Received: 27 November 2018 | Revised: 12 June 2019 | Accepted: 18 June 2019
DOI: 10.1111/csp2.83

Conservation Science and Practice Open Access
A journal of the Society for Conservation Biology
WILEY

CONTRIBUTED PAPER

Long-term effects of energy development on winter distribution and residency of pronghorn in the Greater Yellowstone Ecosystem

Hall Sawyer[1] | **Jon P. Beckmann**[2] | **Renee G. Seidler**[2] | **Joel Berger**[2,3]

[1]Western Ecosystems Technology, Inc., Laramie, Wyoming

[2]Wildlife Conservation Society, North America Program, Bozeman, Montana

[3]Fisheries, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado

Correspondece
Hall Sawyer, Western Ecosystems Technology, Inc., 200 South 2nd Street, Laramie, WY 82070.
Email: hsawyer@west-inc.com

Present address
Renee G. Seidler, Idaho Department of Fish and Game, 4279 Commerce Circle, Idaho Falls, ID 83401.

Funding information
National Geographic Society; Pinedale Anticline Project Office; Questar Corporation; Shell Exploration and Production Company

Abstract

An increasing global demand for energy assures continued disturbance to previously undeveloped landscapes, but understanding broader impacts to wildlife remains elusive. Among groups of species most vulnerable to habitat disruption are those requiring large tracts of land. Pronghorn (*Antilocapra americana*) are an obligate to the open plains and basins that, similar to other transcontinental large herbivores, rely primarily on habitats where development of energy resources such as oil, natural gas, coal, wind, and solar are intensifying. To understand behavioral response to a burgeoning energy development project, we evaluated avoidance, displacement, and winter residency patterns of pronghorn in the southern Greater Yellowstone Ecosystem across a 15-year period using 171 collared individuals. Distance from natural gas well pads increased through time and was concurrent with declines in winter residency. Between 2005 and 2017, we found that (a) pronghorn avoidance of well pads likely increased by 408 m, (b) the overall displacement of pronghorn relative to well pads in the final year of study increased by 800 m, (c) the time pronghorn spent in the study area was reduced by 22% (nearly 1 month), and (d) the percentage of pronghorn leaving the study area increased by 57%. Such directional changes signal a strong behavioral response of an open-plain obligate to energy infrastructure, and together, these metrics indicate that pronghorn response to energy development involves both avoidance of infrastructure and partial abandonment of their traditional winter ranges. While comparable long-term data sets are generally unavailable for other functionally equivalent ungulate groups in similar ecological topographies of Asia, Africa, and South America, our study may serve as a reasonable surrogate and highlights that behavioral changes elicited from energy development which at first appear subtle can proliferate and may portend demographic consequences.

KEYWORDS

Antilocapra americana, avoidance, disturbance, indirect habitat loss, winter range

1 | INTRODUCTION

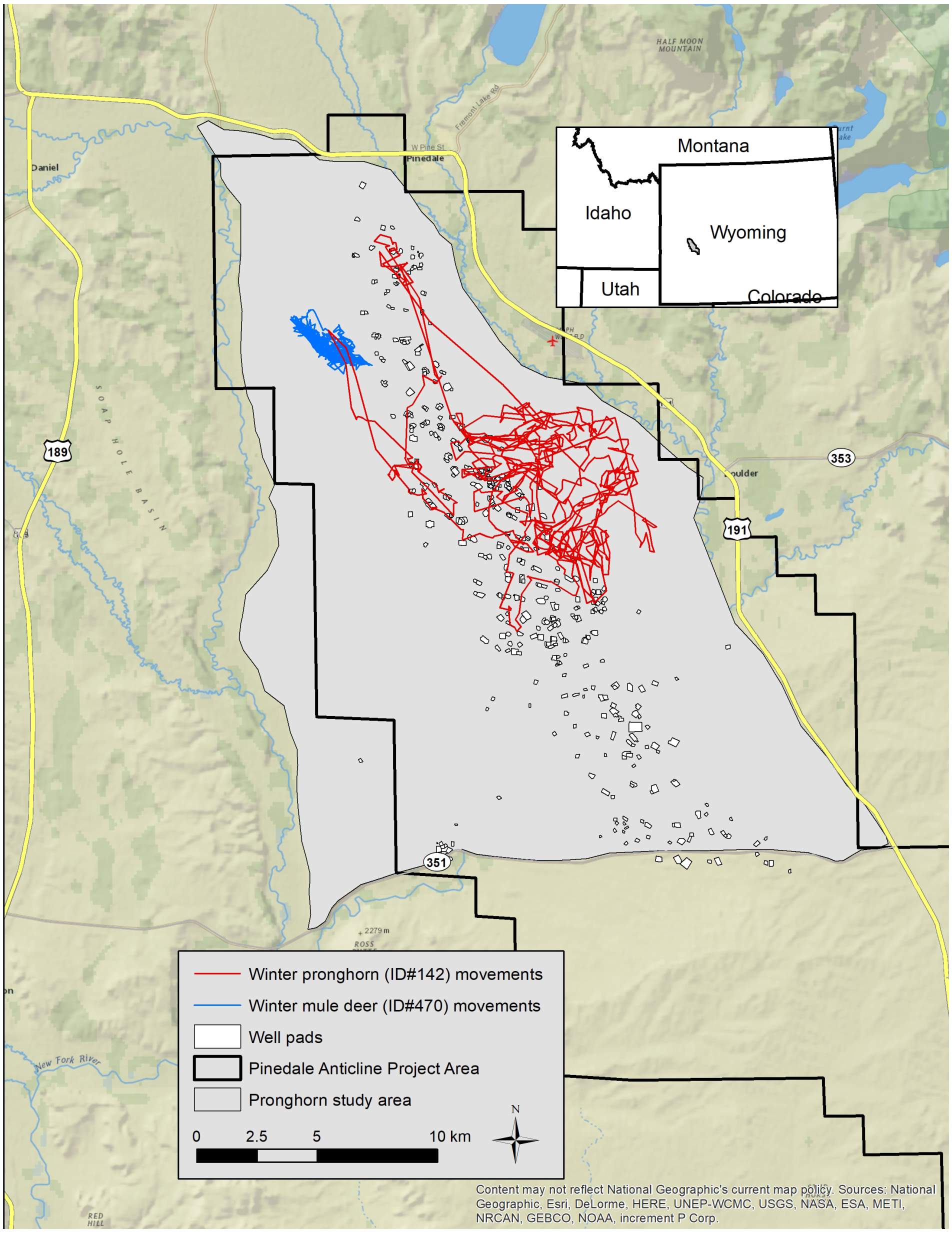
The world's energy needs continue to increase as human populations surge (Kiesecker & Naugle, 2017). From central Asia to Africa and from South to North America, grassland basins and deserts host both a wide array of wild herbivores and abundant energy resources (e.g., oil, natural gas, coal, wind, solar) that are more readily accessible than those situated in mountains or oceans. North America alone hosts an active fossil fuel program where some 50,000 oil and gas wells are added annually (Allred et al., 2015), many of which are located in the open habitats of the basins and plains (Copeland, Doherty, Naugle, Pocewicz, & Kiesecker, 2009). While industrial activities vary regionally and transcontinentally (Harfoot et al., 2018), data on potential impacts are lacking for most species, including such visibly notable species as Bactrian camels (*Camelus bactrianus*) to saiga antelope (*Saiga tatarica*), giraffes (*Giraffa camelopardalis*) to elephants (*Loxodonta africana*), and guanacos (*Lama guanicoe*) to pronghorn (*Antilocapra americana*)—all of which have expansive land requirements. For some ungulates and, more broadly, biological diversity (Canaday & Rivadeneyra, 2001; Harfoot et al., 2018; Suárez et al., 2009), the proliferation of roads associated with development has reduced the amount of habitat and, in some cases, the abundance of species through poaching patterns consistent from Patagonia to eastern Mongolia (Olson et al., 2011; Radovani, Funes, Walker, Gader, & Novaro, 2015). Regardless of geography, energy development projects typically comprise networks of roads and other infrastructure that contribute to habitat fragmentation and adverse effects to wildlife (Kiesecker & Naugle, 2017; Loomis & Haefele, 2017; Naugle, 2011).

