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Where to Forage When Afraid: Does Perceived Risk Impair Use of the Foodscape?

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Where to forage when afraid: Does perceived risk impair use of the foodscape?

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Abstract. The availability and quality of forage on the landscape constitute the foodscape within which animals make behavioral decisions to acquire food. Novel changes to the foodscape, such as human disturbance, can alter behavioral decisions that favor avoidance of perceived risk over food acquisition. Although behavioral changes and population declines often coincide with the introduction of human disturbance, the link(s) between behavior and population trajectory are difficult to elucidate. To identify a pathway by which human disturbance may affect ungulate populations, we tested the Behaviorally Mediated Forage-Loss Hypothesis, wherein behavioral avoidance is predicted to reduce use of available forage adjacent to disturbance. We used GPS collar data collected from migratory mule deer (*Odocoileus hemionus*) to evaluate habitat selection, movement patterns, and time-budgeting behavior in response to varying levels of forage availability and human disturbance in three different populations exposed to a gradient of energy development. Subsequently, we linked animal behavior with measured use of forage relative to human disturbance, forage availability, and quality. Mule deer avoided human disturbance at both home range and winter range scales, but showed negligible differences in vigilance rates at the site level. Use of the primary winter forage, sagebrush (*Artemisia tridentata*), increased as production of new annual growth increased but use decreased with proximity to disturbance. Consequently, avoidance of human disturbance prompted loss of otherwise available forage, resulting in indirect habitat loss that was 4.6-times greater than direct habitat loss from roads, well pads, and other infrastructure. The multiplicative effects of indirect habitat loss, as mediated by behavior, impaired use of the foodscape by reducing the amount of available forage for mule deer, a consequence of which may be winter ranges that support fewer animals than they did before development.

Key words: Behaviorally Mediated Forage-Loss Hypothesis; energy development; forage use; habitat selection; human disturbance; indirect habitat loss; movement patterns; mule deer; Odocoileus hemionus; *perceived risk; time-budgeting behavior.*

Introduction

As the human footprint continues to expand, novel changes to the environment test evolutionary strategies and behavioral plasticity of organisms exposed to change (Sih et al. 2011, Tuomainen and Candolin 2011, Robertson et al. 2013). Indeed, development of infrastructure in previously undisturbed environments often coincides with population declines resulting from habitat loss and fragmentation (Andrén 1994, Fischer and Lindenmayer 2007). In particular, human disturbance associated with energy development can prompt behavioral responses with indirect effects that compound the more obvious direct effects (Sawyer et al. 2009, Polfus et al. 2011, Northrup et al. 2013, Buchanan et al. 2014). For example, behavioral responses to human disturbance can indirectly affect fitness by disrupting acquisition of resources (Frid and Dill 2002, MacLeod et al. 2014). More specifically, human disturbance can alter the way an animal uses forage, which is presumed to

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affect energy intake (Gill et al. 1996, Lima 1998, Frid and Dill 2002, Barboza et al. 2008). Although such behavioral responses can have population-level effects (MacLeod et al. 2014), altered use of forage resulting from behavioral changes is rarely evaluated but remains a probable mechanism triggering population declines associated with human disturbances (Northrup et al. 2013).

Landscape heterogeneity in quantity, quality, and dispersion of forage constitutes the foodscape within which animals make behavioral decisions in the acquisition of food (Charnov 1976, Searle et al. 2007). Within the foodscape, there are numerous constraints that influence foraging behavior and access to available food. For example, large herbivores face constraints inherent to the foodscape, such as availability and quality of forage, that are met with physiological constraints of ingestion and digestion of plants within the foodscape (Searle et al. 2007, Laca et al. 2010). Further, decisions made specific to characteristics of the foodscape face additional external constraints such as conspecific and heterospecific competition and risk of predation (Festa-Bianchet 1988, Spalinger and Hobbs 1992, Kie 1999, Frair et al. 2005, Hebblewhite et al. 2008). In particular, perceived risk of predation can prompt behaviors such as avoiding high-quality habitats, altering movement patterns, and modifying behavioral time budgets (Lima and Dill 1990, Altendorf et al. 2001, Frair et al. 2005, Liley and Creel 2007, Winnie and Creel 2007, Hebblewhite and Merrill 2009, van Beest et al. 2013, Donadio and Buskirk 2016). Although behaviors in response to perceived risk are adaptations that allows large herbivores to co-occur on landscapes with predators, there may be thresholds at which behaviors prompted by perceived risk are no longer advantageous (Brown et al. 1999, Gaynor et al. 2019), resulting in deleterious effects on fitness and demography (Schmitz et al. 1997).

Human disturbance is a form of perceived risk that prompts behavioral responses analogous to those of predation (Frid and Dill 2002, Gavin and Komers 2006, Sawyer et al. 2009, Gaynor et al. 2019). Multiple taxa of large herbivores alter habitat selection, movement patterns, and time-budgeting of foraging behaviors in response to various forms of human disturbance (Dyer et al. 2001, 2002, Sawyer et al. 2006, 2009, 2013, Benhaiem et al. 2008, Stankowich 2008, Proffitt et al. 2013, St-Louis et al. 2013). Not only do behavioral responses to human disturbance occur across multiple spatial and temporal scales (Johnson et al. 2002, Polfus et al. 2011, Northrup et al. 2015), in some instances, they can exceed behavioral responses associated with predation risk (Ciuti et al. 2012, Clinchy et al. 2016). Strong behavioral responses to human disturbance may introduce additional constraints to the acquisition of food and exacerbate limitations to the foodscape. Furthermore, behavioral avoidance of human disturbance can force animals to use less suitable foraging habitat or crowd animals into preferred habitat, thus altering patterns of density dependence throughout the foodscape (Gill et al. 2001). Importantly, human disturbance that prompts avoidance of forage that would otherwise be available may result in indirect habitat loss that far exceeds direct habitat loss (Sawyer et al. 2006, 2009, Polfus et al. 2011, Northrup et al. 2015). Consequently, in systems that are food limited or geographically constrained, indirect habitat loss can reduce nutritional carrying capacity and prompt population declines (McCullough 1979, Hobbs and Swift 1985). Given the pervasive avoidance behaviors and population declines associated with human disturbance (Dyer et al. 2001, Nellemann et al. 2003, Polfus et al. 2011, Buchanan et al. 2014, Northrup et al. 2015, Sawyer et al. 2017), the cumulative effects of direct and indirect losses of forage may be a primary pathway by which human disturbance affects populations (Johnson et al. 2016).

In western Wyoming, oil and natural gas extraction has become widespread among sagebrush–steppe habitats that often are important winter ranges for migratory, large herbivores including mule deer (*Odocoileus hemionus*). Despite the inherent limitations in forage quality associated with high-elevation shrublands, these winter ranges provide crucial habitat for winter survival of mule deer that are exposed to dramatic, seasonal fluctuations in forage availability (Mautz 1978, Korfanta et al. 2015). Mule deer that occupy winter ranges with energy development have altered patterns of habitat and space use that, in some instances, have been linked to lower recruitment rates and reduced abundance (Sorensen et al. 2008, Northrup et al. 2015, Johnson et al. 2016, Sawyer et al. 2017). Yet, the mechanistic connection between avoidance behavior, forage use, and fitness or abundance remains unclear. Further, mule deer populations that concentrate on winter ranges that are food limited (as observed in western Wyoming) may be more sensitive to habitat loss because of inherent limitations of winter ranges (Monteith et al. 2014). Here, we propose the Behaviorally Mediated Forage-Loss Hypothesis, wherein we predict that perceived risk of human disturbance prompts indirect habitat loss from behavioral avoidance, causing a loss of otherwise available forage (Fig. 1). Although the evidence for a pathway by which human disturbance affects populations of large herbivores may appear intuitive, explicit evaluation of behavioral mechanisms behind the correlation between human disturbance and population declines has received little attention (but see Cameron et al. 2005).

