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Research Article

Migratory Disturbance Thresholds with Mule Deer and Energy Development

HALL SAWYER,[1] *Western Ecosystems Technology, Laramie, WY 82070, USA*
MALLORY S. LAMBERT, *Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA*
JEROD A. MERKLE, *Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA*

ABSTRACT Fine-scale movement data has transformed our knowledge of ungulate migration ecology and now provides accurate, spatially explicit maps of migratory routes that can inform planning and management at local, state, and federal levels. Among the most challenging land use planning issues has been developing energy resources on public lands that overlap with important ungulate habitat, including the migratory routes of mule deer (*Odocoileus hemionus*). We generally know that less development is better for minimizing negative effects and maintaining habitat function, but we lack information on the amount of disturbance that animals can tolerate before reducing use of or abandoning migratory habitat. We used global positioning system data from 56 deer across 15 years to evaluate how surface disturbance from natural gas well pads and access roads in western Wyoming, USA, affected habitat selection of mule deer during migration and whether any disturbance threshold(s) existed beyond which use of migratory habitat declined. We used resource and step selection functions to examine disturbance thresholds at 3 different spatial scales. Overall, migratory use by mule deer declined as surface disturbance increased. Based on the weight of evidence from our 3 independent but complementary metrics, declines in migratory use related to surface disturbance were non-linear, where migratory use sharply declined when surface disturbance from energy development exceeded 3%. Disturbance thresholds may vary across regions, species, or migratory habitats (e.g., stopover sites). Such information can help with management and land use decisions related to mineral leasing and energy development that overlap with the migratory routes of ungulates.

KEY WORDS disturbance thresholds, energy development, habitat selection, migratory behavior, movement ecology, mule deer, *Odocoileus hemionus*, ungulate migration.

Advances in tracking technology have revolutionized the study of animal movements through the collection of fine-scale location data (Kays et al. 2015). For terrestrial mammals, and large herbivores in particular, global positioning system (GPS) technology has helped reveal the mechanics of migratory behavior (Bunnefeld et al. 2011, Peters et al. 2019) and the nutritional benefits afforded to animals that migrate (Rolandsen et al. 2017, Middleton et al. 2018). Studies of migratory behavior are advancing our understanding of when, where, how, and why animals move across landscapes (Milner-Guland et al. 2011) and the role of this behavior within ecosystems (Bauer and Hoye 2014). As a result, more emphasis has been placed on conserving migratory species and their corridors (Berger and Cain 2014, Hardesty-Moore et al. 2018, Hays et al. 2019).

Within the western United States, much of the migration focus has been on relatively widespread ungulates such as mule deer (*Odocoileus hemionus*), North America elk (*Cervus canadensis*), and pronghorn (*Antilocapra americana*; Sawyer et al. 2016, Rickbeil et al. 2019, Tack et al. 2019). As part of the growing interest in sustaining migratory populations, new state and federal programs and policies have emerged to better accommodate ungulate migration in management and land use planning at local, state, and federal levels (Middleton et al. 2019). For example, Secretarial Order 3362 issued in 2018 by the United States Department of Interior directs federal agencies to work with western states to enhance the migratory habitat of mule deer, pronghorn, and elk on federal lands (U.S. Department of Interior 2018). In its first year, this federal directive provided $3,209,304 for migration research in 11 western states, made $3,946,392 available for on-the-ground habitat improvements of migratory corridors, and allocated approximately $700,000 for mapping corridors from existing data (C. L. Stemler, U.S. Fish and Wildlife Service, personal communication). Concurrently, the Western Association of Fish and Wildlife Agencies sponsored several migration training workshops for state and federal agencies that reached approximately 300 biologists and administrators. Relatedly, Wyoming began to designate ungulate migration corridors to assist with planning efforts (Wyoming Game and Fish Department 2016), New Mexico passed a Wildlife Corridors Act into law (State of New Mexico 2019), and

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[1]*E-mail: hsawyer@west-inc.com*

Colorado's governor issued an executive order to conserve big game winter range and migration routes (State of Colorado 2019). Collectively, these new programs and policies affirm that migration is important to the annual nutritional cycle of ungulates and that migratory habitat should be given equal consideration with winter and summer range.