Conservation planning requires detailed data on animal movements and behavioral changes associated with various forms of disturbance (e.g., fire, habitat loss, human development), especially with respect to the collapse of migratory ungulate populations (Berger, 2004; Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009). Here, we use 15 years of location data to document how the construction and expansion of a natural gas field in the southern Greater Yellowstone Ecosystem has affected North America's sole endemic living ungulate, the pronghorn. Pronghorn occupy the sagebrush (*Artemisia* spp.) and grassland basins of the Intermountain West—a region that has been dramatically affected by energy development in recent decades (Jones, Pejchar, & Kiesecker, 2015; Leu, Hanser, & Knick, 2008). Efforts to mitigate impacts of large-scale energy development on sagebrush-obligate wildlife have focused primarily on greater sage-grouse (*Centrocercus urophasianus*; Walker, Naugle, & Doherty, 2007; Doherty, Naugle, Walker, & Graham, 2008; Kirol, Beck, Uzurbazar, Holloran, & Miller, 2015) and mule deer (*Odcoileus hemionus*; Sawyer, Nielson, Lindzey, & McDonald, 2006; Sawyer, Korfanta, Nielson, Monteith, & Strickland, 2017; Northrup & Wittemyer, 2013; Lendrum, Anderson, Monteith, Jenks, & Bowyer, 2014; Northrup, Anderson, & Wittemyer, 2015), mainly because sage-grouse have been considered for listing under the Endangered Species Act, and mule deer represent one of the most popular and wide-ranging game species in North America. The concerted efforts around sage-grouse and mule deer have provided extensive knowledge on avoidance behavior, population-level impacts, and mitigation strategies for those species (Naugle, 2011; Northrup & Wittemyer, 2013; Sawyer et al., 2017). Less attention has been given to broad-scale energy development and habitat alteration at the interface of sagebrush habitats and pronghorn populations (Beckmann, Murray, Seidler, & Berger, 2012; Beckmann, Olson, Seidler, & Berger, 2016).

The few pronghorn-specific studies suggest that behavioral responses, such as avoidance, may be difficult to detect or in some cases, may not occur (Beckmann et al., 2012; Christie, Jensen, & Boyce, 2017; Christie, Jensen, Schmidt, & Boyce, 2015)—a sharp contrast from mule deer that show clear responses across regions (Northrup et al., 2015; Sawyer et al., 2006, 2017). For example, Beckmann et al. (2012) showed habitat patches with high levels of drilling activity were used less by pronghorn, but there was no clear relationship between pronghorn use and distance to energy infrastructure. Relatedly, another study in North Dakota found pronghorn avoided roads but not well pads (Christie et al., 2017), whereas Seidler, Long, Berger, Bergen, and Beckmann (2015) found that pronghorn avoided dense energy development during migratory periods. The detection of demographic responses of pronghorn to energy development has been even more challenging (Beckmann et al., 2016), but in North Dakota, population declines have been correlated with increased oil and gas development (Christie et al., 2015). Overall, the small number of studies and lack of long-term study commitment (Kretser, Beckmann, & Berger, 2018) has limited the ability of conservation planners and wildlife agencies to accommodate pronghorn in development plans and mitigation efforts because there is no clear consensus on how or if energy development affects pronghorn (Hebblewhite, 2011).

The study and conservation of species with nomadic or unpredictable movements is more challenging than for species with more static movements (Runge, Martin, Possingham, Willis, & Fuller, 2014), such as mule deer, for example, which travel the same routes and occupy the same confined ranges year after year (Garrott, White, Bartmann, Carpenter, & Alldredge, 1987; Sawyer et al., 2019). Such differences are apparent with mule deer and pronghorn populations in the southern portion of the Greater

Yellowstone Ecosystem (GYE), where mule deer tend to occupy relatively small (~5 km^2; Figure 1) winter ranges and return to them annually (Sawyer et al., 2019). When energy development encroaches on those areas, it is easy to measure and detect individual animals avoiding the developed portions of their winter range (Northrup et al., 2015; Sawyer et al., 2006; Sawyer, Kauffman, & Nielson, 2009). Pronghorn on the other hand, utilize a much larger swath of winter range habitats (~125 km^2; Figure 1) and move about often and unpredictably (Bruns, 1977; Collins, 2016; Kolar, Millspaugh, & Stillings, 2011; Sawyer, Lindzey, & McWhirter, 2005). Not surprisingly, it is more difficult to detect a directional behavioral response to infrastructure when animals are moving around a large area, rather than remaining confined to a smaller area; as highly mobile animals have inherently higher levels of movement variation compared to those that remain more stationary. The challenges associated with detecting behavioral changes in highly mobile species can be accentuated by short-term study, especially in regions prone to variable weather events and environmental conditions (e.g., Jakes et al., 2018). Furthermore, constraining or limiting analyses to political or administrative boundaries may not capture the spatial scale at which some types of behavioral changes are evident. For example, the amount of time that mobile species such as pronghorn spend outside a politically defined project area may, in some cases, provide a useful metric to detect broad-scale behavioral changes concurrent with land-use changes that occur inside the project area, such as energy development.



