

# Noise and landscape features influence habitat use of mammalian herbivores in a natural gas field

Nathan J. Kleist<sup>1,2</sup>  | Rachel T. Buxton<sup>1,3</sup>  | Patrick E. Lendrum<sup>4</sup> | Carlos Linares<sup>5</sup> | Kevin R. Crooks<sup>1</sup> | George Wittemyer<sup>1</sup> 

<sup>1</sup>Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA

<sup>2</sup>National Park Service, Natural Sounds and Night Skies Division, Fort Collins, CO, USA

<sup>3</sup>Department of Biology, Carleton University, Ottawa, ON, USA

<sup>4</sup>Northern Great Plains Program, World Wildlife Fund, Bozeman, MT, USA

<sup>5</sup>Department of Biological Sciences, Boise State University, Boise, ID, USA

## Correspondence

Nathan J. Kleist  
Email: nathan.kleist@gmail.com

## Funding information

National Park Service Natural Sounds and Night Skies Division, Colorado Parks and Wildlife; US Bureau of Land Management and ExxonMobil Production/XTO Energy; Sophie Danforth Conservation Biology Fund

Handling Editor: Elizabeth Derryberry

## Abstract

1. Anthropogenic noise is a complex disturbance known to elicit a variety of responses in wild animals. Most studies examining the effects of noise on wildlife focus on vocal species, although theory suggests that the acoustic environment influences non-vocal species as well.
2. Common mammalian prey species, like mule deer and hares and rabbits (members of the family Leporidae), rely on acoustic cues for information regarding predation, but the impacts of noise on their behaviour has received little attention.
3. We paired acoustic recorders with camera traps to explore how average daily levels of anthropogenic noise from natural gas activity impacted occupancy and detection of mammalian herbivores in an energy field in the production phase of development. We consider the effects of noise in the context of several physical landscape variables associated with natural gas infrastructure that are known to influence habitat use patterns in mule deer.
4. Our results suggest that mule deer detection probability was influenced by the interaction between physical landscape features and anthropogenic noise, with noise strongly reducing habitat use. In contrast, leporid habitat use was not related to noise but was influenced by landscape features. Notably, mule deer showed a stronger predicted negative response to roads with high noise exposure.
5. This study highlights the complex interactions of anthropogenic disturbance and wildlife distribution and presents important evidence that the effects of anthropogenic noise should be considered in research focused on non-vocal specialist species and management plans for mule deer and other large ungulates.

## KEYWORDS

anthropogenic noise, cameras, habitat use, hares, mammal, mule deer, rabbits, soundscape

## 1 | INTRODUCTION

Landscape conversion for energy development is a primary driver of habitat loss in North America. As new technologies enable extraction of previously unattainable resources, millions of hectares are opened up to potential development (International Energy Agency, 2018;

Trainor et al., 2016). An indirect effect of energy extraction that has received less attention is the proliferation of anthropogenic noise, which can influence the behaviour, physiology and distribution of wildlife (Swaddle et al., 2015). Noise from energy development contributes to a doubling of background noise levels in 63% of US protected areas (Buxton et al., 2017), and a wide variety of impacts from

energy development have been documented across wildlife species (Bayne et al., 2008; Francis et al., 2009; Kleist et al., 2018; Northrup & Wittemyer, 2013). Even small increases in noise exposure have been linked to diverse consequences for wild animals, and behavioural impacts may represent the greatest threat (Francis & Barber, 2013; Holt & Johnston, 2014; Injaian et al., 2018; Phillips & Derryberry, 2018).

