Table 2). Individuals near Dunlap (<10 km) showed similar levels of avoidance in both time periods, although there was a non-significant tendency for individuals to avoid turbines at greater distances >5 yr after construction (Fig. 7).

## DISCUSSION

Although wide-ranging negative effects have been documented for other forms of energy development, few studies have evaluated the effects of wind-energy development on

Table 1. Support for final candidate models relating pronghorn selection coefficients for wind turbines to disturbance period (pre-construction, during construction, post-construction) and the proximity of an individual's home range to turbines, south-central Wyoming, USA, 2010–2020. Individual selection coefficients were first estimated using separate logistic regressions for each pronghorn to evaluate habitat selection within the home range for each season.

| Model | $K$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c\ w_i$ | Cum. $w_i$ | LL |
|---|---|---|---|---|---|---|
| Summer | | | | | | |
| Disturbance period × turbine proximity | 7 | 3316.72 | 0.00 | 1.00 | 1.00 | −1651.25 |
| Disturbance period × ln(turbine proximity) | 7 | 3458.44 | 141.72 | 0.00 | 1.00 | −1722.11 |
| Disturbance period | 4 | 3485.89 | 169.17 | 0.00 | 1.00 | −1738.91 |
| Null | 2 | 3486.94 | 170.22 | 0.00 | 1.00 | −1741.46 |
| Turbine proximity | 3 | 3488.84 | 172.12 | 0.00 | 1.00 | −1741.40 |
| ln(turbine proximity) | 3 | 3488.95 | 172.23 | 0.00 | 1.00 | −1741.45 |
| Winter | | | | | | |
| Disturbance period × turbine proximity | 7 | 1923.12 | 0.00 | 0.84 | 0.84 | −954.44 |
| Disturbance period × ln(turbine proximity) | 7 | 1926.49 | 3.38 | 0.16 | 1.00 | −956.12 |
| Disturbance period | 4 | 1934.17 | 11.05 | 0.00 | 1.00 | −963.04 |
| Null | 2 | 1941.05 | 17.94 | 0.00 | 1.00 | −968.51 |
| ln(turbine proximity) | 3 | 1942.67 | 19.55 | 0.00 | 1.00 | −968.31 |
| Turbine proximity | 3 | 1942.72 | 19.60 | 0.00 | 1.00 | −968.33 |



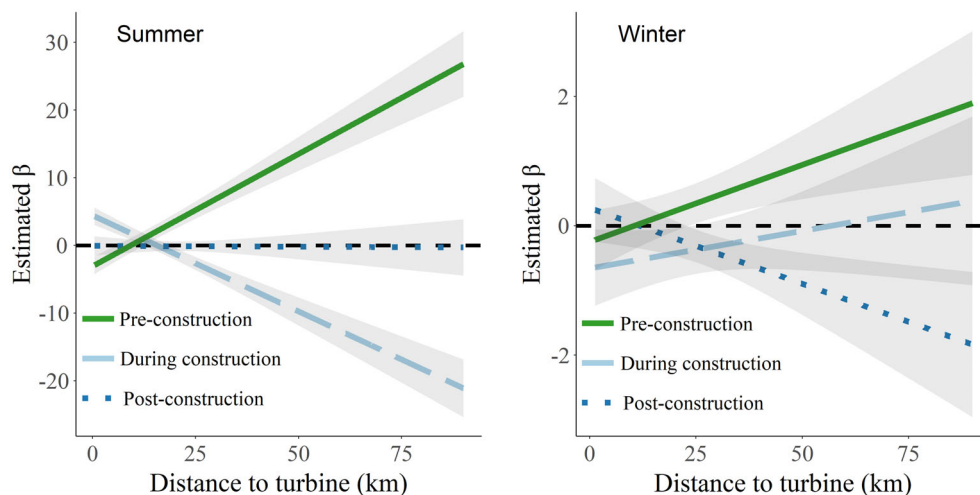Fig. 6. Estimated summer and winter selection coefficients (β) for pronghorn at the third order relative to disturbance period (pre-construction, during construction, post-construction) and the proximity of an individual's home range to wind turbines, south-central Wyoming, USA, 2010–2020.