Content may not reflect National Geographic's current map policy. Sources: National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, increment P Corp.

FIGURE 1 Study area and well pad development relative to the Pinedale anticline project area in western Wyoming, USA. Mule deer #470 and pronghorn#142 data from winter of 2015–2016 illustrate how pronghorn tend to move around larger areas during winter compared with mule deer

We used location data collected from 171 individuals spanning 2 years before and 13 years during development to examine the winter distribution and residency patterns of pronghorn relative to an expanding natural gas project. We annually measured distance to nearest well pad as a metric of avoidance *inside* the project area and evaluated two simple but complementary metrics of residency that captured animal movements *outside* the project area, including the average amount of time animals spent outside of the study area and the percentage of marked animals that left the study area each year. An interpretation of these metrics is as follows. A finding of no change suggests winter distribution and residency patterns remain consistent throughout increasing large-scale energy development. In contrast, an increase in distance from well pad through time is indicative of avoidance behavior, whereas a decrease in the amount of time animals spent in the project area, combined with an increase in the number of animals leaving the project area, indicate lower winter residency rates. While we focus on a North American example, our results emphasize that a longer temporal lens (> 10 yrs) can reveal changes in animal movement and behavior that would otherwise be obscured—a lesson applicable to species and continents beyond North America.

2 | METHODS

2.1 | Study area

Our study area was located inside the Pinedale Anticline Project Area (PAPA) (42.755°N, −109.861°W) of western Wyoming (Figure 1), an area that encompasses the southern extent of the GYE and supports thousands of pronghorn, some of which migrate 160+ km to Grand Teton National Park (Berger, 2004; Berger, Cain, & Berger, 2006; Sawyer et al., 2005). The PAPA is the largest natural gas field in the GYE and encompasses approximately 800 km^2 of high-elevation (2,072–2,370 m) sagebrush (*Artemisia* sp.) and sagebrush-grasslands administered mostly by the Bureau of Land Management (BLM 2000; Figure 1). The BLM approved development of 700 producing well pads, 645 km of pipeline, and 444 km of access roads in July of 2000 (BLM, 2000); most construction did not begin until 2001. An additional 4,400 wells were approved for development in 2008 (BLM, 2008; Figure 2). Winter disturbance included a mix of access roads, active drilling operations, and producing wells. Although some drilling was allowed during winter (Sawyer et al., 2017), the majority of well pads that pronghorn were exposed to during winter months contained wells that were in production phase (Figure 2). Compared with drilling well pads, the lower levels of human activity and traffic at producing well pads tend to have less disturbance on ungulates (Sawyer et al., 2009). The footprint of active wells, access roads and other infrastructure expanded annually over the study period. The PAPA has been designated as crucial pronghorn winter range for more than 50 years (Beckmann et al., 2012) and supports an estimated 1,500–3,000 individuals (Sawyer et al., 2005). Our analysis was restricted to 550 km^2 of the northern half of the PAPA, where GPS monitoring of pronghorn was focused (Figure 1).

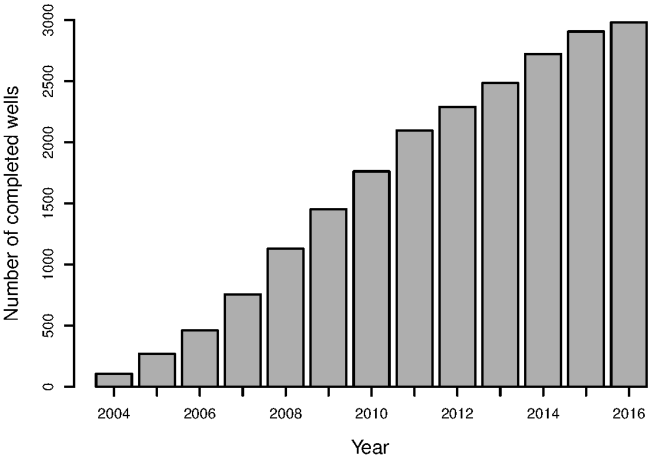


FIGURE 2 Cumulative number of natural gas wells drilled and completed in the Pinedale anticline project area in western Wyoming, USA, 2004–2016. For each winter, pronghorn were exposed to wells drilled in the prior summer

2.2 | Capture and data collection

We collected location data on pronghorn 2 years before development and for 13 consecutive years during development. For the development phase, we used helicopter net-gunning to capture adult (≥1.5 years of age) female pronghorn on winter ranges in the PAPA. We attempted to sample pronghorn in proportion to their abundance, as determined by a pre-capture survey. We captured 150 pronghorn in the study area between December 2005 and March 2016. All pronghorn were equipped with GPS collars (ATS, Isanti, Minnesota and Telonics, Mesa, Arizona) that collected locations every 2–3 hr for 1–2 years. We restricted analyses to animals that collected data for at least 30 days. Overall, we collected 146,432 winter locations inside the study area from 142 individuals across 13 winters, beginning in 2005 and ending in 2017. Fix success of GPS collars was >99% precluding fix-rate or other bias introduced by missing locations (Frair et al., 2010).