New science-based programs that encourage mapping of migratory corridors have helped with management and land use planning (Fraser et al. 2018, Middleton et al. 2019). Yet, when competing land uses overlap (e.g., wildlife, recreation, energy development, livestock grazing), as is often the case on public lands in the western United States, determining the type or level of multiple use can be difficult and controversial. Among the most challenging of these competing land uses has been mineral leasing and development on federal lands that overlap with designated migration corridors.

Mule deer have been at the center of this controversy because their range often overlaps with proposed energy development (Sawyer et al. 2006), their numbers are generally declining (Mule Deer Working Group 2019), they often migrate across a mix of jurisdictional boundaries (Sawyer et al. 2016), and they have been a focal species in much of the research evaluating energy effects on wildlife (Lendrum et al. 2013, Northrup and Wittemyer 2013, Sawyer et al. 2017). For example, studies from across the western United States reported that mule deer avoidance of development in winter range creates large indirect habitat losses (Sawyer et al. 2006, Korfanta et al. 2015, Northrup et al. 2015, Dwinnell et al. 2019) that have been associated with population declines (Johnson et al. 2017, Sawyer et al. 2017). Higher levels of energy development within migratory corridors have also increased the speed at which deer travel and subsequently reduced the amount of stopover habitat (Lendrum et al. 2013, Sawyer et al. 2013, Wyckoff et al. 2018). Although we generally know that less development is better for mule deer, in terms of minimizing negative effects and maintaining habitat function, we often lack detailed information on the amount or level of disturbance that animals can withstand before reducing use of or abandoning an area. As more migratory corridors are identified and used to inform management (Wyoming Game and Fish Department 2016, U.S. Department of Interior 2018, State of Colorado 2019, State of New Mexico 2019), there is increasing need to identify disturbance thresholds—the level of disturbance that elicits an abrupt change in habitat or an ecological process (Groffman et al. 2006)—to ensure migratory routes remain functional.

Given that energy development has become one of the most dominant uses on western rangelands (Naugle 2011, Trainor et al. 2016, Kiesecker and Naugle 2017) and mineral leasing of federal lands continues to increase (Gardner et al. 2019), our goal was to examine how or if natural gas development influences the behavior of mule deer during migration in an open sagebrush (*Artemesia* spp.) region of western Wyoming, USA. Our descriptive study evaluated how surface disturbance from well pads and access roads affects habitat selection of mule deer during migration and whether any disturbance threshold(s) exist beyond which migratory use steeply decline. Our specific objectives were to examine disturbance thresholds at 3 spatial scales—the study area, migratory route, and individual movements—and use those metrics in a weight of evidence approach to identify the relationship between surface disturbance and migratory behavior of mule deer.

STUDY AREA

Our 264-km^2 study area was located in the Pinedale Anticline Project Area (Bureau of Land Management [BLM] 2000), a large natural gas development in western Wyoming (42.755°N, −109.861°W) that provided winter range for thousands of migratory mule deer (Sawyer et al. 2017) and pronghorn (Sawyer et al. 2019*a*). The area comprised mostly federal lands (85%) administered by the BLM and is characterized by high elevation (2,072–2,370 m) sagebrush communities (Sawyer et al. 2006). The climate was characterized by short, dry summers and long, cold winters. Mean temperatures in January and July were −10.7°C and 15.4°C, respectively (BLM 2008). Annual precipitation was approximately 26.9 cm (BLM 2008). Mule deer typically began spring migration to higher elevation summer ranges in late March or early April, and returned during autumn migration in November and December (Sawyer et al. 2005). The open sagebrush landscapes were largely undisturbed until the BLM approved the development of 700 producing well pads, 645 km of pipeline, and 444 km of access roads, beginning in 2000 (BLM 2000). The BLM later approved an additional 4,400 wells (BLM 2008). The deep gas formation was relatively narrow (2–4 km) and bisected the mule deer winter range so that some deer had to move through the development area during their seasonal migrations (Fig. 1). Between 2001 and 2017, approximately 971 ha of sagebrush land cover was converted to roads and well pads (Fig. 2). Of that direct habitat loss, 88% was attributed to well pads with an average size of 3.6 ha (Fig. S1, available online in Supporting Information). During that same period, mule deer abundance decreased by approximately 40% (Sawyer et al. 2017).