While researchers studying noise impacts on animal behaviour have focused primarily on birds and marine mammals (Barber et al., 2010; Parks et al., 2011; Shannon, McKenna, et al., 2016; Slabbekoorn, 2013), animals without highly adapted vocalizations may still be affected by acoustic disturbance. Common prey species like ungulates and leporids (rabbits and hares) are highly attuned to the acoustic environment—relying on sensitive hearing and highly adapted pinna to receive predation cues from the environment (Geist, 1981; Marai & Rashwan, 2004). Quiet environments promote efficient ‘trade-offs’ between vigilance and foraging behaviours, on which these species rely to balance environmental awareness with metabolic needs (Lima & Dill, 1990; Lynch et al., 2015). Anthropogenic noise masks biological sounds and restricts the area within which vigilant prey can receive unobstructed auditory information from the environment (i.e. listening area) by reducing the signal-to-noise ratio of acoustic cues (Kleist et al., 2016; Lohr et al., 2003; Parris & McCarthy, 2013). When prey animals use loud habitats with reduced listening areas, they may perceive enhanced predation risk and heighten vigilance effort at the expense of foraging (Shannon, Cordes, et al., 2014). Conversely, acoustic disturbance can trigger distraction that increases the likelihood of predation (Chan et al., 2010). Such negative impacts may deter prey from areas exposed to noise (Ware et al., 2015) and could significantly reduce the use of otherwise high-quality habitats.

Theory and natural history allude to an impact of noise on ungulates and leporids, yet consideration of noise as an independent driver of behavioural change is relatively understudied in these groups. Research suggests that ungulates respond to loud human disturbances including real and simulated military aircraft overflights (Krausman et al., 1998), recreation (Borkowski et al., 2006), roadways (Buxton et al., 2020; Meisingset et al., 2013) and natural resources extraction (Dyer et al., 2001; Sawyer et al., 2009). However, these studies do not address the potential for noise to exacerbate impacts of habitat conversion, nor do they explicitly consider noise exposure associated with disturbance. When noise has been considered in analyses of disturbance, results appear species- and source specific. For example, caribou *Rangifer tarandus* and pronghorn *Antilocapra americana* reduced the use of habitats exposed to noise from military activity, while white-tailed deer *Odocoileus virginianus* avoided areas exposed to simulated shale gas drilling above 70 dB(C) (Drolet et al., 2016; Landon et al., 2003; Maier et al., 1998). However, neither elk *Cervus elaphus* nor pronghorn using roadside habitats increased activity in response to noise associated with vehicle traffic in Teton National Park, USA (Brown et al., 2012).

Less is known about response to noise in leporids. An extensive history as a laboratory animal shows that extreme acoustic stimuli do have negative physiological consequences in domestic and wild leporids (Franklin et al., 1991; Griffiths et al., 1960). Research

on another small mammal, black-tailed prairie dogs *Cynomys ludovicianus* suggests increased perceived risk may drive behavioural changes (Shannon, Crooks, et al., 2016; Shannon, McKenna, et al., 2016). The lack of research focused on the responses of common mammal species to noise provides an opportunity to expand understanding of how anthropogenic noise impacts the behaviour of these ecologically fundamental species.

We use a large-scale paired camera and acoustic recorder system to examine the effects of noise from shale gas extraction activity on mule deer *Odocoileus hemionus* and leporid *Lepus* sp. & *Sylvilagus* sp. habitat use within fragmented landscapes. Our study design allows us to examine impacts of exposure to a gradient of anthropogenic noise on mammalian herbivores while controlling for the influence of natural and anthropogenic landscape features (Buxton, Lendrum, et al., 2018). Previous results from the study system showed that mule deer avoid active well-drilling sites (Northrup et al., 2015) and roads (Lendrum et al., 2012). Deer also move through disturbed habitats more quickly during migration (Lendrum et al., 2013). Exploring responses to fragmentation in the context of noise may reveal that these stressors interact to drive habitat use patterns (Shannon, Crooks, et al., 2016; Shannon, McKenna, et al., 2016). An initial analysis on potential influences of noise in this system applied on-animal acoustic monitoring to measure vigilance behaviour of mule deer (Lynch et al., 2015). Deer demonstrated increased acoustic vigilance (i.e. listening) when landscape features impeded visual vigilance, and acoustic vigilance varied with levels of noise exposure. This suggests that physical landscape features likely interact with acoustic conditions to drive mule deer behaviour. We build on these results to assess if habitat use of mule deer and leporids was negatively associated with increased exposure to anthropogenic noise across an industrial landscape. Including both mule deer and leporids in models exploring homotypic stressors provides insight into mechanisms that drive species-specific responses to noise and a framework to assess potential mitigation strategies (Northrup & Wittemyer, 2013).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The Piceance Basin is part of the larger Mancos Shale, the second largest natural gas resource in the United States, and has been developed for energy extraction since the early 20th century (Hawkins et al., 2016; Martinez & Preston, 2018). Development of the Mancos Shale is projected to increase throughout the next decade and into the foreseeable future (Bureau of Land Management, 2016; Martinez & Preston, 2018), leading to conversion of sagebrush habitat that is an important resource for over 350 terrestrial species (Knick et al., 2003; Souther et al., 2014; Weller et al., 2002; Wisdom et al., 2005). Although some patches of large, contiguous habitat occur nearby, our study area is marked by a network of well pads, roads, processing facilities and pipelines associated with extraction