We collected pre-development data from 35 pronghorn that were captured with the same methodology during the summer of 1998 in Grand Teton National Park (Sawyer et al., 2005). Unlike the development-phase animals that were equipped with modern GPS collars, we marked these pronghorn with traditional VHF collars (ATS) that were located approximately once per month using aerial telemetry. We note that aerial locations of VHF collars are not as accurate as those from GPS collars, but typically have locational errors within 100 m (Carrel, Ockenfels, Wennerlund, & Devos, 1997; Leptich, Beck, & Beaver, 1994). Overall, we collected 130 winter locations inside the study area from 29 individuals during winters of 1999 and 2000, before energy development.

2.3 | Distance to well pad analysis

In the context of wildlife and energy development, it is often presumed, without evidence, that animals quickly habituate to infrastructure once the construction phase is complete (Sawyer et al., 2017). Habituation assumes that disturbance associated with development elicits a behavioral response (i.e., avoidance) in animals that, after some time, recedes as animals return to using habitats as they did before development. To detect whether pronghorn actually avoided infrastructure, we calculated the mean distance of individuals to the nearest well pad each year. We used well pads as a proxy for energy infrastructure, because they strongly influence winter habitat use of other ungulates and represent the source of most gas-field disturbance (Northrup et al., 2015; Sawyer et al., 2006, 2009). We restricted distance to well pad calculations to pronghorn locations *inside* the study area during winter, defined as December 01 to March 31. For each animal during each winter, we calculated the average distance to nearest well pad and then averaged across animals to estimate a sample mean for each winter, thereby accounting for potential unequal sample sizes in GPS locations and ensuring the animal was correctly treated as the experimental unit (Otis & White, 1999). Annual sample sizes ranged from 9 to 29, with a mean of 17 (Table 1). This analysis was necessarily restricted to development phase data, where we used the mean distance to well pad metric in a linear regression analysis to evaluate trend and generate predictions over the 13 years of development. The difference in predicted values between development year 1 (2005) and 13 (2017) was used to determine whether avoidance increased through time.

We recognized that this analysis may indicate whether avoidance of well pads changed through time, but it does not reveal whether the observed distances in year 1 (2005) were due to avoidance or simply reflect where animals already were prior to development (e.g., 500 m from well pads). To address this shortcoming and quantify long term changes in displacement, we ran a similar analysis, but calculated distance to the well pads present in the last year of study (2017), rather than at the time of observation. While this may seem counter-intuitive, it allows a direct test of the null hypothesis that pronghorn distribution did not change through time; and, importantly, it allows pre-development data to be compared with post-development data (Sawyer et al., 2017). In other words, if animals do not avoid, or are not displaced by well pads, then they should be distributed at similar distances from the 2017 infrastructure, regardless

TABLE 1 Sample sizes of marked pronghorn, mean distance to well pads, average amount of time spent in study area, and percentage of animals that left the study area during each winter, before (1999–2000) and during (2005–2017) energy development in western Wyoming, USA

Winter	*n*	Mean distance to well pad (m) in each year	Mean distance to well pad (m) in 2017	Time (%) in study area	Exit (%) study area
1999	29	NA	798	NA	7%
2000	25	NA	949	NA	4%
2005	18	864	525	96%	17%
2006	9	1,130	877	100%	0%
2007	16	1,889	1,603	88%	37%
2008	17	1,636	1,472	87%	41%
2009	14	1,163	1,012	98%	21%
2010	14	692	630	99%	14%
2011	15	1,596	1,529	95%	6%
2012	15	1,416	1,406	87%	53%
2013	16	1,717	1,688	68%	75%
2014	17	1,556	1,529	86%	35%
2015	16	1,234	1,476	84%	50%
2016	19	1,674	1,658	87%	58%
2017	16	1,613	1,596	70%	81%

of the year. A change in distribution can then be quantified as the difference (m) between well pad metrics calculated in the first year of study and last. Specifically, we used the mean distance to well pad metric in a linear regression analysis to evaluate trends and generate predictions over the 13 years of development, where predicted values between development year 1 and 13 was used to determine changes in displacement. Pre-development data were used as a baseline reference, but excluded from regression analyses because of a 4-year gap between pre-development and development data collection periods (Table 1).

2.4 | Winter residency metrics

We used two independent but complementary metrics to evaluate winter residency of pronghorn. First, we calculated the amount of time that each marked animal spent inside the study area during winter. We averaged this metric across animals to estimate a sample mean for each winter, which we then plotted across the 13 years of development and used as a response variable in a linear regression model to evaluate trend. This metric could not be calculated for the two pre-development years because VHF data were not collected frequently enough to accurately determine time spent in study area. Our second metric calculated the percentage of GPS-collared animals that spent at least 1 day outside of the study area each winter. Although VHF data were limited to monthly locations, we calculated this metric for pre-development years to provide comparison to later years. The percentage of animals leaving the study area each year during development was also used as the response variable in a linear regression model to detect long-term trends. Together, these two metrics provide a clear measure of winter residency through time by quantifying the amount of time spent inside the study area, as well as the percentage of animals leaving the study area.

3 | RESULTS

3.1 | Distance to well pad analysis

Consistent with avoidance behavior, point estimates showed the mean distance to well pad was 750 m larger in 2017 (1,614 m) compared with 2005 (864 m; Table 1). The more conservative regression analysis indicated the mean distance to nearest well pad increased through the 13-year development period (*Distance to well pad* = 1,092 + 34[*year*], r^2 = 0.14, *p* = .211; Table 1, Figure 3) by approximately 34 m per year. In this regression setting, the two-sided *p*-value of .211 provided 78% confidence that the slope was positive. The difference between the predicted distance to well pad in 2005 (1,195 m) and 2017 (1,603 m) suggest avoidance increased by 408 m. Similarly, the regression analysis using only the 2017 infrastructure was concordant with the prior analyses which indicated the mean distance to nearest well pad increased through the 13-year development period (*Distance to well pad* = 708 + 66[*year*], r^2 = 0.36, *p* = .017; Table 1, Figure 4) by approximately 66 m per year. The difference between the predicted distance to well pad in 2005 (908 m) and 2017 (1,708 m) suggest pronghorn were displaced by 800 m during the study period. The predicted distance of 908 m in 2005 was consistent with the average distance of 941 m observed in pre-development years (Table 1, Figure 4).

