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Mule deer and energy development—Long-term trends of habituation and abundance

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Abstract
As the extent and intensity of energy development in North America increases, so do disturbances to wildlife and the habitats they rely upon. Impacts to mule deer are of particular concern because some of the largest gas fields in the USA overlap critical winter ranges. Short-term studies of 2–3 years have shown that mule deer and other ungulates avoid energy infrastructure; however, there remains a common perception that ungulates habituate to energy development, and thus, the potential for a demographic effect is low. We used telemetry data from 187 individual deer across a 17-year period, including 2 years predevelopment and 15 years during development, to determine whether mule deer habituated to natural gas development and if their response to disturbance varied with winter severity. Concurrently, we measured abundance of mule deer to indirectly link behavior with demography. Mule deer consistently avoided energy infrastructure through the 15-year period of development and used habitats that were an average of 913 m further from well pads compared with predevelopment patterns of habitat use. Even during the last 3 years of study, when most wells were in production and reclamation efforts underway, mule deer remained >1 km away from well pads. The magnitude of avoidance behavior, however, was mediated by winter severity, where aversion to well pads decreased as winter severity increased. Mule deer abundance declined by 36% during the development period, despite aggressive onsite mitigation efforts (e.g. directional drilling and liquid gathering systems) and a 45% reduction in deer harvest. Our results indicate behavioral effects of energy development on mule deer are long term and may affect population abundance by displacing animals and thereby functionally reducing the amount of available habitat.

KEYWORDS
avoidance behavior, disturbance, indirect habitat loss, land-use planning, mitigation

1 | INTRODUCTION

Habitat loss and fragmentation are among the most influential factors affecting species distribution and population viability (Fahrig, 2003; Hethcoat & Chalfoun, 2015; Sih, Ferrari, & Harris, 2011). Worldwide, energy development projects are quickly converting native habitats into roads, well pads, pipelines, wind turbines, solar installations and other infrastructure associated with energy production (Leu, Hanser, & Knick, 2008; Rabanal, Kuehl, Mundry, Robbins, & Boesch, 2010; Sih et al., 2011; Walston et al., 2009). The increased rate and extent of energy development is especially evident in western North America (Copeland, Doherty, Naugle, Pocewicz, & Kiesecker, 2009), where advances in drilling technology and regulatory incentives for reducing carbon dioxide emissions have accelerated development of natural gas and renewable energy (McDonald, Fargione, Kiesecker, Miller, & Powell, 2009). Given the spatial extent of current and anticipated future energy development, it is important to understand how energy development affects the distribution and abundance of wildlife to find effective mitigation strategies (Northrup & Wittemyer, 2013) and provide empirical information to aid stakeholders in evaluating the trade-offs associated with large-scale energy development.

Numerous studies have documented ungulates modifying their behavior (i.e. displacement) in response to energy development (Dyer, O'Neill, Wasel, & Boutin, 2001; Nellemann, Vistnes, Jordhøy, Strand, & Newton, 2003; Cameron, Smith, White, & Griffith, 2005; Sawyer, Nielson, Lindzey, & McDonald, 2006; Sawyer, Kauffman, & Nielson, 2009; Lendrum, Anderson, Long, Kie, & Bowyer, 2012; Skarin, Nellemann, Ronnegard, Sandstrom, & Lundqvuist, 2015; Wilson, Parrett, Joly, & Dau, 2016), but the duration of those behavioral responses and their implications for demography are not well established. There remains a common perception that ungulates eventually adapt to altered landscapes and acclimate to energy infrastructure. For example, environmental impact assessments required by the National Environmental Policy Act (NEPA) frequently assume that displacement of ungulates by natural gas development is short term and restricted to the drilling phase, but once a project transitions to the production phase, behavioral impacts attenuate or cease (BLM, 2005, 2006, 2012). Nevertheless, the assumed habituation to energy infrastructure has yet to be tested—a critical piece of information for predicting the effects of development and implementing effective mitigation. If animals habituate to disturbance, then the potential that short-term behavioral responses (e.g. increased vigilance or infrastructure avoidance) translate into fitness consequences is low. Conversely, if animals do not habituate or habituation is delayed for many years, we would expect fitness and population viability to decrease, especially when the disturbance occurs in spatially restricted habitat (sensu Schmitz, Krivan, & Ovadia, 2004) as is common for mule deer winter ranges.