Using three populations of migratory mule deer in western Wyoming, USA, that exist across a gradient of intensity of human disturbance resulting from energy development, we tested the Behaviorally Mediated Forage-Loss Hypothesis by first, measuring behavioral responses of animals when exposed to human disturbance, and second, by linking animal behavior with use of the foodscape along a gradient of human disturbance. Because behavioral responses may vary across spatial

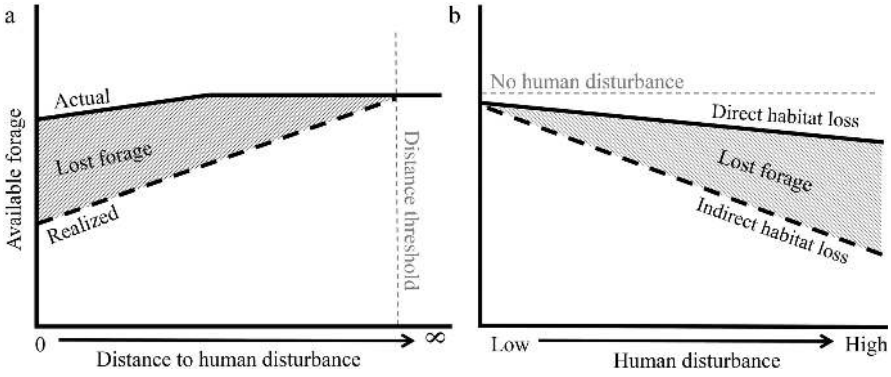

FIG. 1. (a) A conceptual model of the Behaviorally Mediated Forage-Loss Hypothesis. As animals approach human disturbance (e.g., energy development), the actual amount of available forage is diminished because of direct degradation of forage (Walston et al. 2009). Behaviors in response to perceived risk of human disturbance result in a realized availability of forage that is far reduced from the actual available forage. As animals approach human disturbance, the strength of perceived risk increases resulting in greater differences in actual and realized available forage near human disturbance compared with being farther away from disturbance, but there is a distance threshold to which human disturbance no longer affects behavior. The shaded area represents the subsequent lost forage resulting from indirect habitat loss. (b) A conceptual model of the cumulative effects of direct and indirect habitat loss on available forage. Behavioral avoidance resulting in indirect habitat loss further reduces use of available forage near disturbance. The magnitude of the reduction in available forage becomes greater as levels of human disturbance and indirect habitat loss increases. Note that all conceptual models assume that animals are using ranges that are geographically and nutritionally limited.

scales (Johnson et al. 2002, Polfus et al. 2011), we evaluated behavioral responses at different hierarchical scales (Johnson 1980, Searle et al. 2007, Polfus et al. 2011), including habitat selection within winter ranges, movement patterns within home ranges, and time-budgeting behavior within foraging patches. In accordance with the Behaviorally Mediated Forage-Loss Hypothesis, we made the following predictions:

1) Mule deer will exhibit behaviors of perceived risk in response to human disturbance resulting from energy development. Specifically, within winter ranges, mule deer will select for habitats away from human disturbance, will favor movement away from human disturbance within home ranges, and within foraging patches, will increase time spent in vigilant behavior when animals are close to human disturbance; however, the degree of behavioral responses to human disturbance will vary across these hierarchical scales (Polfus et al. 2011).
2) Although mule deer should use habitats based on forage quality and quantity (Brown et al. 1999, Pierce et al. 2004), their avoidance of areas near disturbance will override the preference of forage characteristics. Therefore, use of available forage near disturbance will be lower compared with areas farther away from disturbance, reflecting the effects of indirect habitat loss on realized forage availability (Fig. 1; Gill et al. 1996).

MATERIALS AND METHODS

Study area

Our study was located in western Wyoming, USA, across three discrete mule deer winter ranges at the southern end of the Greater Yellowstone Ecosystem (GYE; Fig. 2). Winter ranges included the Sublette (1,013 km^2), located approximately 5 km southwest of Pinedale, Wyoming (42°44′ N, 109°51′ W), the North Wyoming Range (611 km^2), located immediately northwest of La Barge, Wyoming (42°23′ N, 110°16′ W), and the South Wyoming Range (1,904 km^2) located approximately 25 km west of Kemmerer, Wyoming (41°49′ N, 110°31′ W). The primary vegetation types across all winter ranges were characteristic of a shrub-steppe ecosystem dominated by sagebrush species (*Artemisia tridentata*, *A. nova*) with sparse mountain-shrub communities (*Juniperus scopulorum*, *Cercocarpus* spp., *Amelanchier alnifolia*, *Symphoricarpos oreophilus*, and *Purshia tridentata*) and willow (*Salix* spp.) complexes in riparian areas. Elevations among winter ranges ranged from 2,000 to 2,300 m and mean, annual precipitation (30-yr average; Applied Climate Information System [ACIS], National Oceanic and Atmospheric Administration Regional Climate Centers) varied from 29.0 cm in Sublette (Pinedale, Wyoming; ACIS station 7260; elevation 2188 m) to 26.3 cm in South Wyoming Range (Kemmerer, Wyoming; ACIS Station 5105; elevation 2,112 m) to 16.5 cm in North Wyoming Range (Big Piney, Wyoming; ACIS Station 0695; elevation 2,079 m; data *available online*).[9] Although the GYE supports a suite of predators, including wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), those predators rarely occur on these mule deer winter ranges because of habitat and behavioral constraints, but coyotes (*Canis latrans*) and cougars (*Puma concolor*) do occur commonly. All winter ranges included active oil and natural gas extraction; however, density of development and intensity of human

[9] rcc-acis.org

disturbance differed across winter ranges. In general, the Sublette was characterized by recent (2001 to present) and ongoing natural gas development, including thousands of wells in the Pinedale Anticline Project Area (Bureau of Land Management 2005, 2008). In contrast, the North and South Wyoming Ranges were characterized by established (1919 to 2014) producing oil wells that tend to have a smaller footprint than modern natural gas well pads, which can exceed 8.1 ha (20 ac) when multiple wells are drilled from a single pad. The percent of total habitat characterized as energy infrastructure (e.g., roads and well pads) was 6.2% of North Wyoming Range, 2.1% of Sublette, and 1.1% of South Wyoming Range. Although overall development of infrastructure on Sublette was moderate, directional drilling was implemented allowing for development within concentrated areas. Within the area of concentrated development in Sublette, 8.6% of the total habitat was characterized as infrastructure from energy development. Average traffic volumes during winter among winter ranges were highest on Sublette (3.0 ± 1.4 vehicles/h) compared with lower volumes on North Wyoming Range (0.5 ± 0.1 vehicles/h) and South Wyoming Range (0.4 ± 0.2 vehicles/h; S. Dwinnell, *unpublished data*).

Animal capture and GPS data

Between March 2013 and March 2015, we captured 45 adult female mule deer on Sublette, 48 on North Wyoming Range, and 53 on South Wyoming Range winter ranges via helicopter net-gunning (Webb et al. 2008). Upon each capture, animals were hobbled, blindfolded, and ferried to a processing station (Monteith et al. 2014) where we fit each with a GPS collar (Advanced Telemetry Systems, Isanti, Minnesota, USA and Telonics, Mesa, Arizona, USA) programmed with fix rates ranging between 2 and 5 h. We fit new animals with collars as mortalities occurred. All capture and handling efforts were conducted under compliance with a protocol approved by the Institutional Animal Care and Use Committee at the University of Wyoming (Protocols 20131029MK00036-02 and 20131111KM00040-02), and were in accordance with guidelines of the American Society of Mammalogists (Sikes 2016).