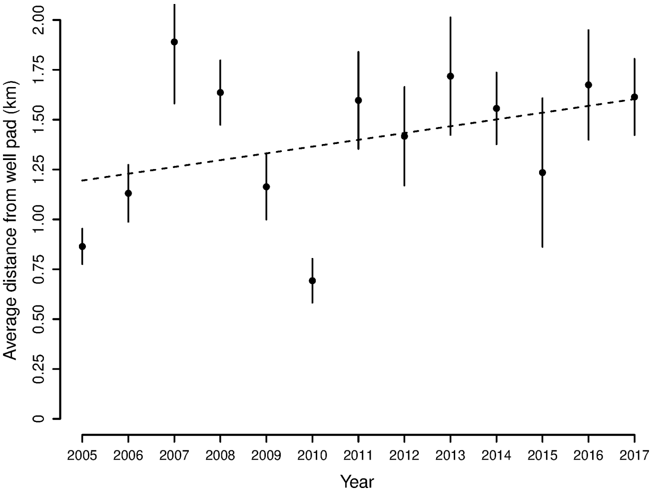


FIGURE 3 Mean distance (±*SE*) from well pad of radio-collared pronghorn during natural gas development (2005–2017) in the Pinedale anticline project area, Wyoming. Dashed line represents fitted regression line that shows a 408 m increase in distance to nearest well pad over the 13-year development period

3.2 | Winter residency metrics

Regression analysis indicated that the average amount of time pronghorn spent inside the study area decreased by 1.7% each year and 22% across the 13-year development period (*time* = 1.00–0.017[*year*], r^2 = 0.39, *p* = .01; Table 1, Figure 5). Concurrently, the percentage of pronghorn that left the study area during each winter increased by 4.7% each year, totaling 57% across the study period (*proportion* = 0.046 + 0.047[*year*], r^2 = 0.47, *p* = .005; Table 1, Figure 5). The predicted 9% of animals leaving the study area in 2005 was consistent with the 6% estimated in pre-development years (Figure 5).

4 | DISCUSSION

The human footprint of energy development and its associated losses in ecosystem services and biodiversity are

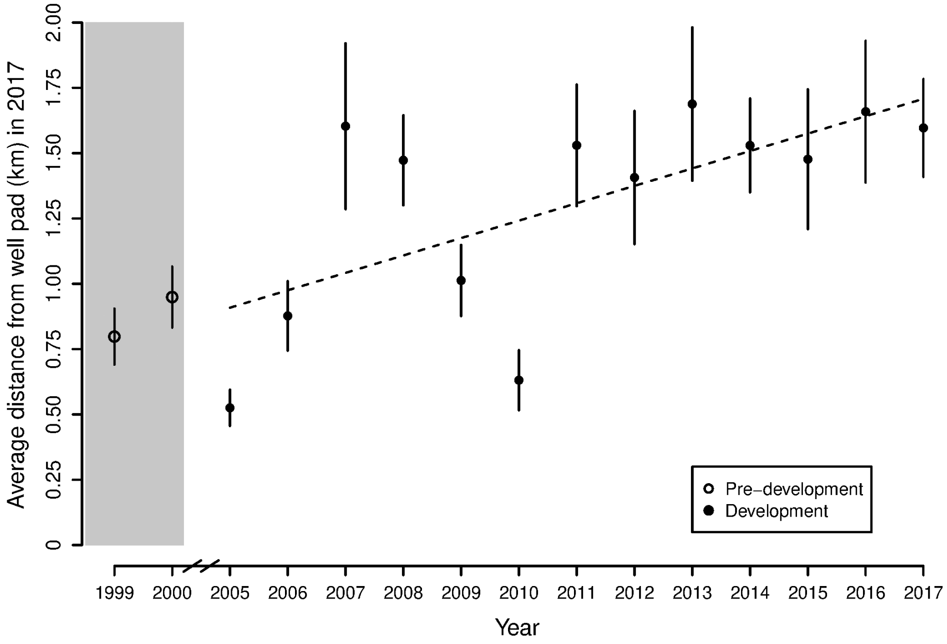


FIGURE 4 Mean distance (±*SE*) from well pads in 2017 of radio-collared pronghorn before (1999–2000) and during (2005–2017) natural gas development in the Pinedale anticline project area, Wyoming, USA. Dashed line represents fitted regression line that shows an 800 m change in distribution over the 13-year development period

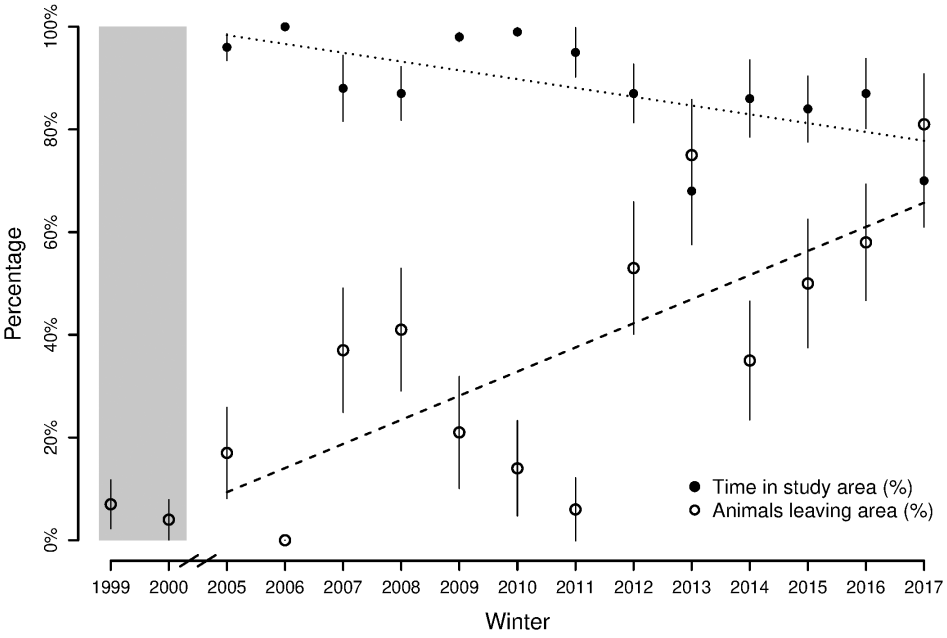


FIGURE 5 Percent time (±*SE*) that radio-collared pronghorn spent inside (solid circles) the study area and associated regression line (dotted line) shows a 22% decrease over the 13-year development period, 2005–2017. The percentage (±*SE*) of marked pronghorn that left the study area (open circles) and associated regression line (dashed line) shows a 57% increase over the 13-year development period, 2005–2017