METHODS

We used helicopter net-gunning to capture 183 adult female mule deer during the winters of 2001 through 2015. We captured all deer 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). We fitted each deer with a GPS-collar (Telonics, Mesa, AZ, USA) programmed to collect locations every 2 or every 3 hours, for up to 2 years. Most individuals ($n = 127$) migrated along the west side of the study area and did not bisect the development area. By necessity, our analyses were restricted to the 56 individuals that migrated directly through, or within approximately 1 km of the gas development study area (Fig. 1). The number of migration sequences varied by year but spanned 15 years.

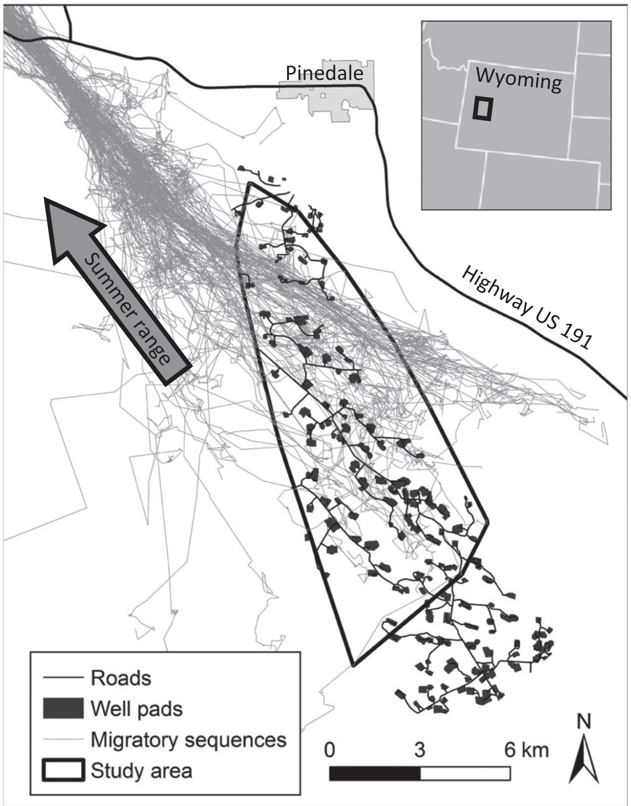

Figure 1. Migratory sequences from global positioning system (GPS)-collared mule deer ($n = 56$) that bisect the Pinedale Anticline natural gas field (~264 km^2) in western Wyoming, USA, 2001–2016.

We conducted a series of analyses to examine whether the amount of surface disturbance from natural gas development influenced the migratory behavior of mule deer. We defined surface disturbance as the amount of native vegetation converted to well pads and access roads, the primary sources of direct habitat loss associated with gas development (Sawyer et al. 2017; Fig. 2). We digitized roads

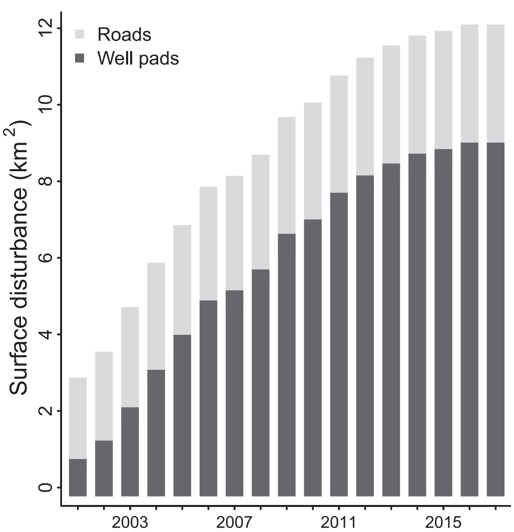

Figure 2. Amount of mule deer habitat converted to well pads and roads during the development of the Pinedale Anticline natural gas field, western Wyoming, USA, 2001–2017.