With 17 years of population monitoring, including pre- and post-development data, we had a unique opportunity to investigate whether mule deer—an iconic and economically valuable species in western North America—habituate to development, while simultaneously monitoring population trends in association with expanding energy development. Our study system in western Wyoming, USA, was conducive to this type of long-term effort for several reasons. First, with the exception of several exploratory wells and one access road, the area was mostly pristine before natural gas development (BLM, 2000). Second, mule deer in the region are migratory and only occupy the gas field during winter months (Sawyer, Lindzey, & McWhirter, 2005) when they are concentrated and easy to count. Third, mule deer show strong fidelity to seasonal ranges (Garrott, White, Bartmann, Carpenter, & Alldredge, 1987; Northrup, Anderson, & Wittemyer, 2016), making them a model species for studying habituation. And lastly, winter conditions in our study area varied across years, allowing us to examine how or if behavioral responses were influenced by environmental conditions.

Previous work in this area documented avoidance of well pads by mule deer during the first 3 years of development (Sawyer et al., 2006), and later indicated that the degree of avoidance was influenced by the amount of human activity at well pads (Sawyer et al., 2009). Our goal was to build on that understanding by determining whether mule deer habituate to disturbance through time by reducing or ceasing avoidance behavior. We used >260,000 global position system (GPS) locations collected from 187 deer before, during, and after development to determine whether distance from infrastructure decreased with time, and whether avoidance behavior was related to winter severity (Parker, Robbins, & Hanley, 1984; Robinson & Merrill, 2012), as declining forage availability and animal condition during severe winters may overwhelm risk aversion as individuals seek limited forage (McNamara & Houston, 1987). We concurrently measured abundance of mule deer, with comparison to a broader geographic region to provide an indirect link between observed behavioral changes (i.e. avoidance or habituation), demography, and energy development. Understanding how or whether mule deer habituate to energy development, and how such behavioral responses might influence the trajectory of those populations, has important management and conservation implications that can help inform future planning.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was situated in the northern half of a large natural gas field in the Upper Green River Basin of western Wyoming (42.755°N, −109.861°W) referred to as the Pinedale Anticline (Bureau of Land Management [BLM], 2000). Our study area was a ~264 km^2 of mule deer winter range characterized by high-elevation (2,072–2,370 m) sagebrush (*Artemisia* sp.) and sagebrush grasslands (Figure 1; Sawyer et al., 2006). Thousands of mule deer from summer ranges in four different mountain ranges annually migrate 30–130 km to winter in this portion of the Pinedale Anticline (Sawyer et al., 2005).

The Pinedale Anticline comprises mostly federal lands (85%) administered by the Bureau of Land Management. Before 2001, this area was relatively undisturbed, with few roads and minimal human activity (Sawyer et al., 2009; Walston, Cantwell, & Krummel, 2009). In July of 2000, the BLM approved development of 700 producing well pads, 645 km of pipeline, and 444 km of access roads in the Pinedale Anticline (BLM, 2000). Most construction activities began in 2001 and the BLM approved an additional 4,400 wells for development in 2008 (BLM, 2008). We defined the predevelopment phase as 1998–2000 and the development phase as 2001 through 2015.