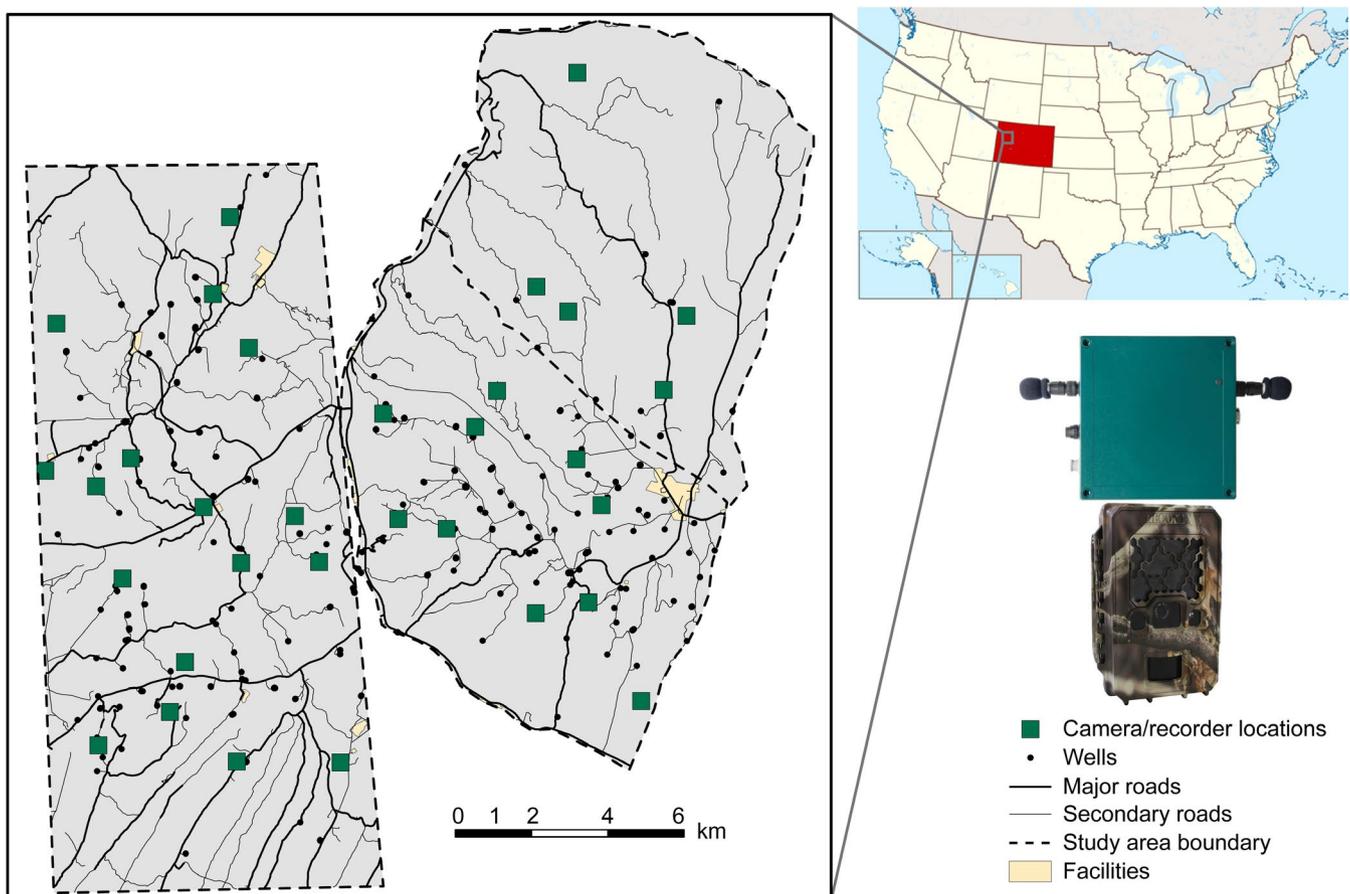
of natural resources. In addition to natural gas development, human activities in the area include winter cattle grazing in valley bottoms and hunting in the fall (Northrup et al., 2015).