(operationally defined based on a width of 10 m) and well pads each year of study using 10-m resolution satellite imagery (Spot Image Corporation, Chantilly, VA, USA), acquired each autumn, following summer construction activities. We evaluated how surface disturbance influenced migratory behavior at 3 spatial scales: study area, migratory route, and individual movement.

At the study area scale, we used a resource selection function (RSF; Manly et al. 2002) to estimate probability of deer use as a function of surface disturbance. We defined our study area by placing a minimum convex polygon around all well pads constructed between 2000 and 2017 (Fig. 1). We then reduced the size of this polygon to encompass only the distribution of observed GPS locations of mule deer during migration (Fig. 1). We isolated migration sequences by identifying start and end dates for spring and autumn migration using net squared displacement (Bunnefeld et al. 2011), with 15 December used as the initial position. We estimated the RSF by comparing the amount of surface disturbance within a buffer around used deer locations ($n = 2{,}779$) to a set of randomly generated available buffered points ($n = 27{,}790$) inside the study area polygon (Fig. 3A). Prior to analysis, we removed migration sequences with <5 used locations within the study area, resulting in a sample size of 49 individuals and 87 migration sequences. We fit RSFs using mixed effects logistic regression and accounted for individual variation within the population by including a random intercept for each migration sequence (Gillies et al. 2006). To determine the appropriate buffer size to calculate surface disturbance around used and available points, we compared models with a linear effect of surface disturbance on habitat selection at 12 different buffers sizes: 50, 100, 150, 200, 250, 300, 350, 400, 450, 500, 750, and 1,000-m radii. Based on the log likelihood values, the 750 m buffer was best supported by the data, and we used this buffer in subsequent analyses (Fig. S2, available online in Supporting Information). To evaluate potential non-linear or threshold effects, we compared models with a linear effect of surface disturbance to models with a threshold effect specified by 1 or 2 linear splines. We iteratively (by 0.25% surface disturbance units) searched for candidate models to determine whether thresholds existed and their surface disturbance values. To control for outliers, we constrained our search for thresholds within 1–23% surface disturbance (i.e., the range of values within 1–99% of surface disturbance values in the observed data). Further, when we considered 2 splines in a single model, we constrained those 2 splines to be >1% surface disturbance units away from each other. We assessed relative empirical support for the models ($n = 3{,}915$) based on Akaike's Information Criterion (AIC), and selected the best-fitting model with the lowest AIC.

At the migratory route scale, we assessed how individuals located their migration route relative to surface disturbance within the study area. We first calculated the 99% contour around a utilization distribution for each migration sequence using the Brownian bridge movement model (BBMM; Horne et al. 2007). Because the migratory routes