Most mule deer within our study were migratory (98.6%) and moved between discrete summer and winter ranges. We isolated GPS locations on winter ranges using plots of net squared displacement (NSD; Turchin 1998) to identify arrival to and departure from winter ranges (Bunnefeld et al. 2011, Aikens et al. 2017). We conducted all subsequent analyses exclusively on GPS locations recorded on winter ranges. To overcome autocorrelation of time series data, we evaluated the autocorrelation function using the nlme package in R and identified 8 h as the interval at which autocorrelation sufficiently diminished ($r < 0.5$). We subsequently rarified all location data to at least 8-h intervals. We rarified collars on fix intervals not easily devisable by eight to the next integer greater than eight (e.g., 2.75 and 5 h intervals were rarified to 11- and 10-h intervals, respectively). Our analyses of GPS data comprised 29,922 locations from 104 individuals for winter 2013–2014 with an average of 271.2 ± 13.1 (mean ± SE) locations per animal and 16,583 locations from 71 individuals for winter 2014–2015 with an average of 230.0 ± 12.7 locations per animal.

Characterizing the foodscape

In 2013, we established 150 forage transects to measure quantity and quality of forage across each winter ranges (50 forage transects per winter range). We selected starting locations of forage transects randomly using a random point generator (splancs package) in R. We restricted starting locations to occur within the 100% minimum convex polygon (MCP) of capture locations during the initial capture in March 2013 for each winter range. We determined orientation of forage transects by following a random azimuth selected from the random starting location. If a forage transect crossed any infrastructure (e.g., roads or well pads), we selected a new azimuth. All transects occurred within patches of sagebrush where over 50% of the shrub species were Wyoming big sagebrush (*A. tridentata wyomingensis*). Wyoming big sagebrush was the dominant forage species of all three winter ranges, and big sagebrush (*A. tridentata*) accounted for over 85% of winter diets for mule deer within our study area (Wyoming Game and Fish Department, *unpublished data*).

In October 2013–2014, before animals arrived to winter range, we evaluated forage quantity by measuring production (i.e., annual leader growth), shrub density, and available biomass of Wyoming big sagebrush along each forage transect. We selected a shrub for production measurements at every third step (equaling roughly 1.5 m) for a total of 25 individual shrubs per transect. For each shrub selected, we measured annual leader growth (mm) on 10 leaders that we chose randomly (Wyoming Game and Fish Department 2007). We measured shrub density of Wyoming big sagebrush by counting each live shrub within a 50-m^2 belt transect along the forage transect. We also evaluated available biomass using reference unit methodology (Kirmse and Norton 1985). We assessed forage quality by evaluating crude protein (i.e., nitrogen), in vitro dry matter digestibility (IVDMD), and plant secondary metabolites (PSMs; including various monoterpene, phenolic, and coumarin compounds) of representative samples of new leader growth collected from a sample of shrubs from each forage transect (see Appendix S1 for details). Monoterpene, phenolic, and coumarin compounds are defensive toxins in sagebrush that can affect nutritional quality of forage for herbivores by prompting increased energy expenditure and nutrient binding when ingested (Dearing et al. 2005).

In May 2014–2015, after animals departed from winter ranges, we revisited the same forage transects to

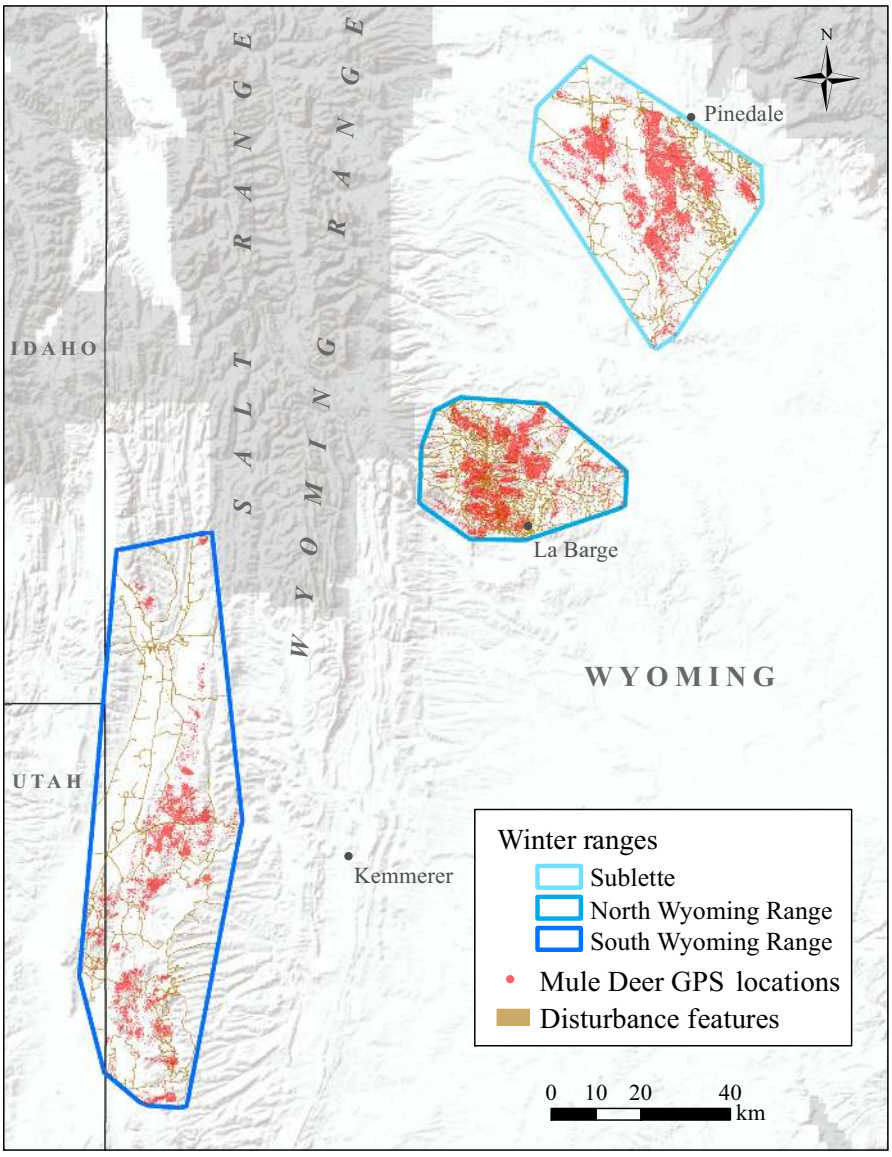

FIG. 2. Study area including three discrete winter ranges for mule deer in western Wyoming, USA (Sublette, North Wyoming Range, and South Wyoming Range), 2013–2015.

evaluate use of forage. Along each transect, we again chose 25 shrubs at every third step and indexed use by randomly selecting ten available leaders and counting the number that were browsed. Evidence of browse on leaders was easily identifiable, and measurements were collected before spring growth occurred (Wambolt 1996, Wyoming Game and Fish Department 2007). Using the same methodology, we also evaluated use over the summer when collecting production measurements in the autumn to account for forage use that may have occurred by other species (e.g., pronghorn [*Antilocapra americana*] and domestic cattle) over the summer; however, use of sagebrush leaders in summer was negligible (<1% across all transects), so we deemed it unnecessary to include summer use as a covariate in subsequent analyses.

We used new leader growth of sagebrush (i.e., sagebrush production) as our metric of forage availability, because new leaders are considered the most important forage item for mule deer in this region overwinter (Wambolt 1996, Korfanta et al. 2015). To create a metric of forage availability across the landscape, we modeled sagebrush production as a function of topography, climate, human disturbance, and vegetation using a random forest regression model across all three winter ranges for 2013 and 2014 (see Appendix S2 for details). We used the resulting raster of predicted sagebrush production (hereafter referred to as sagebrush production;

Appendix S2: Fig. S3) as a key covariate in all subsequent analyses.