expected to intensify, as global energy demand is predicted to increase 65% by 2050 (Kiesecker & Naugle, 2017). Conserving highly mobile species in the face of widespread development is especially challenging because their movements tend to be broader and less predictable than other species (Mueller et al., 2011; Runge et al., 2014). In the absence of long-term data and especially on fine-scale movements, it may not be possible to discern how landscapes are used nor the effects of various types of disturbance. Our 15-year study showed that pronghorn avoidance and displacement from well pads increased through time and revealed a significant decline in winter residency rates concurrent with large-scale natural gas development in the GYE. Between 2005 and 2017 pronghorn avoidance of well pads increased by 408 m and their overall displacement from well pads increased by 800 m. Concurrently, the amount of time pronghorn spent in our 550 km^2 study area declined by 22%, and the proportion of pronghorn leaving the study area increased by 57%. Together these four independent metrics provide strong evidence that pronghorn response to energy development involves avoidance of infrastructure and partial abandonment of their traditional winter ranges.

In contrast to mule deer that consistently avoided well pads throughout the development period in this same study area (Sawyer et al., 2017), pronghorn avoidance appeared to be intermittent until 2011, after which they regularly used areas increasingly distant from well pads compared to earlier years (Figure 3). The consistent avoidance after 2011 suggests a disturbance or risk threshold was exceeded and altered pronghorn behavior. We note, however, that unlike the mule deer research that collected data prior to and during all years of development (Sawyer et al., 2017), our study of pronghorn did not collect data during the first 4 years of development (2001–2004). Certainly the collection of pronghorn movement data through all years of development would strengthen inferences on pronghorn distribution and behavior during the initial years of development. Nonetheless, our 13-years of consecutive data captured 91% of drilling activity (i.e., completed wells) and habitat disturbance associated with this energy project, including an infill plan (i.e., expansion of originally proposed drilling plans) approved in 2008 that increased the number of allowed wells from 700 to 4,400 (BLM 2008). Furthermore, our 2 years of pre-development data, although limited by VHF technology, provided baseline estimates of avoidance and winter residency metrics that were consistent with regression trends revealed from our 13 years of development data.

The predicted distance from nearest well pad in our displacement analysis increased from 908 m in 2005 to 1,708 m in 2017 and presumably led to indirect habitat losses much larger than habitat lost directly to infrastructure (Ciuti et al., 2012; Nellemann & Cameron, 1998; Northrup et al., 2015). Avoidance or displacement can diminish the amount of habitat available to pronghorn (sensu Nellemann, Vistnes, Jordhøy, Strand, & Newton, 2003) and, absent habitat improvements to offset such losses, less habitat equates to fewer animals on the landscape. The impacts of reduced habitat availability on pronghorn are of particular concern in Wyoming, a state that hosts more than half of North America's 800,000 remaining pronghorn (Kauffman et al., 2018).

At broader scales, indirect habitat loss resulting from long-term avoidance or displacement is concerning because of reductions in available habitat (Beckmann et al., 2012; Northrup et al., 2015) and subsequent links to population declines (Sawyer et al., 2017). Of additional concern here, were the diminishing winter residency rates of pronghorn through time, where individuals spent greater amounts of time outside of the study area (i.e., traditional winter range) and a higher proportion of individuals left the study area during winter. It is unclear whether pronghorn abandoning their traditional winter range for 22%, or 26 days, of the winter results in a net habitat loss or increase in energy expenditure, or if it is a behavioral response that allows them to access other high-quality habitat that can offset the direct and indirect habitat losses incurred from energy development. However, given the amount and extent of energy development in the surrounding areas (BLM 1998, 2000, 2018), we suspect that any remaining high-quality habitats not impacted by development are already occupied by other pronghorn and any sort of emigration to these areas would result in competition with conspecifics. In short, it seems unlikely that thousands of pronghorn from our study area could benefit from spending 22% less time in their traditional winter range by seeking out alternative habitat. Rather, given that animals tend to select high-quality habitats (Stephens & Krebs, 1986), combined with the role of cultural transmission in ungulate movements (Couzin, 2018; Jesmer et al., 2018), it seems more likely that displacement of pronghorn from traditional winter range reflects a lower carrying capacity that, in turn, may prompt pronghorn to vacate the area in search of alternative ranges.

Ideally, the consequences of pronghorn avoidance and lower winter residency rates associated with energy development could be measured in terms of demography. Unfortunately, measuring and detecting demographic responses of pronghorn populations can be especially difficult because of their mobility (Runge et al., 2014) and fluctuating densities (Beckmann et al., 2016). Nonetheless, observed behavioral responses to infrastructure have been predicted as a precursor to changes in demography (Beckmann et al., 2012). While there were no demographic metrics collected for marked pronghorn in our study area throughout the entire 13-year development period, the Wyoming Game and Fish Department (WGFD) annually estimated pronghorn abundance for the larger Sublette herd unit that includes our study area and most of the Green River Basin. Those estimates suggest pronghorn declined by 47% between 2005 (est. 57,600) and 2017 (est. 36,000; WGFD 2016), concurrent with widespread natural gas development in the Jonah and Pinedale Anticline gas fields (BLM 1998, 2000, 2008). Relatedly, Christie et al. (2015) found pronghorn declines during the last 10 years of a 30-year study were associated with oil and gas development and a series of severe winters. Certainly, severe winters contributed to population declines documented in the southern GYE by WGFD, but our pronghorn avoidance and winter residency metrics did not appear to be driven by winter severity alone, as evidenced by consistent temporal trends in both metrics, regardless of variable winter conditions that included two severe (2011, 2017), seven average (1999, 2000, 2005, 2006, 2013, 2014, 2016), and six mild (2007, 2008, 2009, 2010, 2012, 2015) winters (Sawyer et al., 2017).