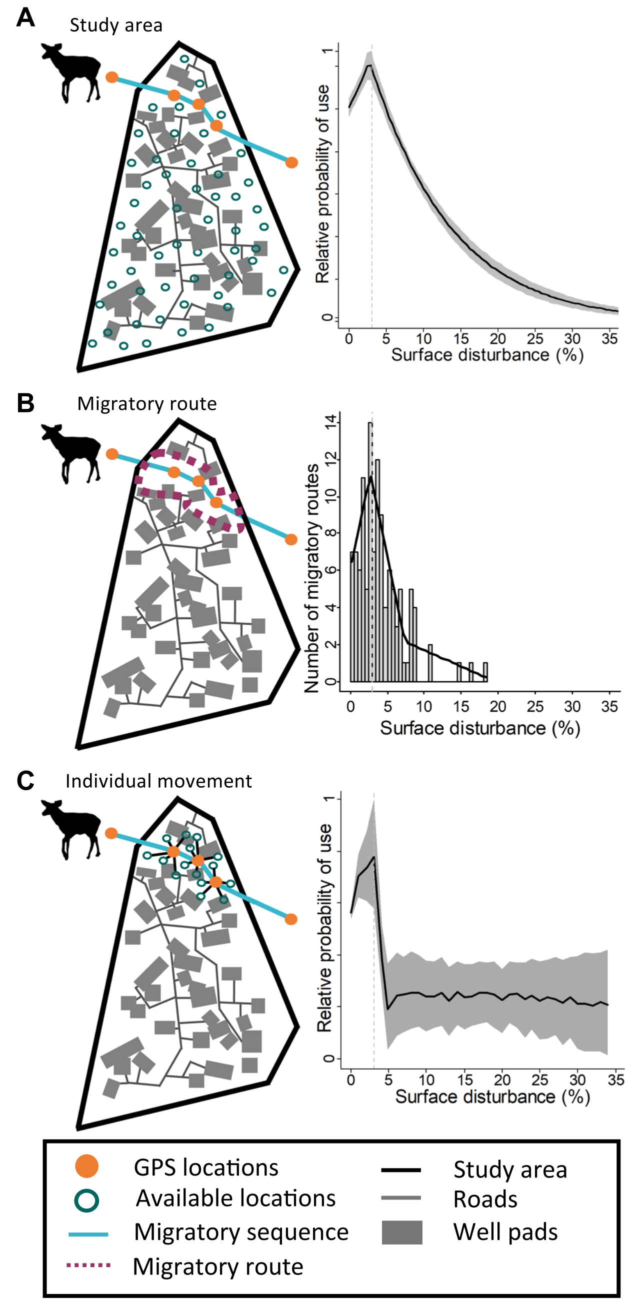

Figure 3. Conceptualized methodology paired with results: A) resource selection function at the study area scale showed a sharp decline in probability of use (95% CI in gray) of migratory habitat when surface disturbance exceeded 3%; B) histogram of surface disturbance within individual migratory routes, as defined by the Brownian bridge movement model, showed mule deer rarely used routes where surface disturbance exceeded 3%; and C) step selection function comparing used to available steps while migrating showed a sharp decline in probability of use (95% CI in gray) when surface disturbance exceeded 3%. Vertical gray dotted lines denote 3% surface disturbance. We calculated surface disturbance within a buffer (radii) of 750 m and 150 m around used and available points for the study area (A) and individual movement (C) scales, respectively. We analyzed all 3 spatial scales using migration sequences collected from 56 individual mule deer in the Pinedale Anticline gas field, western Wyoming, USA, 2003–2017.

of these deer extended 50–100 km beyond the gas field, we clipped the 99% contour of each individual's migration sequence to our defined study area (Fig. 1) so that we could restrict our analysis to migratory segments (56 individuals, 112 migration sequences) within the study area (Fig. 3B). We then calculated the amount of surface disturbance in each of the migratory routes and plotted a histogram (with 30 bins) of the percent of surface disturbance within each clipped migration route. To evaluate potential non-linear or threshold effects, we used the segmented package in R (R Core Team 2019) to assess empirical support for 1 or 2 linear splines across the range of surface disturbance values in the histogram.

At the individual movement scale, we assessed whether surface disturbance influenced the movements of deer through the gas field using a step selection function (SSF) framework (Fortin et al. 2005). For each migration sequence, we isolated steps (i.e., pairs of sequential source and target points) and generated 25 possible target points from each known source point by sampling from the step and turning angle distributions within the population. We then compared surface disturbance between used and available steps (Fig. 3C). To focus our inference on when individuals were migrating (i.e., not stopped over) within or near the gas field, we included only steps where either the used or available steps landed within 1 km of a well pad and the individual had moved >50 m between the source and target point. Subsequently, the SSF was based on 7,163 steps from 56 individuals (145 migration sequences). Mean number of steps per migration sequence was 49 ± 52 (SD). We parameterized all SSFs using conditional logistic regression, with each stratum identified as a used point and the paired 25 available target points. We calculated standard errors and 95% confidence intervals for parameters using generalized estimating equations (GEE), which account for temporal autocorrelation and a lack of independence within each individual's movements (Craiu et al. 2008). We assigned all strata for a given migration sequence a unique cluster in the GEE analysis. We included step length and its log to take into account heterogeneity in the availability domain (Forester et al. 2009) and to explicitly model the step length distribution (Avgar et al. 2016). Similar to the study area analyses, we evaluated a range of buffer sizes (25, 50, 100, 150, 200, 250, 300, 350, 400, 450, and 500-m radii) and concluded a 150-m radius was most appropriate for calculating surface disturbance (Fig. S3, available online in Supporting Information). To evaluate potential non-linear or threshold effects, we compared models with a linear effect of surface disturbance to models with a threshold effect specified by 1 or 2 linear splines. Using the same methods as the study area scale, we iteratively searched for candidate models to determine whether thresholds existed and their surface disturbance values. To control for outliers, we constrained our search for thresholds within 1–31% surface disturbance (i.e., the range of values within 1–99% of surface disturbance values in the observed data). We assessed relative empirical support for the models ($n = 7{,}259$) based on the lowest quasi-likelihood under independence criterion (QIC) value, which accounts for non-independence among observations within a cluster (Craiu et al. 2008). We conducted analyses at all 3 spatial scales using the program R (R Core Team 2019).