Human disturbance metrics

We used remotely sensed data of roadways and infrastructure associated with energy development (e.g., well pads, holding facilities, and processing stations; Appendix S1: Table S1) to create a disturbance layer across our study area. We used roadway data collected from the Topologically Integrated Geographic Encoding and Referencing (TIGER; United States Census Bureau 2013) road database. We removed all roadways classified as two-tracks from the roadway layer because snow accumulation and road closures in winter prohibited access to these roads. We merged all remaining roadways into one layer using ArcGIS 10.3 (ESRI, Redlands, California, USA). We extracted spatial data for energy development from a digital layer representing oil and natural gas development scars in 2012 (Energy Development of Southwestern Wyoming, U.S. Geological Survey; Biewick and Wilson 2014 [these were the most current and comprehensive data available at the time of the study]). Within this digital layer, all development scars were annotated with information on feature type (e.g., well pad, holding facility, etc.), dates of operation, and activity status. We extracted polygons of all features still active in 2012 allowing us to use the most up-to-date and comprehensive data available on status of energy development throughout our three winter ranges. We then merged polygons of active energy development features with the roadway polygon to create a spatial polygon layer of all infrastructure associated with energy development. Using the spatial layer of all infrastructure associated with energy development, we calculated Euclidian distances of forage transects and GPS locations of deer to development, hereafter referred to as the metric of distance to disturbance. Additionally, we created a raster layer at a 100-m resolution of distance to disturbance across the whole study area using the Raster package in R.

Well pads, specifically, have been shown to prompt behavioral responses of avoidance in mule deer within our study area (Sawyer et al. 2006). To account for the increased human activity associated with well pads and the consequential effect of well pads on animal behavior, we created an additional metric of disturbance that was weighted by the distance to nearest well pad. The metric of human disturbance weighted by well pads was calculated by multiplying the distance to nearest disturbance feature by the distance to the nearest well pad feature (Fig. S1). Hereafter, we referred to this weighted metric as the weighted distance to disturbance. We used the two metrics of human disturbance, (1) the distance to disturbance and (2) the weighted distance to disturbance, in all subsequent analyses of animal behavior and use of forage.

Time-budgeting behavior

We evaluated time-budgeting behavior through behavioral observations conducted on radio-collared mule deer during daylight hours. Between January and March 2014, we relocated collared animals using radio telemetry and spotting scopes from the ground. We made every effort to avoid detection, and observations were terminated if animals in the group displayed any indication of detection. Once the target animal was located, we conducted focal-animal sampling for 15 min (Benhaiem et al. 2008), wherein we observed and recorded behaviors associated with foraging (e.g., feeding and chewing), resting, locomotion, and perceived risk (e.g., vigilance; see Appendix S1: Table S2 for breakdown of behaviors recorded). We were interested in behaviors of perceived risk that could hinder food intake; therefore, we recorded exclusively vigilant behavior and vigilance while chewing as separate behaviors because animals that multi-task vigilant behaviors with chewing do not assume the costs of reduced food intake (Fortin et al. 2004*a*). We also noted group size because it can affect vigilant behavior (Fortin et al. 2004*b*, Liley and Creel 2007). Between January and March 2014, we collected time-budgeting information from 177 separate observations conducted on 62 individuals across all three winter ranges.

Analysis of animal behavior

Modeling approach.—We implemented separate analyses to evaluate behaviors relative to landscape characteristics at three spatiotemporal scales, including (1) habitat selection within winter range, (2) movement patterns within home ranges, and (3) time-budgeting of vigilant behavior. Before conducting behavioral analyses, we first established a base model that included topographic and climate characteristics known to influence behavior of ungulates (Avgar et al. 2013, Northrup et al. 2015, Merkle et al. 2016). We determined variables within our base model for all subsequent analyses based on habitat selection within the winter range using a generalized linear mixed model (GLMM) with a negative binomial distribution. We used a negative binomial distribution to account for overdispersion in count data (White and Bennetts 1996). Competing models for our base model included candidate covariates of cumulative snow depth, cumulative snow water equivalent (i.e., SWE), heat level index (i.e., HLI), topographic roughness, and topographic radiation aspect index (i.e., TRASP; Appendix S2: Table S1). We evaluated all possible combinations of covariates and did not include collinear variables ($|r| > 0.5$) in the same model (Doherty et al. 2012, Monteith et al. 2014). We used Akaike Information Criterion corrected for sample size (AIC_c) to rank models and selected covariates within the model with the lowest AIC_c to serve as our base model for all subsequent analyses.

To evaluate the relative influence of forage availability (i.e., sagebrush production) and human disturbance on habitat selection and movement patterns, we used our base model and added all possible combinations of human disturbance metrics (i.e., either distance to disturbance or weighted distance to disturbance) and forage availability. Because group size can influence vigilance, we included group size as an additional covariate in analysis of time-budgeting behavior. We tested support for nonlinear terms informed by expected diminishing responses to disturbance and interactions between disturbance metrics and forage availability to evaluate the potential for a trade-off between responses to human disturbance and available forage. We also included an interaction between human disturbance and group size in our analysis of time-budgeting behavior because vigilance can decrease as group size increases (Fortin et al. 2004*b*, Liley and Creel 2007). We then used AIC_c, ΔAIC_c, and Akaike weights (w_i) for model selection. Although animals have been observed to modulate human disturbance by increasing use near development at night when human activity is diminished (Dzialak et al. 2011, Northrup et al. 2015), we were more interested in overall effects of human disturbance and, therefore, did not differentiate between day and night behaviors in our analyses. For models of movement patterns within home ranges, we used quasi-likelihood under the independence model criterion (QIC) to account for non-independence among observations within individual animals (Craiu et al. 2008). We did not include collinear covariates ($|r| > 0.5$) in the same competing model, and standardized all covariates to allow for direct comparisons of effect size. We considered any model within 2.0 ΔAIC_c (or ΔQIC), of the top model to be a potential alternative, and considered alternative models to be noncompetitive if the addition of parameters failed to improve maximized log likelihood (or quasi-likelihood), and if 95% CI of the additional parameters overlapped zero (Burnham and Anderson 2003).

Habitat selection within winter range.—We used a resource selection function (RSF) to evaluate selection of landscape characteristics for animals within winter ranges. We generated one random (i.e., available) location (using sp package in R) for each used location (n = 42,575) within the 100% MCP of GPS locations for each winter range. We used a GLMM with a binomial distribution to evaluate selection by mule deer based on use and availability of landscape characteristics (Johnson et al. 2006). We established a random intercept for each individual animal to account for repeated sampling of individuals (Zuur et al. 2007). We also included winter range (i.e., Sublette, North Wyoming Range, or South Wyoming Range) and year as nuisance parameters. Next, we added the base model, and the covariates sagebrush production, human disturbance metrics (i.e., either distance to disturbance or weighted distance to disturbance), and an interaction between sagebrush production and human disturbance metrics to evaluate the potential for a tradeoff between selection of forage and disturbance. We tested support for a quadratic term for each metric of disturbance that allowed for a nonlinear relationship that may reflect a diminishing effect of disturbance on selection as distance increases (Sawyer et al. 2006, 2009). Following model selection, we ensured that variance inflation factors (VIF) for all variables within the top model did not exceed 2.0, and used a K-fold cross-validation (k = 5) to evaluate robustness of the top model (Boyce et al. 2002).