Whether in Wyoming and Colorado, Mongolia or Kazakhstan, Patagonia or Southern Sudan, a wide array of functionally equivalent ungulates occupy seasonal environments where various forms of energy development are converting native habitats to infrastructure. Few regions of the globe remain unaffected by the exploration and production of the next fuel or electron. Although the open plains and basins, and the large herbivores they support, are at particular risk to development and associated effects, little is known about how such species respond to broad-scale disturbance. Yet such information is vital for conservation action and land-use planning to ensure population persistence for species like pronghorn. Regardless of taxa, human disturbance tends to reduce animal movements – behaviors that can broadly affect species persistence and ecosystem function (Tucker et al., 2018). Our work demonstrates that pronghorn in the southern GYE changed behavior in response to energy development by avoiding infrastructure and abandoning their traditional winter range for nearly a quarter of the winter. While the demographic consequences remain unclear, we suggest that such behavioral changes be viewed as cautionary because they could signal broader effects on pronghorn abundance and viability in the GYE.

ACKNOWLEDGMENTS

Pronghorn collaring studies were funded by Shell Exploration and Production Company, Questar Corporation, Ultra Resources, Inc., and the Pinedale Anticline Project Office. We thank the Bureau of Land Management and Wyoming Game and Fish Department for logistical support. Quicksilver Aviation and Native Range provided safe and efficient capture services. The Wildlife Conservation Society helped support this study. H.S. received support for this project from the National Geographic Society.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

H.S. conceived the ideas and designed methodology; all authors collected the data; H.S. and R.G.S. analyzed the data; H.S. led writing of manuscript; all authors reviewed, edited, and approved the final manuscript.

DATA ACCESSIBILITY

All summarized data presented in Table 1. GPS location data are available through the Wyoming Game and Fish Department's Movebank.org portal at https://www.movebank.org/node/124178 or the Wyoming Migration Initiative Data Viewer at https://migrationinitiative.org/dataviewer.

ETHICS STATEMENT

Ethical clearances were not required for this study, however all animals were captured following protocols consistent with the University of Wyoming Institutional Animal Care and Use Committee and recommendations of the American Society of Mammalogists (Sikes et al., 2011).

ARTICLE IMPACT STATEMENT

Pronghorn response to energy development involves avoidance of infrastructure and partial abandonment of their traditional winter ranges.

ORCID

Hall Sawyer https://orcid.org/0000-0002-3789-7558
Jon P. Beckmann https://orcid.org/0000-0002-4406-7667

REFERENCES

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.

Beckmann, J. P., Murray, K., Seidler, R. G., & Berger, J. (2012). Human-mediated shifts in animal habitat use: Sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. *Biological Conservation*, *147*, 222–233.

Beckmann, J. P., Olson, S. H., Seidler, R. G., & Berger, J. (2016). Sub-lethal effects of energy development on a migratory mammal-the enigma of North American pronghorn. *Global Ecology and Conservation*, *6*, 36–47.

Berger, J. (2004). The last mile: How to sustain long-distance migration in mammals. *Conservation Biology*, *18*, 320–331.

Berger, J., Cain, S. L., & Berger, K. M. (2006). Connecting the dots: An invariant migration corridor links the Holocene to the present. *Biology Letters*, *2*, 528–531.

Bruns, E. H. (1977). Winter behavior of pronghorns in relation to habitat. *Journal of Wildlife Management*, *41*, 560–571.

Bureau of Land Management. (1998). *Jonah Field II Natural Gas Development Project - Record of Decision*. Rock Springs, WY: Rock Springs District Office.

Bureau of Land Management. (2000). *Pinedale Anticline Natural Gas Field Exploration and Development Project - Record of Decision* (BLM/WY/PL-00/026+1310). Pinedale, WY: Pinedale Field Office.

Bureau of Land Management. (2008). *Final Supplemental Environmental Impact Statement for the Pinedale Anticline Oil and Gas Exploration and Development Project - Record of Decision* (BLM/WY/PL-08/029+1310). Pinedale, WY: Pinedale Field Office.

Bureau of Land Management. (2018). *Normally Pressured Lance Natural Gas Development Project - Record of Decision* (BLM/WY/PL-18/011+1310). Pinedale, WY: Pinedale Field Office.

Canaday, C., & Rivadeneyra, J. (2001). Initial effects of a petroleum operation on Amazonian birds: Terrestrial insectivores retreat. *Biodiversity and Conservation*, *10*, 567–595.

Carrel, W. K., Ockenfels, R. A., Wennerlund, J. A., & Devos, J. C. (1997). Topographic mapping, Loran-C, and GPS accuracy for aerial telemetry locations. *Journal of Wildlife Management*, *61*, 1406–1412.

Christie, K. S., Jensen, W. F., & Boyce, M. S. (2017). Pronghorn resource selection and habitat fragmentation in North Dakota. *Journal of Wildlife Management*, *81*, 154–162.

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. *Biological Conservation*, *192*, 445–453.

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS One*, *7*, e50611.

Collins, G. H. (2016). Seasonal distribution and routes of pronghorn in the northern Great Basin. *Western North American Naturalist*, *76*, 101–112.

Copeland, H. E., Doherty, K. E., Naugle, D. E., Pocewicz, A., & Kiesecker, J. M. (2009). Mapping oil and gas development potential in the US intermountain west and estimating impacts to species. *PLoS One*, *4*, 1–7.

Couzin, I. D. (2018). Collective animal migration. *Current Biology*, *28*, R952–R1008.

Doherty, K. E., Naugle, D. E., Walker, B. L., & Graham, J. M. (2008). Greater Sage-Grouse winter habitat selection and energy development. *Journal of Wildlife Management*, *72*, 187–195.

Frair, J. L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N. J., & Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2187–2200.

Garrott, R. A., White, G. C., Bartmann, R. M., Carpenter, L. H., & Alldredge, A. W. (1987). Movements of female mule deer in northwest Colorado. *Source: The Journal of Wildlife Management*, *51*, 634–643.

Harfoot, M. B. J., Tittensor, D. P., Knight, S., Arnell, A. P., Blyth, S., Brooks, S., … Burgess, N. D. (2018). Present and future biodiversity risks from fossil fuel exploitation. *Conservation Letters*, *11*, e12448.

Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P. G. M., & Berger, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, *7*, 55–76.

Hebblewhite, M. (2011). Effects of energy development on ungulates. In D. E. Naugle (Ed.), *Energy development and wildlife conservation in western North America* (pp. 71–94). Washington, DC: Island Press.