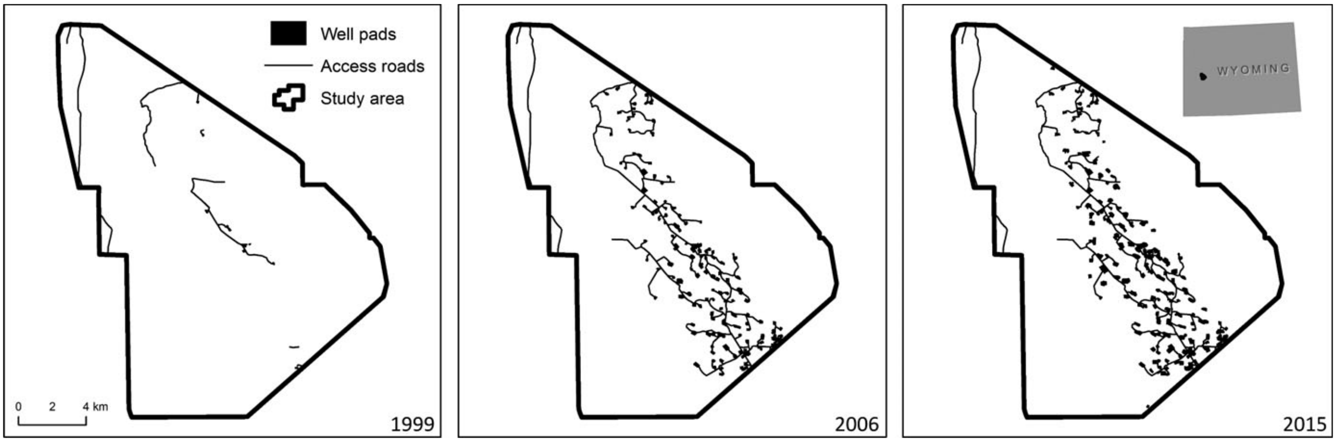

FIGURE 1 Access roads and well pads within the winter range for mule deer on the Pinedale Anticline in western Wyoming, USA, 1999–2015

The development phase included active drilling operations in some locations and production with reduced human activity and ongoing reclamation efforts in other locations. Drilling was limited to 1–6 active rigs on the northern half of the study area during most winters. The majority of well pads that mule deer were exposed to during winter months contained wells that were completed and producing natural gas.

The estimated 5,200 mule deer that wintered on the Pinedale Anticline when the study began were hunted from mid-September through the first week of October, while they still occupied their mountain summer ranges. In response to declining deer numbers observed during the study period, the Wyoming Game and Fish Department implemented several management changes aimed at increasing mule deer abundance, including shortening the hunting season by approximately 1 week and reducing the number of nonresident licenses by 50%. Overall, mule deer harvest decreased gradually through the study period and by 2015, both male (n = 1,861) and female (n = 115) harvest were ~45% less than harvest levels during 2000 (Wyoming Game and Fish Department, 2015).

2.2 | Deer capture and data collection

We used helicopter net-gunning to capture adult (≥1.5 years of age) female deer on winter range. We attempted to sample deer in proportion to their abundance, as determined by a precapture survey. All mule deer 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 & Gannon, 2011). We radio-collared 93 animals before gas development, between February 1998 and December 2000. Of those, 79 were equipped with very high-frequency (VHF) collars (Advanced Telemetry Systems, Isanti, Minnesota, USA) that were located by ground telemetry every 10–14 days throughout the winter. The remaining 14 collars were global positioning system (GPS) collars (Telonics, Mesa, AZ, USA) programmed to collect locations every eight hours for one winter. Although 93 animals were captured before development, we restricted our analysis to those with a minimum of 20 locations (n = 23; 8 GPS and 15 VHF) collected between 1 December and 31 March.

We captured another 183 animals during the development phase (2001 through 2015) and equipped them with GPS collars (Telonics) that collected locations every two hours. Here, we restricted our analysis to animals with a minimum of 100 GPS locations (n = 164) to ensure each animal collected at least one week of location data. Overall, we collected 1,739 winter locations from 23 individuals during the predevelopment phase, and 262,991 locations from 164 animals during the development phase. Fix success of GPS collars was >99% precluding fix rate or other bias introduced by missing locations (Frair et al., 2010).

2.3 | Direct habitat loss

We calculated direct habitat loss as acres of sagebrush and grassland converted to energy infrastructure each year. We used ARCGIS (Environmental Systems Research Institute, Redlands, CA, USA) to digitize roads and well pads, the main forms of infrastructure on the Pinedale Anticline, from satellite images (Spot Image Corporation, Chantilly, VA, USA) collected in early autumn each year after annual construction activities were complete but before snow accumulation. We based acreage estimates associated with roads on an average road width of 10 m.

2.4 | Habituation

When applied to mule deer and energy development, habituation assumes that disturbance associated with energy development elicits a behavioral response (i.e. avoidance) in animals that, after some time, gradually erodes or dissipates. We tested whether mule deer decreased their average distance from infrastructure through time, which would provide evidence of habituation. We used well pads as a proxy for energy infrastructure, because they strongly influence winter habitat use of mule deer (Northrup, Anderson, & Wittemyer, 2015; Sawyer et al., 2006, 2009). Rather than use well-pad infrastructure from each year, we based our analysis of avoidance of infrastructure on well pads that were present the last year of study in 2015. Doing so allowed us to directly test the null hypothesis that deer distribution has not changed through time. Specifically, if animals habituate to development (i.e. show attenuated avoidance), then they should be distributed a similar distance from the 2015 infrastructure, regardless of the year. Moreover, if initial displacement occurs but animals habituate thereafter, then average distance from the 2015 infrastructure may initially rise but should eventually decrease to predevelopment levels.