In early summer 2015, paired acoustic recorders and camera traps were deployed in the South Magnolia (83 km<sup>2</sup>), North Magnolia (79 km<sup>2</sup>) and Ryan Gulch (141 km<sup>2</sup>) regions of the Piceance Basin in Northwestern Colorado, USA (Figure 1). These three sites comprise the majority of designated critical overwintering habitat for one of the largest migratory mule deer herds in the United States, estimated to number between 21,000 and 27,000 individuals (Lendrum et al., 2017; White & Lubow, 2007). This central portion of the Piceance Basin is characterized by sagebrush *Artemisia tridentata* flats and the piñon pine *Pinus edulis*–Utah juniper *Juniperus osteosperma* shrubland complex that defines much of the Colorado Plateau ecoregion (Sleeter et al., 2012). A detailed account of vegetation structure at our study sites was previously reported by Lendrum et al. (2012). Elevation of study sites ranged from 1,675 to 2,285 m and the topography of the region is typified by large, steep drainages, providing aspect diversity that gives deer access to more favourable conditions even during severe winters (Bartmann et al., 1992).

The three study areas experienced substantial energy development, where the density of well pads varied from relatively low in North Magnolia (<0.05 pads/km<sup>2</sup>) to moderate in Ryan Gulch (0.37 pads/km<sup>2</sup>) and high in South Magnolia (0.70 pads/km<sup>2</sup>; Lendrum et al., 2012). This study was conducted during a post-drilling, production phase, where the human activity and noise in the region was reduced compared to active-drilling phases. To space devices evenly and create a gradient of exposure to industrial landscape features, we subdivided the area into a 5 by 5 km grid and randomly selected four sites that were >500 m from any infrastructure, four sites that were <500 m from active processing facilities that generate noise pollution and 24 sites that were <500 m from producing well pads.

## 2.2 | Cameras and acoustic recorders

Thirty-two pairs of acoustic recording devices (Song Meters Model SM2, Wildlife Acoustics Inc.) and camera traps (RECONYX PC 800 digital cameras, Figure 1) were deployed beginning 22 May 2015. This method of pairing camera traps and acoustic



**FIGURE 1** Placement of acoustic recorders and camera traps (devices pictured on the right) in the Piceance Basin, an area highly impacted by shale gas development in northwest Colorado. Devices were placed at sites far from oil and gas infrastructure, near noisy facilities and near wells where activity ceased at different times from the present. Study areas outlined by dashed border are Ryan Gulch (left), North Magnolia (right upper), South Magnolia (right lower)

recorders offers a continuous and non-invasive collection of data that improves upon the use of either technology separately by simultaneously capturing both wildlife and human activity (Buxton, Lendrum, et al., 2018). We placed each acoustic recorder and camera pair as close as possible to the randomly chosen location, while also retaining proximity to specific features such as animal movement routes and water sources expected to maximize capture probability. Cameras were positioned on a post or tree at a height of approximately 40 cm, facing perpendicular to the expected direction of animal travel approximately 3 m from the anticipated site of capture (Lendrum et al., 2017). Equipment failure resulted in 20–32 acoustic recording devices being active at a time (Table S1). Acoustic devices recorded continuously for 2 hr after sunset and sunrise and for 5 min each 30-min period for the rest of the day and night. Recordings were collected at a sample rate of 22,050 Hz after sunrise to capture birds, mammals and insects. Cameras were pointed at natural habitat that was representative of the surrounding environment and not at features associated with oil and gas development. We visited camera traps to change batteries every 6 months, and acoustic devices opportunistically each 2–4 months, where external 6-volt battery life resulted in 2-week to 1-month gaps in recordings each 2 months. Camera trap triggers were set on high sensitivity and programmed to take three pictures after triggering by motion and heat—maximizing detection of small mammals while still allowing larger bodied animals to be readily detected (Wellington et al., 2014). This approach may have resulted in more false triggers due to increased wind sensitivity but reduced the chance of missed animal detections. We used CPW Photo Warehouse (version 4.0; Ivan & Newkirk, 2016) to identify and store the species in each photograph. Combined collection resulted in 2,217 days of data from cameras and recorders. Combined collection days at each site varied from a high of 144 days/site to a low of 8 days/site. The average number of combined camera and recorder observation days at each site was 69.28 days—exceeding the recommended number of sampling occasions needed to adequately detect mule deer or leporids for camera-trap sampled occupancy modelling (Shannon, Lewis, et al., 2014).