Movement patterns within home range.—We used a step-selection function (SSF) model to evaluate whether animals were moving toward or away from various landscape characteristics of their home ranges. We identified used steps for individuals as the Euclidian distance between consecutive GPS locations (Fortin et al. 2009). From each used location (n = 41,584), we then generated 25 available steps at random lengths and angles chosen from the distribution of step lengths and turning angles for all animals. We calculated the difference in values of all covariates between the starting location of each step and ending location of the same step, which allowed for evaluation of whether animals were moving away from or toward various landscape characteristics. We used conditional logistic regression to evaluate the relative influence of forage availability and human disturbance on selection of movements (Merkle et al. 2015). We identified stratum within the model as each used step and the 25 available steps associated with the used locations. Furthermore, strata for each individual animal within a given year were assigned a unique cluster (Merkle et al. 2016). For SSFs, we included the base model, along with the addition of sagebrush production, human disturbance metrics, and their interactions to evaluate tradeoffs. We did not include the variables winter range and year because those variables were partially redundant with the clustering of individual animals per year in the SSF. Following model selection, we ensured that VIF for all variables within the top model did not exceed 2.0 and validated the top model using a K-fold cross-validation (k = 5; Fortin et al. 2009).

Time-budgeting of foraging behavior.—We used a generalized linear model with a negative binomial distribution, which accounts for overdispersion of count data (White and Bennetts 1996) to evaluate the time animals spent in vigilant behavior relative to group size, sagebrush production, and human disturbance metrics. We evaluated how human disturbance interacted with sagebrush production and group size by including interactions among these variables. We tested support for log-transformation of terms for distance to disturbance and weighted distance to disturbance to account for diminishing effects of disturbance as distance increases.

Following model selection, we assessed model fit by evaluating pseudo R^2.

Analysis of forage use

We evaluated use of available forage along each forage transect as a function of forage availability and quality, and proximity to human disturbance. We used a negative binomial GLM to model forage use at each transect as a function of the base model and metrics of forage availability and quality and human disturbance. We chose a negative binomial distribution because forage use was assessed using count data, and use of a Poisson distribution violated assumptions of overdispersion. Variables of forage availability included shrub density, available biomass, and sagebrush production, whereas variables of quality included metrics of crude protein, IVDMD, and PSMs, including phenolics, coumarins, and monoterpenes (i.e., alpha-pinene, alpha-phellandrene, beta-pinene, bornyl-acetate, camphene, camphor, myrcene, and 1,8-cineole).

Similar to our modeling approach for behavior, we used an information theoretic approach for model selection and evaluation of variable importance. We used a multi-step approach to assess variable importance in predicting use of forage. Starting with covariates of the base model, we added metrics of forage quantity (i.e., shrub density, available biomass, and sagebrush production) and considered the quantity metric within the model with the lowest AIC_c having the most support in predicting use of forage. We then retained the best supported model for forage quantity, and repeated the same approach to identify variables of quality (i.e., crude protein, IVDMD, phenolics, coumarins, alpha-pinene, alpha-phellandrene, beta-pinene, bornyl-acetate, camphene, camphor, myrcene, and 1,8-cineole) that influenced use of forage. Finally, using the model with the most support, we evaluate the relative influence of human disturbance metrics on use of forage. We tested support for log-transformation of terms for distance to disturbance and weighted distance to disturbance to account for potentially asymptotic relationship associated with diminishing effects of disturbance as distance increases. To account for a potential tradeoff between forage availability and human disturbance, we included an interaction between sagebrush production and human disturbance metrics in competing models. We ensured that VIF for all variables within the top model did not exceed 2.0, and we evaluated model fit by calculating pseudo R^2.

Quantifying loss of forage

To evaluate the cumulative effects of human disturbance on forage use, we quantified the overall loss of forage resulting from both direct and indirect habitat loss. We calculated forage loss under the assumption that animals were geographically constrained to their respective winter ranges and did not disperse to new home ranges outside of the traditional winter range, a notion supported by previous and long-term research in our study area (Sawyer et al. 2006, 2009, 2017). We quantified direct habitat loss by calculating the proportion of the area of infrastructure (i.e., roads and well pads) within each winter range. We calculated total areas of winter ranges using the MCP (100% isopleth) of GPS locations of deer within each winter range. We quantified the loss of available forage resulting from avoidance of human disturbance (i.e., indirect habitat loss) based on model predictions from the negative binomial GLM for use of forage of each winter range. To exclusively quantify loss of available forage resulting from indirect habitat loss, we restricted predictions of use of forage to areas with no infrastructure. We did this by clipping all roads and well pads from the MCP of each winter range (using ArcGIS10.3), and projected predicted use of forage onto the resulting layer at a 100-m resolution. We used all covariates that occurred in the top model that had a spatial reference. For covariates without spatial references that spanned the study area (e.g., non-raster data such as covariates of forage quality), we assigned the mean value for each winter range to all cells within the final MCP of the winter range.

We then quantified loss of available forage from indirect habitat loss in three steps. First, we simulated use of forage under conditions of minimal perceived risk of disturbance by setting the parameter for distance to disturbance to the maximum value within our data range, minimizing the effect of disturbance to the greatest extent within our data range, and summed the total use of forage for each winter range (i.e., use of forage without disturbance). Next, we predicted use of forage when parameters for distance to disturbance were set to the actual values for each winter range and summed the total use of forage (i.e., use of forage with disturbance). We measured loss in available forage by calculating the proportional difference between use of forage with and without the effect of human disturbance. Finally, to evaluate the magnitude of indirect habitat loss relative to direct habitat loss, we calculated the ratio of the percent of direct habitat loss to the percent of indirect habitat loss.

Results

Animal behavior

The base model with the most support ($w_i = 1.00$) included the climate variable of snow water equivalent (i.e., SWE) and topographic variables of heat level index (i.e., HLI) and roughness. Covariates within the base model were included in all subsequent analyses.

Habitat selection on winter ranges by mule deer was influenced by an interaction between sagebrush production and the distance to disturbance weighted by distance to well pad (Appendix S3: Table S1). Relative

probability of use decreased closer to disturbance but with a diminishing effect as distance to disturbance increased; however, sagebrush production, roughness, and SWE had a greater relative effect size compared with the weighted distance to disturbance and HLI (Table 1). Probability of use increased with sagebrush production, roughness, weighted distance to disturbance, and HLI but decreased with SWE. Sagebrush production had the greatest influence on selection by deer and probability of use increased as sagebrush production increased. Moreover, sagebrush production influenced selection relative to disturbance in that the negative effect of disturbance on habitat selection was dampened as sagebrush production increased; thus relative probability of use near disturbance increased as sagebrush production increased (Fig. 3). The *k*-fold cross-validation indicated acceptable model fit for the top model with the Spearman's rank correlation coefficient (r_s) of 0.99 ± 0.01 (mean ± SD) for used locations.

Selection of movement steps within home ranges was most influenced by distance to disturbance, sagebrush production, and roughness (Appendix S3: Table S2 and Table 1). Although SWE and HLI were included in the top SSF model, they were not significant in predicting selection in movement steps. Based on our SSF, mule deer selected for movements away from disturbance and toward habitats with high sagebrush production and roughness (Fig. 4). Selection in movements away from disturbance had a greater effect on movements than selection for movements toward sagebrush production and roughness. The *k*-fold cross-validation indicated satisfactory robustness for the SSF with r_s mean of 0.67 ± 0.08 for observed steps.