For each animal during each winter, we calculated the average distance to nearest well pad based on the 2015 infrastructure, making an individual deer the sample unit. We then averaged across animals within each year to estimate a sample mean for each winter before (1999–2000) and during (2001–2015) development. We used a standard two-sample *t* test ($\alpha = 0.10$) to determine whether the mean distances of deer from nearest well pad each year differed between predevelopment and development (2001–2015) years. Recognizing that animals may not habituate during the first several years following disturbance (e.g. Sawyer et al., 2006, 2009), we also tested for differences between the mean distance to well pads before development (1999–2000) and the last 3 years of the study (2013–2015), which included wells mostly in production.

To evaluate effects of winter snowpack on distribution of mule deer (Parker et al., 1984; Robinson & Merrill, 2012), we also categorized each winter as mild, average or severe based on snow cover observed during early- (December) and late-winter (February) helicopter surveys. In addition to snow cover, we also noted snow depths at capture sites in December and across the study area during aerial surveys in February. Mild winters (2002, 2006–2009, 2011, 2014) were characterized by large patches (>50% of study area) of open ground where sagebrush was entirely exposed. Average winters (1998–2001, 2004–2005, 2012–2013, 2015) had continuous snow cover, but snow depths did not bury sagebrush. In contrast, severe winters (2003, 2010) had complete snow coverage that buried sagebrush so that shrubs were not visible in >50% of the study area. We pooled animals based on categories of winter severity and used 95% confidence intervals to evaluate whether winter severity influenced the distance to well pads.

2.5 | Abundance

We estimated abundance of mule deer using helicopter counts of animals in a random sample of 2.59-km^2 quadrats (Freddy et al., 2004). Each year, we conducted counts in February when winter snowpack concentrated animals on winter range and improved visibility. The same observer (HS) conducted every year of the survey. Quadrats covered 25% ($n = 18$) of the study area in 2001, 50% ($n = 34$) from 2002 through 2010, and 68% ($n = 46$) 2011 through 2015. The number of quadrats was increased in 2002 and 2010 to improve precision of estimates.

For each quadrat, a real-time flight path was traced into a GPS and once the perimeter of the quadrat was established, all animals within the quadrat were counted. We recognize that group size and vegetative cover may influence probability of detection (Samuel, Garton, Schlegel, & Carson, 1987), but we did not correct for potential visibility bias because detection rates are generally high in open habitats (Freddy et al., 2004) and obtaining a minimum count was sufficient for the purposes of our study. We used abundance and variance estimators based on equal-sized sampling units and a simple random sample (Thompson, White, & Gowan, 1998). We assessed for a temporal trend in abundance using least-squares regression, weighted by the inverse of the standard error in each annual estimate, thereby assigning more weight to years with estimates of greater confidence. To complement the regression analysis, we also calculated the percent change in abundance based on point estimates from 2001 and 2015.

To compare abundance of mule deer on the Pinedale Anticline with regional population trends, we used abundance estimates from the Wyoming Game and Fish Department for the entire Sublette Herd Unit—a 15,792 km^2 area that encompasses the Pinedale Anticline. The WGFD used a model-based approach developed by White and Lubow (2002) that considers several key demographic parameters, including adult survival, recruitment, sex and age composition, and harvest statistics (Morrison, 2012) to calculate abundance. Importantly, other mule deer winter ranges in the Sublette Herd Unit were not affected by energy development.

3 | RESULTS

3.1 | Direct habitat loss

Well pad and road construction resulted in direct habitat loss to mule deer winter range of approximately 2,360 acres (9.5 km^2), or 3.5% of the study area (Figure 2). Well pads accounted for 88% of direct habitat loss, whereas roads contributed 12%. Direct habitat loss increased steadily through the first 10 years of development followed by an asymptote during the remaining 5 years.

3.2 | Habituation

Avoidance behavior was variable, but did not decrease with time through the development phase; in all but 3 years, mule deer occupied areas further away from well pads during the development phase than predevelopment (Figure 3). Overall, during the development phase, mule deer were 913 m further from well pads (2,187 ± 108 m, mean ± *SE*) compared with mule deer before (1,274 ± 196 m, mean ± *SE*) development (Figure 4; $t_{36.97} = -4.08$, $p < .001$). Similarly, mule deer from the last three years of development were 1.38 km further from well pads (2,655 ± 278 m) compared with mule deer before development (Figure 4, $t_{42.32} = -4.05$, $p < .001$).