### 2.3 | Noise indices

Because our total acoustic dataset from the Piceance consisted of over 10 TB with >2,000 days of recordings from 32 sites spanning May 2015–November 2015, our ability to listen to all recordings or observe them using spectrograms was limited. Therefore, we calculated noise indices to indicate the energy of anthropogenic noise in acoustic recordings (Buxton, McKenna, et al., 2018). To do this, we manually summarized anthropogenic noise sources in a subset of recordings (the first 5 min of each half hour between 08:00–12:00 for 2–3 randomly selected recording days at each of 31 sites; 4,100 min) and used these identified sounds to develop a model of anthropogenic noise levels. Manual event identification

was carried out by a trained technician using the software Raven Pro 1.5 (Cornell University) to visualize spectrograms and listen to audio files. Window settings were standardized (FFT, brightness and contrast) to ensure spectrogram properties were consistent across observations. Following a training period, the technician was presented with a test dataset of at least 10 randomly selected audio clips with a known number of anthropogenic noises to ensure they were able to correctly identify most (>90%) sounds. The technician then identified and selected each instance of anthropogenic or geophysical (rain, wind and thunder) sound, collecting the measurements of average power (dB) and average total energy (dB) from each (Table S2).

Acoustic indices summarize the distribution of acoustic energy by estimating the variation and energy of sounds in a recording (Buxton, McKenna, et al., 2018). We converted all audio data to 1 s 1/3 octave band SPLs measured as  $Leq_{1s}$  from 12.5 to 8,000 Hz (Merchant et al., 2015). This coarser resolution is commonly used in noise studies and requires less storage space and shorter computation time than wav files. We computed a total of 30 indices for each day of recording (Table S3).

To predict the daily energy of anthropogenic noise across the entire acoustic dataset, we used a random forest (RF) machine learning procedure (Breiman, 2001; `RANDOMFOREST` package; Liaw & Wiener, 2002). Using the subset of recordings measured by a technician, global RF models were built using all 30 noise indices as predictor variables and either average power or average total energy of anthropogenic noise events as response variables. We used a model selection procedure to select noise indices used as covariates in the final RF model used for prediction (`RFUTILITIES` package; Murphy et al., 2010). Similar to the frequently reported acoustic measurement  $L_{max}$ , which reports the loudest sound level occurring during a specified time period (Francis & Barber, 2013), our approach using noise indices accounts for intermittent, distinct noise disturbances rather than measuring over time with a continuous, integrated measurement such  $L_{50}$ .

### 2.4 | Statistical approach

We used occupancy models in the R package `UNMARKED` (version 12–3; Fiske & Chandler, 2011) to explore habitat selection patterns in leporids and mule deer. The binary response variable was daily detection and we include both site and observation-level covariates in double right-hand sided models using the function ‘`occu`’, which fits the single-season occupancy model from Mackenzie et al. (2002). The global model included an observation-level covariate for daily power of anthropogenic noise (`DailyPwr`) and site-level covariates including elevation (Elev, m), transformed aspect (North) and land cover type. Although multiple land cover classes exist in the region, our study area is dominated by piñon-juniper (44%) and sagebrush (39%), with all other types being relatively rare. Therefore, to simplify our approach, we combined all land cover types into the binary variable ‘`Overstorey`’, which

distinguished treed areas from open areas calculated using data from the Colorado Vegetation Classification Project (Northrup et al., 2015). Elevation and aspect were calculated in a digital elevation model at a resolution of 30 m (<http://datagateway.nrcs.usda.gov/>) using ArcGIS 10.5 (Esri), and the variable 'North' was a cosine transformation of aspect (Olaya, 2009).