RESULTS

Regardless of spatial scale, mule deer rarely used areas with more than 3% surface disturbance during migration. At the study area scale, relative probability of use declined as surface disturbance increased ($\beta = -0.066 \pm 0.005$ [SE], $P < 0.001$); however, we had support for 1 break point at 2.75% (Fig. 3A). Within 2 AIC units of this top model, the first break point ranged from 1.75% to 4.75% (Table S1, available online in Supporting Information). Below 2.75%, mule deer used areas of higher surface disturbance more than available ($\beta_{spline1} = 0.08 \pm 0.02$). Above 2.75%, mule deer used surface disturbance less than it was available (Fig. 3A; $\beta_{spline2} = -0.10 \pm 0.007$). Nearly 50% of observed locations occurred at surface disturbances below 2.75%, and 92% of locations occurred at surface disturbances below 10%.

At the migratory route scale, a histogram of surface disturbance within migratory routes showed that 50 of 117 migration sequences of the mule deer migrated in routes with <3% surface disturbance (Fig. 3B). When surface disturbance exceeded 3%, we detected a decline in migratory use, and only 5 individuals ever used routes with >9% surface disturbance (Fig. 3B). Accordingly, in the analysis of thresholds with the histogram, we had support for 2 breakpoints at 2.7% and 7.4% ($\beta_{spline1} = 1.88 \pm 1.18$; $\beta_{spline2} = -3.79 \pm 1.25$, $\beta_{spline3} = 1.73 \pm 0.43$).

At the individual movement scale, we found that relative probability use declined linearly as surface disturbance increased ($\beta = -1.12 \pm 0.31$, $P < 0.001$); however, we had support for 2 break points at 3.5% and 4.5% (Fig. 3C). Within 2 QIC units of this top model, the first break point ranged from 2.75% to 3.75% (Table S2, available online in Supporting Information). Below 3.5%, mule deer used surface disturbance according to its availability ($\beta_{spline1} = 2.15 \pm 2.04$). Above 3.5%, mule deer used surface disturbance much less than it was available (Fig. 3C; $\beta_{spline2} = -37.54 \pm 9.6$, $\beta_{spline3} = -0.230 \pm 0.34$). The individual movement scale contained larger amounts of variation than the study area scale, as evidenced by the wide confidence intervals. Nonetheless, 92% of all steps occurred at locations with <3.5% surface disturbance.

DISCUSSION

A growing understanding of migration ecology has created new opportunities to incorporate ungulate migration routes into land use planning and management across jurisdictions (Middleton et al. 2019). One such opportunity is the ability to map migratory routes to consider in the context of broad-scale energy development (e.g., resource management plans, oil and gas guidelines, National Environmental Policy Act documents). Although GPS technology now makes it relatively simple to identify where a particular ungulate herd migrates, it has been much more difficult to determine how much disturbance animals can accommodate in their migratory routes. Our 15-year study suggests that mule deer are sensitive to well pad surface disturbance during migration. Regardless of spatial scale, the likelihood of individuals migrating through a particular area generally declined as surface disturbance increased, and this avoidance was pronounced above 3% surface disturbance.