Mule deer response to well pads was inversely related to winter severity. Avoidance decreased during severe winters; however,

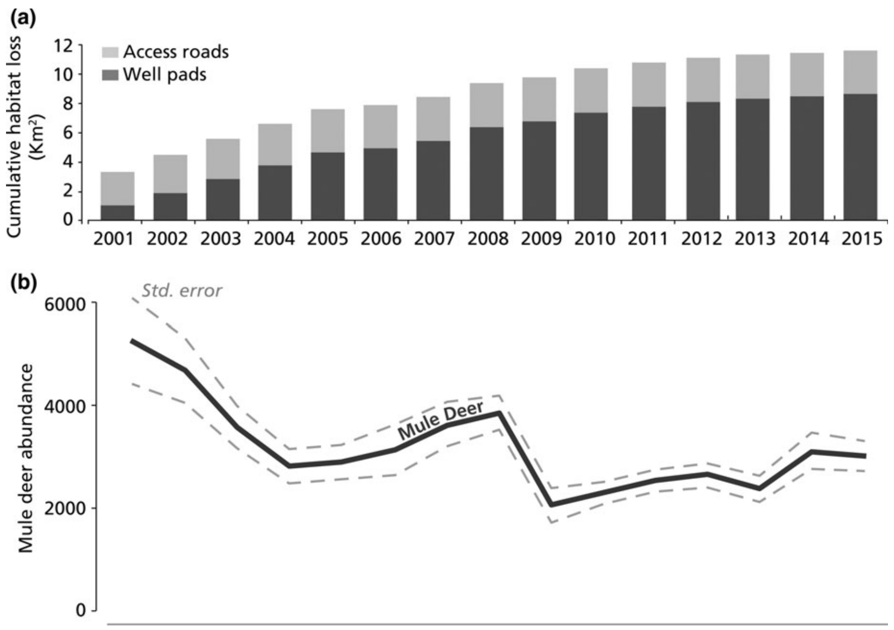

FIGURE 2 Direct habitat loss associated with access roads and well pads (a) and annual estimates ($\pm SE$) of abundance of mule deer (b) in the Pinedale Anticline, Wyoming, 2001–2015

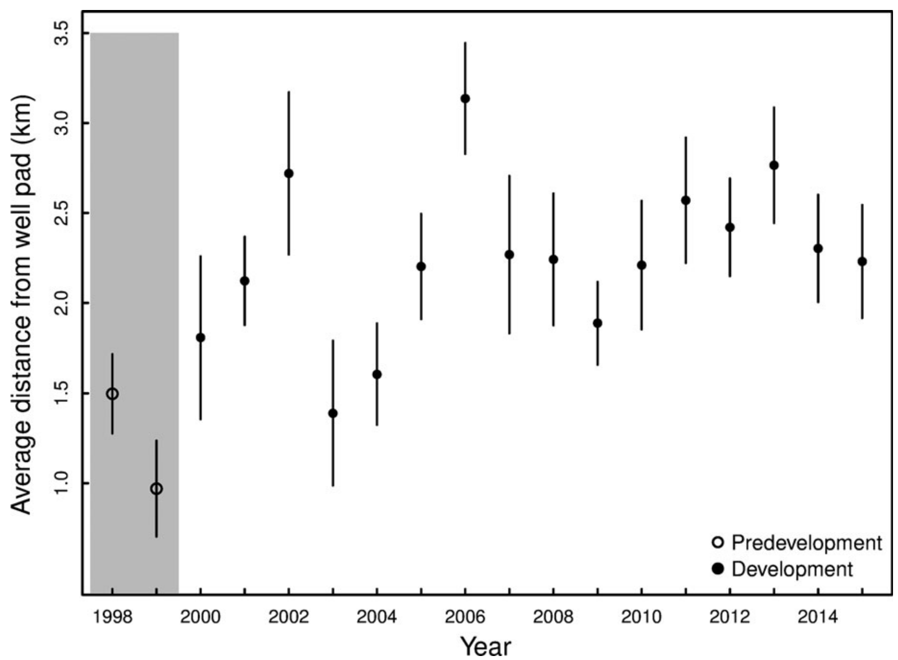

FIGURE 3 Average distance ($\pm SE$) to nearest well pad of radio-collared mule deer (n = 187) before and during natural gas development in the Pinedale Anticline, Wyoming, USA, 1998–2015

proximity to well pads was still lower during the years before development, both of which were average winters (based on 95% CIs). Aversion to well pads ranged from 2,418 ± 148 m during mild winters to 2,118 ± 134 m in average winters and 1,858 ± 273 m during severe winters (Figure 5).