The interactive relationship between distance to disturbance and group size had the greatest influence on time spent in vigilant behavior, followed by sagebrush production (Appendix S3: Table S3 and Table 2). As animals got closer to disturbance, time spent in vigilant behavior increased, albeit by a small amount, time spent vigilant by a solitary animal was reduced by only 3.24 s at 1,000 m, compared with 0 m, from disturbance. Furthermore, the negative effect of distance to disturbance was dampened as group size increased, and animals in large groups near disturbance spent relatively less time exclusively vigilant compared with animals in small

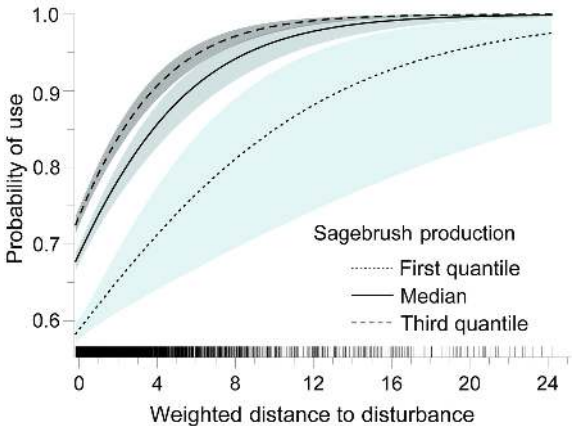

FIG. 3. The nonlinear (quadratic) relationship between probability of habitat use (RSF) by mule deer within winter ranges as a function of the interaction between sagebrush production and the weighted distance to disturbance. Each line represents the relationship between the weighted distance to development that is centered on zero and the probability of habitat use, including 95% confidence bands, while sagebrush production is held constant at the first quantile (9.5 mm), median (19.3 mm), and third quantile (24.2 mm). We measured sagebrush production as average leader growth of sagebrush (mm) along the forage transect on winter ranges of mule deer in western Wyoming, USA, 2013–2015.

TABLE 1. Coefficients, odds ratios, and 95% confidence intervals of covariates of the fixed effects of the top resource selection function (RSF) and step-selection function (SSF) models used to predict habitat selection and movement of mule deer in western Wyoming, USA, 2013–2015.

Covariate	Relative effect size	Relative odds ratio	Lower CI	Upper CI
Resource selection function				
Snow water equivalent	−0.230	0.794	0.778	0.811
Heat level index	0.003	1.003	0.987	1.018
Roughness	0.293	1.341	1.317	1.365
Weighted distance to disturbance	−0.619	0.538	0.516	0.516
Weighted distance to disturbance^2	0.224	1.251	1.183	1.322
Sagebrush production	0.475	1.608	1.577	1.640
Weighted distance to disturbance^2 × sagebrush production	0.123	1.131	1.087	1.176
Step-selection function				
Snow water equivalent	0.000	1.000	1.000	1.000
Heat level index	−0.466	0.628	0.275	1.432
Roughness	0.029	1.030	1.002	1.058
Distance to disturbance	0.030	1.031	1.004	1.058
Sagebrush production	0.019	1.019	1.014	1.024

Note: All covariates were scaled to be centered on zero and coefficients represent the relative effect size.

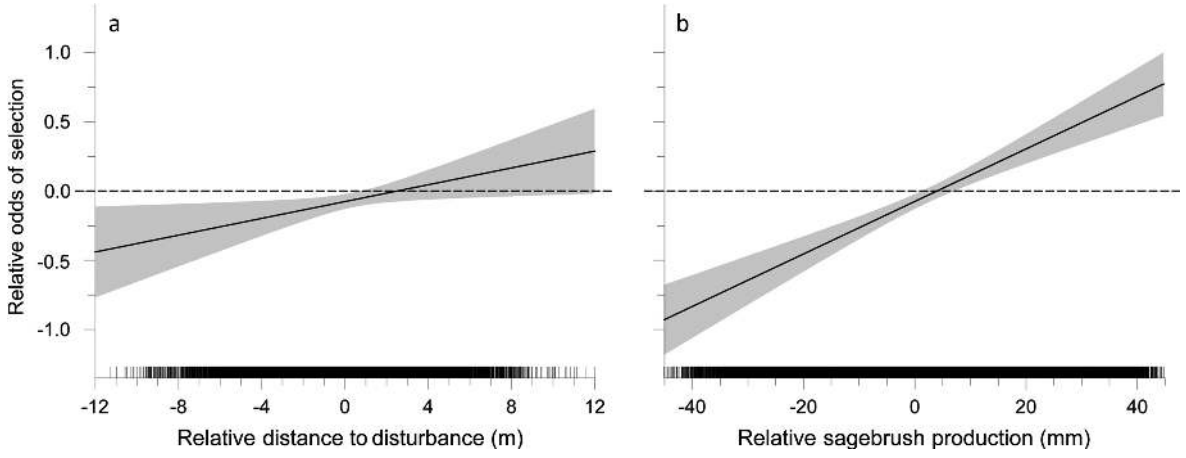

FIG. 4. Relative odds of selection, including 95% confidence bands, in movement patterns (SSF) by mule deer within home ranges as a function of (a) distance to disturbance and (b) sagebrush production. Relative distance to disturbance was the difference in the distance to disturbance (m) from the source location to the ending location of the step. Positive values represent movements away from disturbance whereas negative values are movements toward disturbance. Relative sagebrush production was calculated similarly, but positive values represent movements toward patches of higher sagebrush production relative to the source location and negative values represent movements away from patches of higher sagebrush production. Sagebrush production was measured as average leader growth of sagebrush (mm) along the forage transect on winter ranges of mule deer in western Wyoming, USA, 2013–2015.

groups (Fig. 5). In addition, vigilance decreased as sagebrush production increased. Pseudo R^2 for our top model was low (5.15% of variation was explained by the model), but the model carried 100% of the AIC_c weight and ranked 60.51 ΔAIC_c points better than the null model.

Forage use on the landscape

Covariates of forage quantity and quality with the most support in predicting use of forage included shrub density, crude protein, IVDMD, phenolics, alpha-pinene, beta-pinene, and 1,8-cineole. In addition to the aforementioned variables and those within the base model (i.e., SWE, HLI, and roughness), forage use was influenced by an interaction between weighted distance to disturbance and sagebrush production (Appendix S3: Table S4). Sagebrush production and weighted distance to disturbance had a greater effect on use of forage compared with all other variables (Table 3). Sagebrush production had the greatest relative influence on use of forage; use increased with sagebrush production. In contrast, forage use decreased nonlinearly as the weighted distance to disturbance decreased, but that effect interacted with sagebrush production in that the decreasing use of forage in proximity to disturbance was dampened when sagebrush production was high (Fig. 6). The top model (pseudo $R^2 = 0.26$) carried 96% of the AIC_c weight and was 6.8 ΔAIC_c better than the next competing model.

TABLE 2. Coefficients and 95% confidence intervals of covariates of the top model predicting time-budgeting of vigilant behavior.

Covariate	Coefficient	Lower CI	Upper CI
Snow water equivalent	0.146	0.026	0.271
Heat level index	0.113	0.019	0.205
Roughness	−0.054	−0.160	0.053
Group size	−0.087	−0.194	0.026
Distance to disturbance	−0.155	−0.264	−0.044
Sage production	−0.180	−0.295	−0.068
Group size × distance to disturbance	0.403	0.286	0.523

Notes: Model evaluated the relative effect of group size, sagebrush production, and human disturbance on the time mule deer spent vigilant on winter ranges in western Wyoming, USA, 2013–2015. All covariates were scaled to be centered on zero and coefficients represent the relative effect size.