ungulates, despite the sharp increase in interest and demand. Using data from pronghorn monitored over a decade in a landscape containing multiple developing and existing wind-energy facilities, we found evidence for displacement in recent years and some evidence of avoidance for individuals that were within 10 km of turbines. The variability we documented for pronghorn is in stark contrast, however, to the consistent and sustained avoidance of oil and gas development documented in other ungulates (Sawyer et al. 2006, 2009, 2017, Buchanan et al. 2014). Instead, pronghorn were highly variable in their fine-scale habitat selection, varying in both strength and direction resulting in no population-level selection for any variable we evaluated, with avoidance only apparent in close proximity to turbines. Pronghorn are unique in North

Table 2. Support for final candidate models relating pronghorn selection coefficients for wind turbines to time period (short-term, long-term) and the proximity of an individual's home range to turbines for pronghorn that were in close proximity to the Dunlap wind-energy facility. Individual selection coefficients were first estimated using separate logistic regressions for each pronghorn to evaluate habitat selection within the home range for each season.

| Model | $K$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c\ w_i$ | Cum. $w_i$ | LL |
|---|---|---|---|---|---|---|
| Summer | | | | | | |
| Turbine proximity | 3 | 173.66 | 0.00 | 0.40 | 0.40 | −83.63 |
| Null | 2 | 175.18 | 1.52 | 0.19 | 0.59 | −85.49 |
| ln(turbine proximity) | 3 | 175.40 | 1.74 | 0.17 | 0.76 | −84.50 |
| Time period | 3 | 176.23 | 2.57 | 0.11 | 0.87 | −84.91 |
| Time period × turbine proximity | 5 | 176.63 | 2.97 | 0.09 | 0.97 | −82.79 |
| Time period × ln(turbine proximity) | 5 | 178.57 | 4.91 | 0.03 | 1.00 | −83.76 |
| Winter | | | | | | |
| Time period × turbine proximity | 5 | 137.32 | 0.00 | 0.51 | 0.51 | −63.11 |
| Turbine proximity | 3 | 137.54 | 0.22 | 0.45 | 0.96 | −65.56 |
| ln(turbine proximity) | 3 | 143.23 | 5.91 | 0.03 | 0.99 | −68.40 |
| Time period × ln(turbine proximity) | 5 | 145.13 | 7.81 | 0.01 | 1.00 | −67.02 |
| Null | 2 | 157.43 | 20.12 | 0.00 | 1.00 | −76.61 |
| Time period | 3 | 159.46 | 22.14 | 0.00 | 1.00 | −76.52 |

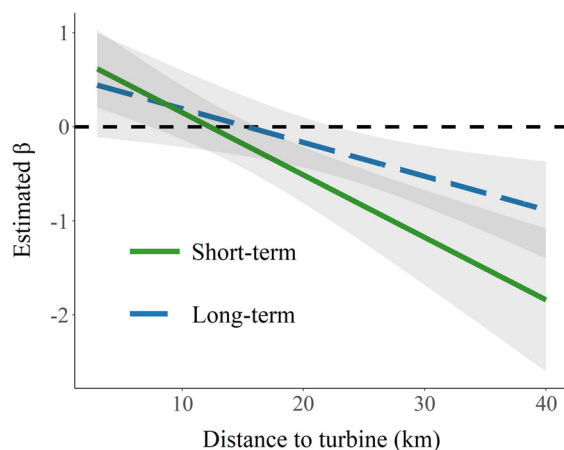

Fig. 7. Estimated winter selection coefficients (β) at the third order for pronghorn around the Dunlap wind-energy facility relative to time period (short-term, long-term) and the proximity of an individual's home range to wind turbines, south-central Wyoming, USA, 2010–2020.

America in that they have larger and more unpredictable movements than other ungulates (Kolar et al. 2011, Kauffman et al. 2018, Sawyer et al. 2019), which, combined with individual and environmental variation such as harsh winters, could make their responses to disturbance inconsistent across years and studies, complicating conservation and management strategies.