Recognizing that migratory behavior decreases as disturbance increases adds to a growing body of knowledge of how development affects ungulate migration (Lendrum et al. 2012, 2013; Sawyer et al. 2013; Blum et al. 2015; Wyckoff et al. 2018). In practice, however, managers would benefit from knowing the threshold at which surface disturbance becomes problematic, to better balance competing land uses like energy development and wildlife habitat protection. For example, resource management plans, energy development guidelines, and other planning documents often need to specify the specific level(s) of disturbance allowed in particular management areas or parcels. More broadly, information on disturbance thresholds is needed to ensure ungulate migration routes remain functional (Sawyer et al. 2013). All 3 of our metrics indicated the surface disturbance threshold after which migratory routes were rarely used by deer was approximately 3% (2.75–3.50%). Surface disturbance did not negatively affect the probability of deer using a migration route until it reached 3%, but once that threshold was exceeded, migratory use declined, regardless of spatial scale. This non-linear response suggests that mule deer can tolerate low levels of disturbance through short segments (1–3 km) of their migratory route. The fact that all 3 metrics point to a threshold effect suggests that migratory mule deer are sensitive to energy development during migration and that migratory use and function deteriorate in routes or regions where surface disturbance exceeds approximately 3%.

Although our study could not address the specific mechanism by which migratory use diminished (e.g., demographic or behavioral changes) in disturbed areas, previous studies have reported that high levels of energy development, and specifically well pads, can change migratory behavior of mule deer and reduce the amount of stopover habitat (Sawyer et al. 2013). One key difference between our study and Sawyer et al. (2013) is that we used surface disturbance rather than well pad density as our metric of development intensity. Traditionally, regulatory work associated with oil and gas development has used well pad density as a metric of development intensity to help planning and mitigation efforts (BLM 2000, Doherty et al. 2008, Harju et al. 2010, Plumb et al. 2019). For example, the oil and gas guidelines developed for mule deer by the Western Association of Fish and Wildlife Agencies (Lutz et al. 2011) consider well pad densities of 1 pad/2.58 km^2 to have minimal effects, 2–4 pads/2.58 km^2 to have moderate effects, and >4 pads/2.58 km^2 to greatly affect mule deer. Relatedly, Sawyer et al. (2013) documented changes in the migratory behavior of mule deer in an area with well pad densities of approximately 7 pads/2.58 km^2 but no changes in area with 4 pads/2.58 km^2. This metric was intuitive and easily measured in earlier decades when most oil and gas pads were similar size (~1 ha). But, now the size of well pads can vary substantially (e.g., 0.5–16 ha; Fig. S1), depending on the type and depth of gas formation being drilled (e.g., coal-bed methane vs. deep shale gas) and how many wells are drilled from each pad. A case in point, contrast our study where average well pad size was 3.6 ha with Sawyer et al. (2013) where average well pad size was 0.6 ha. Recognizing that potential effects associated with 0.6-ha well pads are not equivalent to 3.6-ha well pads, we chose to use surface disturbance rather than well pad density as our metric for development intensity.

Perhaps more importantly, unlike well density, the surface disturbance metric can serve as a common disturbance currency among development types, whether oil and gas, wind turbines, or solar arrays. Conservation efforts associated with greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) recognize the utility of the surface disturbance metric and have adopted best management practices and policies that focus on limiting surface disturbance rather than well pad densities (Copeland et al. 2013, Gamo and Beck 2017). For example, area of disturbance in core sage-grouse habitat in Wyoming may not exceed 5% (State of Wyoming 2015). Such practices across sage-grouse range have indirectly benefitted migratory ungulates, including pronghorn and mule deer (Copeland et al. 2014, Tack et al. 2019).