3.3 | Abundance

Based on regression analysis, mule deer abundance on the Pinedale Anticline declined by 36% over the 15-year development period (*Abundance* = 3,834 – 95 [*year*], r^2 = .299, p = .034; Figure 2). Concurrently, population estimates for the Sublette herd unit declined by 16% (*Abundance* = 28,464 – 338 [*year*], r^2 = .171, p = .07). Based on point estimates alone, the Pinedale Anticline declined by 42% between 2001 and 2015, whereas the Sublette herd declined by 9% (Table 1).

4 | DISCUSSION

Following fifteen years of natural gas development in western Wyoming, mule deer did not habituate to disturbance and continued to avoid energy infrastructure. Even during the last 3 years of development when most wells were in production and well pads were in various states of reclamation, we found no evidence of habituation. Instead, mule deer used areas that averaged nearly 1 km further

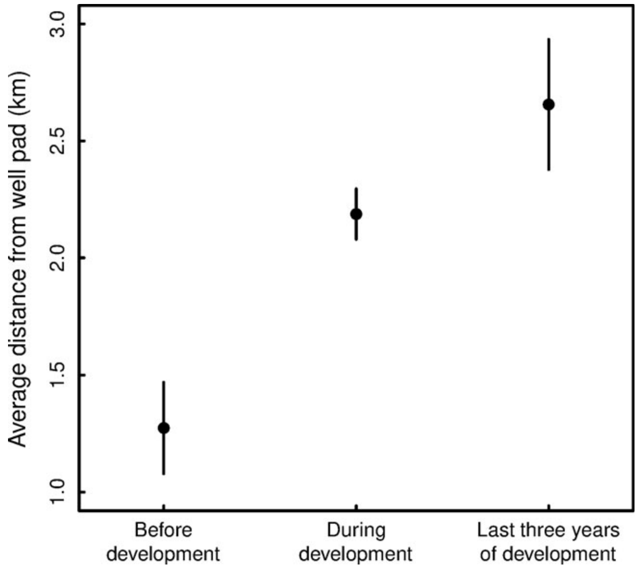

FIGURE 4 Average distance (±*SE*) to nearest well pad of mule deer (n = 187) before development (1998–1999), during all years of development (2000–2015), and the last 3 years of development (2013–2015)

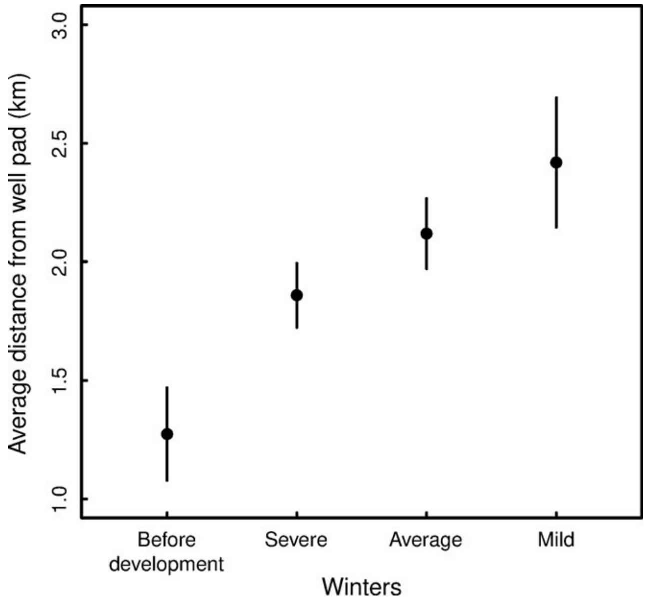

FIGURE 5 Average distance (±*SE*) to nearest well pad of radio-collared mule deer (n = 187) before development (1998–1999) compared with years of development (2000–2015) during severe (n = 2), average (n = 7), and mild (n = 6) winters

TABLE 1 Mule deer abundance estimates and standard errors for study area in Pinedale Anticline and the larger Sublette Herd Unit, 2001–2015