Finally, we explored several site-level covariates that describe the levels of anthropogenic disturbance associated with natural gas development, including the site-averaged daily power of anthropogenic noise (AvgPwr); time since well pad drilling (WellYrs); the number of well pads within a 500-m radius of the survey point (Wells0\_500); and distance (m) to the nearest road (Roads), pipeline (Pipes), natural gas facility (Facs) and well pad (Wells). The variable 'AvgPwr' is a site-level variable calculated by averaging the daily power of anthropogenic noise across all survey days for each site. We acquired well pad location and history data from the Colorado Oil and Gas Conservation Commission (<http://cogcc.state.co.us>). A roads layer was derived by combining the TIGER/Line shape files of the US Census Bureau (<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>) and the Colorado Department of Transportation shape files (<http://apps.coloradodot.info/dataaccess/>). We considered county roads as primary roads and spur roads used for purposes of natural gas extraction as secondary roads, but we were unable to differentiate the levels of vehicle use among roads. Locations of pipelines were obtained from the Bureau of Land Management White River field office. Facilities included operation centres of frequent human activity and compressor stations (Lendrum et al., 2018). The spatial and temporal information for all landscape disturbances were validated or corrected with National Agriculture Imagery Program aerial images (<http://datagateway.nrcs.usda.gov/>) from 2009, 2011, and 2013, 2015 (Lendrum et al., 2018). We calculated Pearson correlation coefficients ( $r$ ) for all continuous variables and used a cut-off of 0.5 to identify any variables with potential collinearity. Using this method, we removed distance to pipeline due to correlation with two variables, distance to roads ( $r = 0.59$ ) and distance to well pad ( $r = 0.53$ ). There was also correlation between distance to well pad and well pad density ( $r = -0.59$ ), and we retained distance to well pad for consistency with other covariates.

We included both observation-level covariates and site-level covariates that could reasonably influence the daily detection of the target species in the observation process model ( $p$ ), and only used covariates that were supported by our previous research. Prior to model fitting, we standardized all numerical covariates by subtracting the mean and dividing by the standard deviation (Schielzeth, 2010). Our final global model for mule deer and leporids included five covariates on detection ( $p$ ): the average daily power of anthropogenic noise, overstorey class, and distance to nearest road, natural gas facility and well pad. Final global models included eight covariates on occupancy ( $\psi$ ): average site-level power of anthropogenic noise, overstorey class, elevation, northness, time since drilling, and distance to nearest road, natural gas facility and well pad.

After finalizing the structure of the global models, we performed a parametric bootstrap goodness-of-fit test to assess the adequacy of the model structure given its fit to the data. We simulated 1,000 sets of data based on parameter estimates and refit the model to each new dataset, and computed a chi-square fit statistic (Fiske & Chandler, 2019). After assessing global model fit, we used the function 'pdredge' in the R package MuMIn (Version 1.43.6; Barton, 2020) to rank models. We considered all candidate models  $<\Delta 2\text{AIC}$  from the top performing model to be equally supported and thus employed a model-averaging approach to determine importance of coefficients included across this subset. We calculated 95% confidence intervals of model-averaged estimates and considered coefficients with 95% CI that did not include 0 to have a significant effect on habitat use. We then used the averaged model to predict occupancy and detection probabilities across the range of each covariate by holding other covariates at their mean, or in the case of the categorical variable for overstorey, at the mode. Prior to plotting the predicted detection and occupancy probabilities, we back-transformed these estimates and unscaled the x and y axes for ease of interpretation.

We also determined overall site detection and occupancy for each model  $<\Delta 2\text{AIC}$  from the top model using the linear combination method from Unmarked. We set linear predictors from each model to their mean, incorporated both levels of categorical predictor overstorey and back-transformed the estimates of  $\psi$  and  $p$  to obtain probability. All analyses and model projections were conducted in Microsoft R Open version 3.5.3.