Loss in forage

Throughout our study area, use of available forage on winter range decreased 10.5% with human disturbance on the landscape compared with the model simulating near absence of human disturbance (Fig. 7). Direct habitat loss resulting from construction of infrastructure across all winter ranges accounted for 2.3% of habitat loss; therefore, for every 1% of direct habitat loss, there was an additional 4.6% indirect loss of forage resulting from the reduction in use of forage near disturbance. Loss of available forage to avoidance of human disturbance (i.e., indirect habitat loss) varied among winter ranges with the greatest reduction occurring on Sublette (19.5% reduction), then South Wyoming Range (10.6% reduction), followed by North Wyoming Range (4.3%

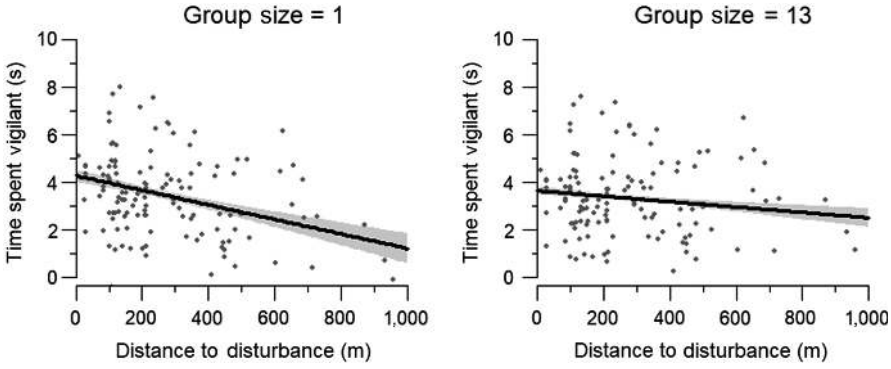

FIG. 5. The effect of group size = 1 compared with group size = 13 on time (s) spent in exclusively vigilant behavior by mule deer as a function of distance to disturbance (m), including 95% confidence bands, on winter ranges in western Wyoming, USA, 2013–2015. Median group size was 13 animals. Regressions are plotted on a zoomed-in time scale of 10 s to show the predicted response of vigilance to distance to disturbance, but behavioral data were collected during 900-s observations.

TABLE 3. Coefficients and 95% confidence intervals of covariates of the top model predicting use of forage.

Covariate	Coefficient	Lower CI	Upper CI
Heat level index	−0.018	−0.051	0.015
Snow water equivalent	−0.007	−0.047	0.034
Roughness	0.081	0.045	0.116
Shrub density	−0.058	−0.088	−0.028
Crude protein	0.098	0.064	0.133
In vitro dry matter digestibility	−0.059	−0.087	−0.030
Phenolics	−0.019	−0.050	0.012
Alpha-pinene	0.018	−0.011	0.049
Beta-pinene	0.022	−0.008	0.052
1,8-cineol	−0.055	−0.109	−0.001
Sagebrush production	0.147	0.110	0.185
ln(weighted distance to disturbance)	0.125	0.090	0.160
ln(weighted distance to disturbance) × sagebrush production	−0.051	−0.080	−0.023

Notes: Model evaluated the relative effect of landscape characteristics, forage quality and quantity, and human disturbance on mule deer use of available forage (i.e., sagebrush) on winter ranges in western Wyoming, USA, 2013–2015. All covariates were scaled to be centered on zero and coefficients represent the relative effect size.

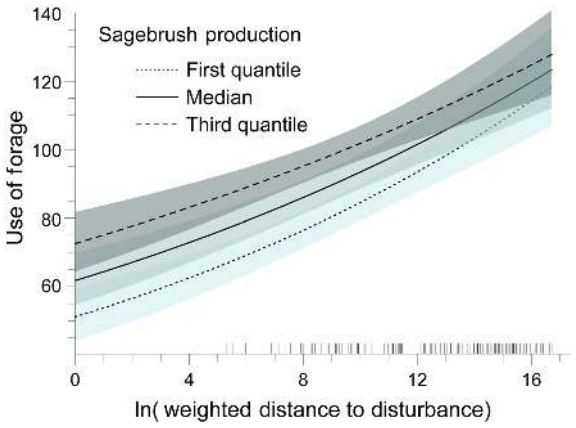

FIG. 6. The relationship between use of forage (i.e., sagebrush) by mule deer as a function of the interaction between sagebrush production and the ln-transformed weighted distance to disturbance. We measured use of forage as a count of sagebrush leaders browsed along a forage transect on winter range in western Wyoming, USA, 2013–2015. Each line represents the relationship between distance to development and use of forage, including 95% confidence bands, while sagebrush production was held constant at the first quantile (14.4 mm), median (21.1 mm), and third quantile (27.4 mm). Sagebrush production was measured as average leader growth of sagebrush (mm) along forage transects on winter ranges.

reduction). Reductions in use of forage equate to an additional loss of forage of 9.3% on Sublette, 9.6% on South Wyoming Range, and 0.7% on North Wyoming Range for every 1% increase in direct habitat loss. Overall loss in forage (direct habitat loss + indirect habitat loss) for winter ranges resulted in 21.6% loss on Sublette, 11.0% loss on South Wyoming Range, and 10.5% loss on North Wyoming Range (Fig. 7). Overall forage loss across the study area was 12.8%.

DISCUSSION

Mule deer avoided perceived risk of energy development at multiple scales that resulted in a net loss of forage that otherwise would have been available, a finding that supports the Behaviorally Mediated Forage-Loss Hypothesis. Across three winter ranges and different development scenarios, mule deer avoided areas close to disturbance (Fig. 3), tended to move away from disturbance (Fig. 4), and increased vigilant behavior when near disturbance (Fig. 5). The effect of human disturbance on mule deer varied by spatial scale, where movement patterns within home ranges were more strongly affected compared with broader-scale behaviors of habitat selection of winter range; while within foraging patches, observed changes in vigilant behaviors were negligible. Mule deer selected for areas with high

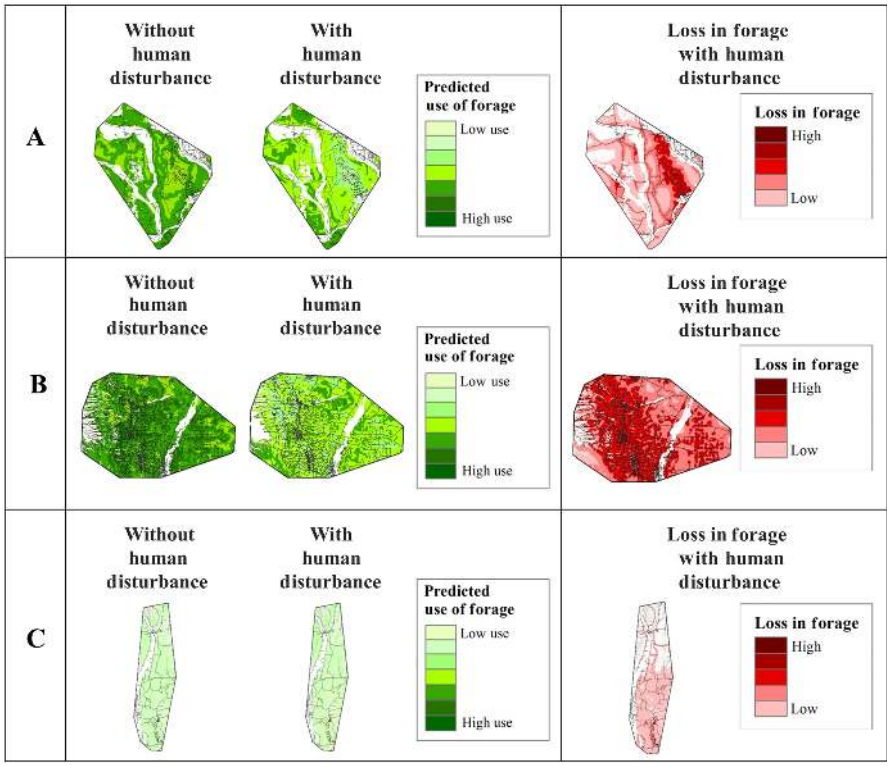

FIG. 7. Predicted use of forage across winter ranges (A, Sublette; B, North Wyoming Range; and C, South Wyoming Range) in western Wyoming, USA, 2013–2015, resulting from the negative binomial GLM with value of weighted distance to disturbance set to the maximum value within our data range, simulating use of forage with the minimal effect of disturbance (use of forage without disturbance) and with the actual values of the weighted distance to disturbance (use of forage with disturbance). Loss of forage with disturbance is the reduction in use of forage in the presence of disturbance, as calculated by the difference in use of forage modeled without disturbance and modeled with disturbance. Note, loss of forage assumes that animals on winter ranges are geographically limited and do not disperse to new winter ranges.

foraging opportunities, but their use of available forage near energy development was never realized to the same potential as similar forage patches farther from development (Fig. 6). The trade-off between seeking areas of high forage availability while avoiding disturbance limited use of available forage and caused indirect habitat loss that far exceeded direct habitat loss.