The annual differences in selection across years and the lack of population-level selection at finer scales across all individuals correspond with the mixed and variable responses previously documented for pronghorn in response to oil and gas development (Beckmann et al. 2012, Christie et al. 2017, Reinking et al. 2019), but are in marked contrast to the consistent and sustained avoidance of oil and gas development exhibited by other ungulates, including mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*; Sawyer et al. 2006, Sawyer et al. 2009, Buchanan et al. 2014, Northrup et al. 2015, Sawyer et al. 2017), and indicator species such as greater-sage grouse (*Centrocercus urophasianus*; Northrup and Wittemyer 2013, Kirol et al. 2020). Overall, the variable results across studies could be due to differences in the physical footprint of development, the habitat suitability of the site, or species-specific differences in behavior. Energy developments can vary in both the number and densities of wells or turbines and the amount of associated human activity, both of which have been shown to influence wildlife responses (Sawyer et al. 2009). Human activity is typically higher at oil and gas wells compared to wind turbines (Jones and Pejchar 2013, Taylor et al. 2016,

LeBeau et al. 2017), which could explain different responses to the two types of development. The development footprint and activity at existing wind-energy facilities could be low enough to make effects difficult to detect or only apparent at short distances, as suggested by the avoidance behavior only documented for individuals within 10 km of the Dunlap wind-energy facility. In addition, pronghorn near wind-energy facilities only avoided turbines under construction during the summer, which coincided with the peak of human activity. Development, particularly for existing and proposed wind-energy facilities, has also been concentrated in critical winter range for pronghorn and continued use of these high-quality areas by pronghorn may be due to a lack of suitable alternatives (Smith et al. 2020). Thus, while pronghorn appeared to select for turbines in some seasons and years, this was simply an artifact of the fact that turbines were initially installed in some of the highest quality winter range and does not suggest that turbines are improving habitat for pronghorn.

Perhaps more importantly, though, as shown by the inconsistent results across years and individuals in our study, pronghorn as a species are variable in their habitat selection behavior, which can lead to different results across studies, complicate population-level conclusions, and make it more difficult to detect development effects until a critical threshold of development has been reached. These findings highlight the need for multi-year studies with large sample sizes to capture annual and individual variation in behavior as done in this study. Relative to other ungulates in North America, pronghorn have much larger seasonal ranges and less predictable migrations, which can make it more difficult to detect a directional response to disturbance (Sawyer et al. 2005, 2019, Kolar et al. 2011). While some individuals and populations have consistent seasonal migrations (Sawyer et al. 2005, Jacques et al. 2009), pronghorn often have mixed migratory strategies and use facultative winter migrations to respond to severe environmental conditions (White et al. 2007, Kolar et al. 2011, Jakes et al. 2018). Compared to seasonal migrations of ungulates such as deer and elk, this variability, particularly the use of facultative migrations, is closer to the nomadism displayed by Mongolian gazelles

(*Procapra gutturosa*), which is related to broadscale landscape unpredictability (Olson et al. 2010, Mueller et al. 2011). These unpredictable movements can complicate inferences regarding both the effects of disturbance and appropriate conservation measures (Olson et al. 2010, Sawyer et al. 2019). In our study, pronghorn migrated up to 80 km away from wind-energy facilities in 3 yr during particularly harsh winters, which could have contributed to the annual variation we saw in habitat selection behavior, although the years in which animals migrated were not correlated with trends in home range selection relative to turbines. There was evidence for displacement during the three most recent summers and the most recent winter of the study, however, which could suggest either that effects are only apparent in the long-term after development or that effects only manifest after a certain threshold of development, such as with the construction of additional wind-energy facilities in our study. Overall, the ability of species to incorporate flexible movement strategies is important for individuals responding to both environmental change and anthropogenic disturbance. Elements of energy development, such as roads and fences, can be barriers to pronghorn movement (Jakes et al. 2018, Jones et al. 2019, Reinking et al. 2019, Xu et al. 2021) and can therefore affect habitat quality.

The avoidance behavior documented for individuals in close proximity to turbines in our study concurs with the only other study evaluating the effects of wind energy development on habitat selection by pronghorn, which evaluated habitat selection for individuals within 5 km of a wind-energy facility and found that pronghorn avoided turbines after development when selecting habitat within their winter home ranges (Smith et al. 2020). We also found evidence for avoidance during the summer, but only relative to turbines under construction, which was likely driven by the increase in human activity associated with construction. Although our work builds on data collected for that original study, we found more variable effects, particularly a lack of population-level selection within the home range for other habitat and anthropogenic variables. Smith et al. (2020) did not incorporate individual-level models when evaluating small-scale selection, which could explain differences

in results regarding fine-scale selection. It is well-documented that not accounting for individual variability can mask individual-level selection strategies and can lead to overconfident estimates of precision (Gillingham and Parker 2008, Schielzeth and Forstmeier 2009, Leclerc et al. 2016, Muff et al. 2019), which could explain the inconsistencies between studies at the third order. Given the amount of individual variation we found, we suggest that individual differences in behavior are strong drivers of population-level habitat selection and should be accounted for in future studies. Furthermore, Smith et al. (2020) only focused on responses to a single wind-energy facility, Dunlap, whereas we included all existing and under-construction wind-energy facilities in our analysis, so it is possible that we captured more landscape-scale responses to wind energy development.