Winter	Pinedale anticline		Sublette herd unit	
Year	Estimate	*SE*	Estimate	*SE*
2001–02	5,228	820	32,011	n/a
2002–03	4,676	614	28,881	n/a
2003–04	3,564	395	29,670	n/a
2004–05	2,818	325	24,115	n/a
2005–06	2,894	311	24,215	n/a
2006–07	3,156	470	24,699	n/a
2007–08	3,638	424	27,200	n/a
2008–09	3,850	322	26,732	n/a
2009–10	2,088	325	24,630	n/a
2010–11	2,318	212	23,426	n/a
2011–12	2,553	210	20,652	n/a
2012–13	2,652	220	21,969	n/a
2013–14	2,405	243	22,900	n/a
2014–15	3,121	325	26,337	n/a
2015–16	3,030	266	28,976	n/a

from well pads compared with animals before development occurred. Although avoidance behavior of mule deer was consistent through the study period, the magnitude of avoidance was mediated by winter severity. Assuming nutritional condition of mule deer deteriorates with winter severity, such an outcome is consistent with theoretical (Frid & Dill, 2002; Lima & Dill, 1990) and empirical (Beale & Monaghan, 2004; Brown & Kotler, 2004) predictions of response to predation risk. Animals in poor condition should be less risk averse in their behavior, thereby favoring energetic gain and forgoing risk avoidance, whereas animals in good condition can afford to be more risk averse (Houston, McNamara, & Hutchinson, 1993; McNamara & Houston, 1986). We hypothesize that mild winters increased foraging opportunities and better maintained nutritional condition, whereas decreased access to forage and increased energy expenditures during severe winters diminished body condition and limited ability of mule deer to modify behavior in response to disturbance. Moreover, reduced use of forage near infrastructure may well have resulted in unused, but available forage for individuals willing to venture close to the perceived risk—a hypothesis that warrants testing. Regardless of the underlying mechanism, such plasticity in behavioral avoidance to winter severity highlights the importance of long-term studies, to ensure animal response is measured across a variety of environmental conditions (Monteith et al., 2014). For example, had our data from the development phase included only 2 years that were both severe winters, we would have incorrectly concluded that mule deer habituated to well pads.

Long-term avoidance behavior is problematic because indirect habitat loss reduces the size of winter range available for mule deer —habitat that would otherwise be used is functionally unavailable to the animals that occupy the range (Korfanta, Mobley, & Burke, 2015; Northrup et al., 2015; Sawyer et al., 2006). Winter range for temperate ungulates is often geographically restricted, particularly in migratory herds, so that habitat loss cannot be offset by simple range expansion. Thus, when habitat is lost directly through conversion to infrastructure and additionally through behavioral avoidance, carrying capacity is also reduced. Although it may be possible to improve the quality of winter range in areas with longer growing seasons or where tree removal can promote new shrub growth (e.g.

Bergman, Doherty, White, & Freddy, 2015), few viable options exist for improving winter ranges that are semi-arid at high elevation and dominated by sagebrush (Korfanta et al., 2015). Notwithstanding range expansion or habitat improvement to offset habitat loss, we would expect population size to decline through density-dependent mechanisms (sensu Bartmann, White, & Carpenter, 1992; Bowyer, Bleich, Stewart, Whiting, & Monteith, 2014).

Indeed, mule deer on the Pinedale Anticline decreased by 36% following 15 years of natural gas development and persistent avoidance of infrastructure. This decline occurred despite a series of mostly mild and average winters across the 17-year study period and a 45% reduction in harvest intended to bolster mule deer numbers (Wyoming Game and Fish Department, 2015). Although our results are consistent with a population decline caused by indirect habitat loss and ensuing density dependence, the observed population decline could alternatively be explained by: (1) widespread mule deer declines across a larger region; or (2) emigration of mule deer from the study area to avoid disturbance. Nevertheless, abundance estimates from the Sublette herd unit declined by only 16% during the same period—a decline that largely may have been caused by trends on the Pinedale Anticline, which was included within the Sublette herd unit. Likewise, emigration was an unlikely explanation for population decline as <2% (n = 3) of the 183 mule deer captured in the PAPA switched winter ranges during the course of study. Mule deer show strong fidelity to their seasonal ranges (Garrott et al., 1987; Monteith et al., 2014), so it is not surprising that mule deer did not abandon their range, even in response to novel disturbance (Northrup et al., 2016). Directly linking behavioral changes to demography in large terrestrial systems is challenging because true experimentation with replication and controls is rarely feasible. Nonetheless, our study suggests that measurable demographic consequences can be expected with large-scale energy development when native habitats are converted to infrastructure that animals avoid. We note that such effects could be lessened in regions where rugged topography and vegetation structure provide refugia and allow deer to mediate avoidance behavior (Northrup et al., 2015).