Jakes, A. F., Gates, C. C., Decesare, N. J., Jones, P. F., Goldberg, J. F., Kunkel, K. E., & Hebblewhite, M. (2018). Classifying the migration behaviors of pronghorn on their northern range. *Journal of Wildlife Management*, *82*, 1229–1242.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., … Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, *361*, 1023–1025.

Jones, N. F., Pejchar, L., & Kiesecker, J. M. (2015). The energy footprint: How oil, natural gas, and wind energy affect land for biodiversity and the flow of ecosystem services. *Bioscience*, *65*, 290–301.

Kauffman, M. J., Meachum, J. E., Sawyer, H., Steingisser, A. Y., Rudd, W. J., & Ostlind, E. (2018). *Wild migrations: Atlas of Wyoming's ungulates*. Corvallis, OR: Oregon State University Press.

Kiesecker, J. M., & Naugle, D. E. (2017). *Energy sprawl solutions: Balancing global development and conservation. Page energy sprawl solutions: Balancing global development and conservation*. Washington, DC: Island Press.

Kirol, C. P., Beck, J. L., Uzurbazar, S. V., Holloran, M. J., & Miller, S. N. (2015). Identifying Greater Sage-Grouse source and sink habitats for conservation planning in an energy development landscape. *Ecological Applications*, *25*, 968–990.

Kolar, J. L., Millspaugh, J. J., & Stillings, B. A. (2011). Migration patterns of pronghorn in southwestern North Dakota. *Journal of Wildlife Management*, *75*, 198–203.

Kretser, H. E., Beckmann, J. P., & Berger, J. (2018). A retrospective assessment of a failed collaborative process in conservation. *Environmental Management*, *62*, 415–428.

Lendrum, P. E., Anderson, C. R., Monteith, K. L., Jenks, J. A., & Bowyer, R. T. (2014). Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. *Mammalian Biology*, *79*, 369–375.

Leptich, D. J., Beck, D. G., & Beaver, D. E. (1994). Aircraft-based LORAN-C and GPS accuracy for wildlife research on inland study sites. *Wildlife Society Bulletin*, *22*, 561–565.

Leu, M., Hanser, S. E., & Knick, S. T. (2008). The human footprint in the west: A large-scale analysis of anthropogenic impacts. *Ecological Applications*, *18*, 1119–1139.

Loomis, J., & Haefele, M. (2017). Quantifying market and non-market benefits and costs of hydraulic fracturing in the United States: A summary of the literature. *Ecological Economics*, *138*, 160–167.

Mueller, T., Olson, K. A., Dressler, G., Leimgruber, P., Fuller, T. K., Nicolson, C., … Fagan, W. F. (2011). How landscape dynamics link individual- to population-level movement patterns: A multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*, *20*, 683–694.

Naugle, D. E. (2011). *Energy development and wildlife conservation in western North America*. Washington, DC: Island Press.

Nellemann, C., & Cameron, R. D. (1998). Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. *Canadian Journal of Zoology*, *76*, 1425–1430.

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., & Newton, A. (2003). Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological Conservation*, *113*, 307–317.

Northrup, J. M., Anderson, C. R., & Wittemyer, G. (2015). Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. *Global Change Biology*, *21*, 3961–3970.

Northrup, J. M., & Wittemyer, G. (2013). Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters*, *16*, 112–125.

Olson, K. A., Mueller, T., Kerby, J. T., Bolortsetseg, S., Leimgruber, P., Nicolson, C. R., & Fuller, T. K. (2011). Death by a thousand huts? Effects of household presence on density and distribution of Mongolian gazelles. *Conservation Letters*, *4*, 304–312.

Otis, D. L., & White, G. C. (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management*, *63*, 1039–1044.

Radovani, N. I., Funes, M. C., Walker, R. S., Gader, R., & Novaro, A. J. (2015). Guanaco *Lama guanicoe* numbers plummet in an area subject to poaching from oil-exploration trails in Patagonia. *Oryx*, *49*, 42–50.

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G., & Fuller, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment*, *12*, 395–402.

Sawyer, H., Kauffman, M. J., & Nielson, R. M. (2009). Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, *73*, 1052–1061.

Sawyer, H., Korfanta, N. M., Nielson, R. M., Monteith, K. L., & Strickland, D. (2017). Mule deer and energy development—Long-term trends of habituation and abundance. *Global Change Biology*, *23*, 4521–4529.

Sawyer, H., Lindzey, F., & McWhirter, D. (2005). Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin*, *33*, 1266–1273.

Sawyer, H., Merkle, J. A., Middleton, A. D., Dwinnell, S. P. H., & Monteith, K. L. (2019). Migratory plasticity is not ubiquitous among large herbivores. *Journal of Animal Ecology*, *88*, 450–460.

Sawyer, H., Nielson, R. M., Lindzey, F., & McDonald, L. L. (2006). Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management*, *70*, 396–403.

Seidler, R. G., Long, R. A., Berger, J., Bergen, S., & Beckmann, J. P. (2015). Identifying impediments to long-distance mammal migrations. *Conservation Biology*, *29*, 99–109.

Sikes, R. S., Gannon, W. L., & The Animal Care and Use Committee of the American Society of Mammalogists. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, *92*, 809–823.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.

Suárez, E., Morales, M., Cueva, R., Bucheli, U. V., Zapata-Ríos, G., Toral, E., … Olalla, V. J. (2009). Oil industry, wild meat trade and roads: Indirect effects of oil extraction activities in a protected area in North-Eastern Ecuador. *Animal Conservation*, *12*, 364–373.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., van Moorter, B., Alberts, S. C., … Mueller, T. (2018). Moving in the anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*, 466–469.

Walker, B. L., Naugle, D. E., & Doherty, K. E. (2007). Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management*, *71*, 2644–2654.

Wyoming Game and Fish Department. (2016). *Job Completion Report.* Cheyenne, WY: Green River Region.

How to cite this article: Sawyer H, Beckmann JP, Seidler RG, Berger J. Long-term effects of energy development on winter distribution and residency of pronghorn in the Greater Yellowstone Ecosystem. *Conservation Science and Practice*. 2019;1:e83. https://doi.org/10.1111/csp2.83