While we found strong population-level selection for other habitat variables when choosing a home range, pronghorn exhibited high individual variability when selecting habitat within the home range that varied in both strength and direction, equating to a lack of population-level selection for any variable we evaluated. This does not suggest that the habitat variables were not important, but that their influence on individuals differed such that there were no strong patterns across all pronghorn. While previous studies have found evidence for small-scale habitat selection by pronghorn at the population level (Reinking et al. 2019, Smith et al. 2020), the majority did not evaluate individual-level models and so likely underestimated the amount of individual variation and overestimated precision for population-level estimates (Schielzeth and Forstmeier 2009). Research on habitat selection typically lumps inter-individual patterns, focusing on inferences at the population scale (Leclerc et al. 2016). However, if individual differences are correlated with fitness, they can have important ecological and evolutionary implications (Réale et al. 2010, Sih et al. 2012, Leclerc et al. 2016). Including behavioral variability is therefore important for studies of animal space use and habitat selection (Merrick and Koprowski 2017).

Behavioral variability can complicate conservation and management, however. Management by necessity focuses on population-level processes, but this is not always feasible, particularly when individuals respond differently to disturbance resulting in non-significant selection at the population level. Instead, management could focus on maintaining behavioral diversity in populations that do not exhibit clear population-level patterns. Research on a variety of taxa, including anadromous fish, migratory birds, and migratory ungulates, has found that a portfolio of varied life-history traits, such as multiple migratory strategies, can improve both population resilience and stability (Schindler et al. 2010, Gilroy et al. 2016, Lowrey et al. 2020). The amount of individual variation in habitat selection behavior suggests that some pronghorn were able to adapt to disturbance, whether through behavioral avoidance or because the disturbance did not represent a significant threat to that individual. However, the steady accumulation of increased disturbance, including roads, fences, wind turbines, and oil and gas wells, could reach a threshold at which consistent behavioral responses are apparent (Sawyer et al. 2020) and there may be additional effects, such as demographic consequences, that we were not able to evaluate in this study. Our system may be approaching such a threshold, because although our results suggest that small-scale avoidance behavior relative to wind-energy facilities has not changed in the long-term, there was a trend toward increased displacement at the home-range level during the study. Providing sufficient natural and heterogeneous habitat to support diversity in behavioral strategies could be an important goal of management to maintain stable populations, particularly for variable species such as pronghorn or where strong directional responses to disturbance are not apparent (Merrick and Koprowski 2017).

## Conclusions

Although the lack of consistent negative effects of wind turbines on pronghorn across years suggests that wind energy development may have less severe and more intermittent effects on pronghorn than oil and gas development has had on other ungulates, there was a trend toward increased displacement during the study and behavioral avoidance was apparent for

individuals near turbines. Knowledge of behavioral changes, such as altered habitat selection, is critical, because this is a primary way in which long-lived species are impacted by novel disturbances (Sawyer et al. 2009). However, the highly variable habitat selection and movement of pronghorn, across both individuals and years, may make effects of wind energy development difficult to detect. Some individuals, particularly those close to wind-energy facilities, did avoid turbines, which could translate to population-level behavioral or demographic changes over time and affect the resilience and stability of the population. In addition, our study focused on habitat selection during key seasonal time periods, but wind-energy development could affect ungulates during other time periods, such as migration, or have demographic consequences that may not manifest in behavioral changes. This complexity suggests that improved understanding would result if species responses to disturbances were monitored over the long-term and included both behavioral and demographic changes. Over time, the accumulation of development, including wind turbines, roads, and fences, can both limit movement and fragment habitat, potentially reaching a critical threshold beyond which populations are negatively impacted.

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## Data Availability Statement

Data are available from the USGS ScienceBase: https://doi.org/10.5066/P9YHHYKD

## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3850/full