Overall, indirect habitat loss decreased available forage by an additional 4.6% for every 1% of direct habitat loss associated with energy development. The magnitude of indirect habitat loss varied among winter ranges (Fig. 7). Specifically, for every 1% of direct habitat loss, the indirect losses of available forage increased an additional 9.1% on Sublette, but only 0.7% on the North Wyoming Range. We suspect that disparities in indirect habitat loss among winter ranges was a function of differences in topography, intensity of energy development, and forage availability between North Wyoming Range and Sublette. For example, the North Wyoming Range was more topographically diverse compared with Sublette (North Wyoming Range mean slope, 3.7% ± 0.6%; Sublette mean slope, 1.2% ± 0.6%). Indeed, as observed in other studies, mule deer selected for rugged habitats and variable topographical features that provide refugia and can ameliorate the effects of human disturbance (Edge and Marcum 1991, Rowland et al. 2005, Northrup et al. 2015). Additionally, the intensity of human disturbance (as measured by traffic volumes), which can affect the magnitude of behavioral responses (Sawyer et al. 2009), was markedly lower on North Wyoming Range (0.5 ± 0.14 vehicles/h) relative to that observed on Sublette (3.0 ± 1.4 vehicles/h). Lastly, energy development on North Wyoming Range has been present as early as the 1920s, whereas development on Sublette began in the 2000s. The lessened degree of indirect habitat loss on the North Wyoming Range may be suggestive of habituation; however, after 15 yr of monitoring on Sublette winter range, deer have not displayed any indication of habituation to the existing infrastructure and disturbance (Sawyer et al. 2017).

We expect the dampened effect of development on the North Wyoming Range was mostly related to topographical ruggedness and human disturbance levels, but our data indicate that differences in forage availability (i.e., sagebrush production) among winter ranges also influenced how deer used their foodscape. Sagebrush

production, as measured by new leader growth, was nearly 1.5 times higher on North Wyoming Range (31.6 ± 2.4 mm) than Sublette (21.2 ± 2.0 mm). For large herbivores on winter range, quality of winter forage is typically low (Mautz 1978, Parker et al. 2005, Bishop et al. 2009, Korfanta et al. 2015), and availability can vary widely, making forage availability perhaps the primary constraint of winter ranges (Wallmo et al. 1977, Johnson et al. 2001). Accordingly, forage use was influenced more strongly by availability of new growth than by its quality (i.e., crude protein, PSM concentrations, and digestibility). Further, animals selected for areas with high sagebrush production, and the effect of human disturbance on use of forage was dampened when sagebrush production was high. The notion that indirect habitat loss can be reduced by increasing forage availability may have important management implications (but see Korfanta et al. 2015), but the degree to which sagebrush production dampens the negative effects of human disturbance may vary annually with climatic conditions, because of the influence of precipitation and spring temperatures on annual leader growth (see Appendix S2; Korfanta et al. 2015). Hence, the interactive effects between climate, human disturbance, and forage availability is a complex dynamic that requires careful consideration of habitat conditions when planning future development and mitigating ongoing projects.

Although human disturbance often coincides with behavioral responses and observed population-level effects on herbivores (Andrén 1994, Fischer and Lindenmayer 2007, Hess and Beck 2012, Sawyer et al. 2017), revealing the specific mechanism between the two has been challenging (Gill et al. 1996). Our findings supporting the Behaviorally Mediated Forage Loss Hypothesis are a step towards understanding the potential population-level consequences. Indirect habitat loss resulting from persistent avoidance of energy development has been documented previously in our study system and that of others (Polfus et al. 2011, Sawyer et al. 2017). Yet, until now, it was unclear if such alterations in space use near disturbance affected use of food because animals can modify behaviors at different spatiotemporal scales to compensate for shifts in behavior at a different scale (Kie 1999, Searle et al. 2007). For example, animals may feed at night to acquire food while avoiding perceived risk (Northrup et al. 2015, Gaynor et al. 2018), or animals may minimize time spent in risky foraging patches by altering foraging behavior to maximize food intake, thus, resulting in little net loss of available forage (Kie 1999). Despite the various behaviors animals can use to ensure use of available forage in areas of perceived risk, mule deer on winter range avoided human disturbance at multiple spatial scales, thereby hampering the way animals made use of available forage.

Reductions in nutritional carrying capacity are implicit in losses of available forage (Bowyer et al. 2014, Monteith et al. 2014). Populations below nutritional carrying capacity may be less affected by loss of forage because displacement, or shifts in animal use away from disturbance, may not constrain forage availability for individuals (Beckmann et al. 2012). Simply put, per capita food resources that remain sufficient to buffer populations from density-dependent pressures could minimize the potential for demographic consequences (Stewart et al. 2005). Conversely, for populations at or near nutritional carrying capacity, even minimal reductions in available forage could result in substantial effects on population demographics (Stewart et al. 2005, Bowyer et al. 2014, Monteith et al. 2014, 2015). On winter ranges where food is already nutritionally limited (Hobbs and Swift 1985), behaviorally mediated loss in forage resulting from human disturbance may easily prompt density-dependent feedbacks, resulting in an initial reduction in nutritional condition of individuals, serving as the proximate cause for population declines where energy development occurs (Cameron et al. 2005). When indirect habitat losses are magnified and long term, the subsequent loss of forage could have clear and lasting effects on population abundance, as has been observed in our study system (mule deer declined by 36% during 15 yr of energy development on Sublette winter range; Sawyer et al. 2017). Nevertheless, understanding the nutritional relationships between behavior and population dynamics before and after energy development is still needed to provide the final mechanistic link to population declines coincident with energy development in critical habitats.

To meet global demands for energy resources, oil and gas resources will continue to be extracted from critical wildlife ranges, including winter ranges of migratory, large herbivores (Johnson et al. 2016). Accordingly, understanding how those disturbances associated with energy development can affect behavior, foraging, and ultimately, population dynamics will help identify ways to minimize the effects (Northrup et al. 2013). Large herbivores have adapted to the naturally occurring constraints of their foodscape, but certain levels of human disturbance appear to prompt behaviors across multiple scales that, in turn, result in exaggerated losses of forage. Recognizing the cumulative losses of forage is key to providing wildlife managers and industry with realistic expectations of population effects that are likely to ensue on winter ranges where energy development occurs. Such knowledge can guide the evaluation of tradeoffs between energy development and the performance and abundance of large herbivore populations. Although the cumulative losses in forage resulting from direct and indirect habitat loss and the ensuing density-dependent feedbacks may be the only mechanism necessary to cause population declines, understanding the nutritional relationships between human disturbance and behavior are the next steps in developing a comprehensive understanding of how human disturbance can affect population dynamics and how to manage those relationships.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1972/full

Data Availability

Associated data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cr90637