### 3 | RESULTS

Mule deer were observed a total of 172 out of 2,017 camera trap days with at least one detection at 27 out of 32 possible sites. The parametric bootstrap goodness-of-fit test suggested that global model fit was adequate ( $p = 0.36$ ). All models in the subset  $<\Delta 2\text{AIC}$  included the same five detection covariates: observation-level covariates for the average daily power of anthropogenic noise and site-level covariates for overstorey and distance to the nearest natural gas facility, road and well pad. All three candidate models received similar Akaike weights and including covariates on occupancy only led to minimal changes in model fit (Table 1).

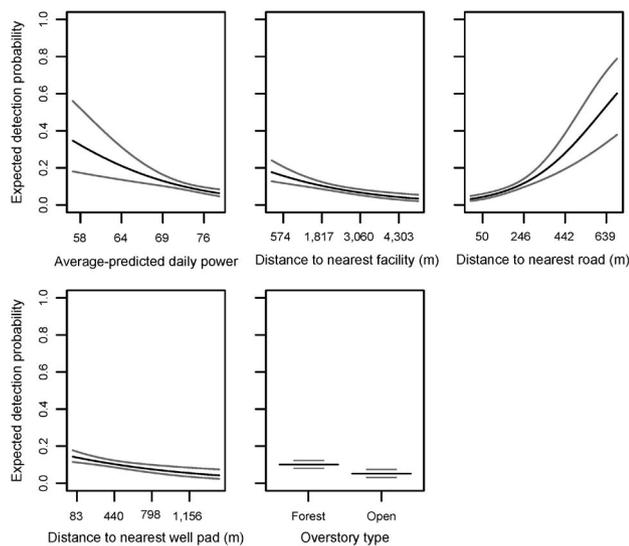
Averaged estimates of the three candidate models  $<\Delta 2\text{AIC}$  show that mule deer detection probability was reduced at sites with greater average daily power of anthropogenic noise (Table 2; Figure 2), ranging from a high of  $0.35 \pm 0.10$  at 57.26 dB to a low of  $0.06 \pm 0.01$  at 77.74 dB. Mule deer detection also was less likely further from natural gas facilities and well pads (Table 2; Figure 2; Supporting information: Results). Mule deer detection probability increased farther from roads (Table 2; Figure 2), reaching a high of  $0.60 \pm 0.11$  at 648.87 m and a low of  $0.03 \pm 0.01$  at 1.17 m. Finally, mule deer detections were less likely in habitat with open canopy (Table 2; Figure 2; Supporting information: Results). The three candidate models for mule deer also contained covariates on occupancy, though occurrence was high across sites and 95% confidence

**TABLE 1** Selection table of candidate single season occupancy models ( $\Delta 2\text{AICc}$ ) for mule deer. Covariates with  $p$  indicate an effect on detection while those with  $\psi$  are an effect on occupancy. The *Daily noise* covariate for  $\psi$  is the site average daily power of anthropogenic noise. The variables *Elevation* and *Northness* were not included in the detection model. All numerical covariates were standardized for comparison between effects prior to model fitting and are presented on the logit scale. The inclusion of a categorical predictor in a model is indicated by a plus symbol. 'k' denotes parameters estimated

Rank	Model	Intercept	Daily noise	Facilities	Roads	Wells	Over-storey	Elevation	Northness	Adj $R^2$	k	LogLik	AICc	$\Delta$	Weight
1	$p$	-2.19	-0.29	-0.48	0.87	-0.34	+	NA	NA	0.93	10	-562.90	1,156.27	0	0.35
	$\psi$	230.64		88.75	-156.79			120.76							
2	$p$	-2.19	-0.29	-0.48	0.87	-0.34	+	NA	NA	0.93	10	-562.92	1,156.31	0.04	0.35
	$\psi$	327.24			-197.19			204.03	71.71						
3	$p$	-2.19	-0.29	-0.48	0.87	-0.34	+	NA	NA	0.93	10	-563.05	1,156.58	0.31	0.30
	$\psi$	159.23	32.51		-109.43			122.03							
Null	$p$	-2.48						NA	NA	0	2	-604.85	1,214.12	57.85	0
	$\psi$	23.24													