Because habituation occurs at the individual level (Bejder, Samuels, Whitehead, Finn, & Allen, 2009), the ideal study design would follow the same animals through the entire study period. In our instance, the length of study far exceeded the average lifespan (10 years) of a mule deer. In lieu of collecting longitudinal data from the same individuals for 17 years, our sampling of new animals each year with GPS collars that functioned 1–3 years provided annual snapshots of how the deer population used winter range relative to development. As the original population from 1998 senesced, the proportion of deer in the population that were born into a disturbed landscape gradually increased so that all or most animals alive from 2008 through 2015 wintered among gas development for their entire life. Population turnover, combined with long-term behavioral responses, indicates an inability of individuals, across generations, to habituate to gas development even if they have been exposed to infrastructure their entire lives.

Our findings contradict many NEPA documents (e.g. Environmental Impact Statements, Environmental Assessments) that guide federal land use on millions of acres in the western USA and consider natural gas development a short-term impact to which animals can readily habituate once drilling activities are complete (e.g. BLM, 2005, 2006, 2012). We understand that a paucity of data on the long-term impacts of development likely led to this type of conclusion in the NEPA process. However, our long-term dataset comprising multiple generations of animals indicates that avoidance of energy infrastructure is a long-term effect that can be associated with significant population declines.

Energy development planning on federal land seeks to avoid negative effects on wildlife populations through best management practices and mitigation measures (see Northrup et al., 2013), as in our study area where onsite mitigation included: (1) installation of a pipeline liquids gathering system that substantially reduced truck traffic and other human activities (Sawyer et al., 2009); (2) drilling of multiple wells (up to 24) from a single pad to minimize direct habitat loss; and (3) an innovative mitigation fund that financed fence modifications, water development, conservation easements, and other projects. Onsite mitigation efforts effectively reduced the amount of human disturbance and habitat loss (Sawyer et al., 2009) and may have lessened avoidance and averted an even larger population decline. Nonetheless, the remaining population-level effects were considerable and not fully offset through mitigation or best management practices.

Our work has important implications for applying the mitigation hierarchy (Council on Environmental Quality, 2000), which seeks to reduce negative effects of development by sequentially avoiding, minimizing, and offsetting impacts. First, effective mitigation seeks to match the mitigation activity with the duration of the impact (Council on Environmental Quality, 2000). Our study indicates that impacts of energy development in sagebrush steppe can be long term, if not permanent, and mitigation measures should be accordingly long term. Second, minimizing impacts through onsite mitigation, although desirable for species that exhibit high site fidelity, may not be possible. Onsite mitigation was insufficient to abate behavioral and demographic consequences to mule deer during our study. Third, given the limitations of onsite mitigation, avoidance of impacts by strategically foregoing leasing or reducing intensity of development of critical habitats is likely the most effective approach to averting population-level impacts. And finally, where avoidance and minimization are not possible or effective, offsite mitigation approaches such as biodiversity offsets or conservation banks that aim to compensate for biological impacts in one area with protected or improved habitat elsewhere (Bull, Suttle, Gordon, Singh, & Milner-Gulland, 2013; Carroll, Fox, & Bayon, 2008) are untested but warrant consideration.

Our results are consistent with a growing body of work illustrating the behavioral effects of human disturbance on ungulates (Beckman, Murray, Seidler, & Berger, 2012; Ciuti et al., 2012; Johnson & Russell, 2014; Northrup et al., 2015) and the links between broad-scale development and demographic consequences (Cameron et al., 2005; Christie, Jensen, Schmidt, & Boyce, 2015; Johnson et al., 2017). Previous literature suggests that energy development, especially when placed in critical habitat, alters ungulate behavior which may be an early warning sign of demographic effects to come (Beckman et al., 2012; Northrup et al., 2015; Sawyer et al., 2006). Unfortunately, studies rarely have predevelopment or baseline data and are typically short term (2–3 years), which can make it difficult to document the magnitude and persistence of behavioral responses or to connect them to demography (Hebblewhite, 2011; Northrup et al., 2012). Our long-term study refutes the prevailing notion that mule deer habituate to human disturbance, and instead, demonstrates that energy development can have long-term consequences for deer populations simply through avoidance behavior and the indirect habitat loss that ensues. Furthermore, as the NEPA process is based on full disclosure of the potential impacts from a proposed action, our work indicates that future impact assessments should disclose that the impacts to ungulate habitat in the shrub-steppe environment of the West may well be long-term and perhaps an irretrievable commitment of resources.

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