Our disturbance threshold of 3% for migratory routes of mule deer carries several important caveats. First, the configuration and juxtaposition of surface disturbance is an important factor to consider in development plans. Specifically, given a set amount of allowable surface disturbance (e.g., 3%), it is preferable for that disturbance to be in the form of fewer large blocks rather than many small blocks (Theobald et al. 1997, Lenth et al. 2006, Doherty et al. 2010). We conducted our work in a region where average well pad sizes were relatively large (3.6 ha), so it is possible that threshold levels may vary in development scenarios characterized by smaller or larger well pad sizes, simply because of differential fragmentation effects (Swift and Hannon 2010). Second, the width of the gas field in our study area where deer migrated was relatively narrow, ranging from 1.5 km to 3.0 km. In fact, deer could potentially see undisturbed land on the other side of the gas field as they entered it. We suspect that if deer had to migrate longer distances through similar development, disturbance thresholds may be further reduced. For example, the intensively developed area where Sawyer et al. (2013) documented increased rates of migratory deer movement was 6.4 km wide, and mean well pad surface disturbance was only 1.8%. A third consideration is that we conducted our study in an open sagebrush landscape, where disturbance effects appear to be exacerbated compared to more vegetated and topographically diverse areas such as pinyon (*Pinus contorta*)–juniper (*Juniperus scopulorum*) woodlands (Lendrum et al. 2012, Northrup et al. 2015). For example, avoidance distances of wintering mule deer from well pads in open shrublands (~900 m; Sawyer et al. 2017) were twice as large as those reported in more rugged terrain with trees (~400 m; Northrup et al. 2015). Also, Lendrum et al. (2012) reported mule deer could migrate through developed gas fields when concealment cover, in the form of pinyon and juniper trees, was available. Fourth, the migratory routes of mule deer have an internal anatomy that includes stopover sites, where animals spend most of their time foraging and resting, in addition to route segments that animals move quickly through (Sawyer and Kauffman 2011). Our migratory route and individual movement analyses focused on route segments that were used primarily for movement rather than stopover habitat. We caution against applying our results to stopover habitat because those migratory segments are important for tracking vegetation green-up (Merkle et al. 2016, Aikens et al. 2017) and are characterized by low human disturbance (Monteith et al. 2018). A final caveat is that migratory behavior of mule deer is not apparently as flexible or plastic as other ungulates (Sawyer et al. 2019*b*). The migratory patterns of mule deer appear to be strongly influenced by memory (Merkle et al. 2019). With such rigid behaviors, mule deer may be less adaptive to rapidly changing landscapes than elk that routinely exhibit flexible migratory behavior (Eggeman et al. 2016, Peters et al. 2019). Ecological thresholds triggered by habitat loss or fragmentation tend to be lower when available habitat is restricted (Monkkonen and Reunanen 2007, Swift and Hannon 2010), as it appears to be with the relatively fixed migratory routes and behavior of mule deer.

The conservation of migratory ungulates in the western United States relies on state and federal management; states have authority to manage wildlife populations, whereas habitat is generally managed by federal agencies (i.e., BLM, U.S. Forest Service, National Park Service). Accordingly, federal land use decisions can influence migratory populations via effects on habitat. Mineral leasing and subsequent development of energy resources continue to pose serious management challenges for a variety of wildlife (Doherty et al. 2008, Naugle 2011, Hethcoat and Chalfoun 2015, Sawyer et al. 2019*a*). In some instances, energy development projects that overlap with ungulate migration routes or winter ranges can have long-term negative effects on populations (Johnson et al. 2017, Sawyer et al. 2017). Determining which parcels should be leased or how intensive a parcel should be developed are difficult decisions that could be better informed by knowing the level(s) and type(s) of disturbance that species can tolerate in their various seasonal ranges. As the migratory routes are increasingly recognized as a critical part in the nutritional strategy (Aikens et al. 2017) and management (U.S. Department of Interior 2018) of ungulates, we suggest that wildlife managers adopt a conservation model similar to sage-grouse (e.g., State of Wyoming 2015), where management practices aim to minimize surface disturbance (i.e., below disturbance thresholds) in critical habitats such as migratory routes.

MANAGEMENT IMPLICATIONS

Better understanding the relationship between surface disturbance and migratory behavior can help with management and land use decisions related to mineral leasing and energy development that overlap with the migratory routes of ungulates. Specifically, state wildlife agencies can use this type of information to refine oil and gas guidelines for mule deer, comment on proposed federal mineral leases that overlap with migratory routes, and evaluate land-use decisions on parcels where state permitting (e.g., executive order or state trust land) is required. Similarly, federal land managers (e.g., BLM) can consider the 3% disturbance threshold in their leasing decisions and associated stipulations, and more broadly in resource management plan revisions. We encourage agencies tasked with managing other ungulate species affected by energy development to use this work as a first step to begin unraveling how disturbance thresholds may vary by species, region, and disturbance type.

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