Covariate	Estimate	SE	95 CI lower	95 CI upper
$p$ (Intercept)	-2.19	0.10	-2.39	-1.99
$p$ (Daily power)	-0.29	0.08	-0.44	-0.14
$p$ (Facilities)	-0.48	0.11	-0.69	-0.27
$p$ (Roads)	0.87	0.15	0.58	1.16
$p$ (Wells)	-0.34	0.10	-0.53	-0.15
$p$ (OverstoreyOpen)	-0.69	0.21	-1.10	-0.28
$\psi$ (Intercept)	242.51	3,152.08	-5,935.44	6,420.47
$\psi$ (Average power)	9.80	20.55	-17.90	82.93
$\psi$ (Elevation)	149.94	2,145.34	-4,054.84	4,354.73
$\psi$ (Facilities)	31.31	31.31	NaN	NaN
$\psi$ (Northness)	24.78	258.19	-781.51	924.93
$\psi$ (Roads)	-156.48	2074.91	-4,223.23	3,910.26

**TABLE 2** Full model-averaged coefficients and 95% confidence intervals for subset of models  $<\Delta 2\text{AIC}$  from top model for mule deer



**FIGURE 2** Effects of covariates predicted from averaged subset containing all models  $<\Delta 2\text{AIC}$  on detection probability of mule deer. Grey lines indicate 95% confidence interval

intervals overlapped 0 (Table 2). This suggests no clear pattern in site characteristics that was discernable through the modelling process. Given predictors from Model 1 (Table 1), the overall probability of daily detection was  $0.07 \pm 0.01$ , and the overall predicted probability that a site was occupied was  $1.00 \pm <0.01$ .

Leporids were observed a total of 311 out of 2,217 camera trap days, with at least one detection at 26 out of 32 sites. The parametric bootstrap goodness-of-fit test for the global model suggested that the model structure was adequate ( $p = 0.95$ ). Both models explaining leporid habitat use that were  $<\Delta 2\text{AIC}$  of the top model included distance to the nearest natural gas facility, road and well pad. In the case of leporids, the two candidate models each contained detection covariates for the distance to the nearest natural gas facility, road and well pad. However, there was no support for an effect of anthropogenic noise or overstorey type on leporid detection (Table 3).

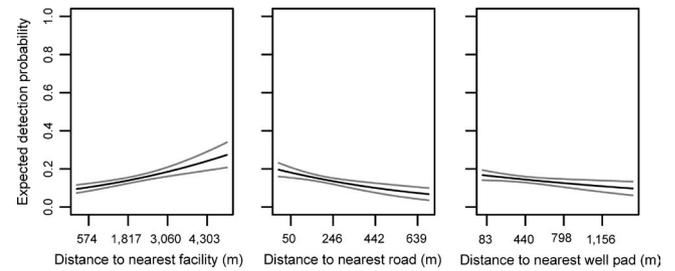
Averaged estimates of the two candidate models  $<\Delta 2\text{AIC}$  show that detection probability of leporids increased further from natural gas facilities (Table 4; Figure 3; Supporting information: Results) and decreased further from roads (Table 4; Figure 3; Supporting

**TABLE 3** Selection table of candidate single season occupancy models (<math>\Delta AIC</math>) for leporids. Covariates with  $p$  indicate an effect on detection while those with  $\psi$  are an effect on occupancy. The *Daily noise* covariate for  $\psi$  is the site average daily power of anthropogenic noise. The variables *Elevation* and *Northness* were not included in the detection model. All numerical covariates were standardized for comparison between effects prior to model fitting and are presented on the logit scale. 'k' denotes parameters estimated

Rank	Model	Intercept	Daily noise	Facilities	Roads	Wells	Overstorey	Elevation	Northness	Adj $R^2$	k	LogLik	AICc	$\Delta$	Weight
1	$p$	-1.79		0.34	-0.29	-0.16		NA	NA	0.81	6	-861.27	1737.90	0	0.68
	$\psi$	31.03					-18.10								
2	$p$	-1.78		0.33	-0.27	-0.16		NA	NA	0.82	7	-860.37	1739.40	1.51	0.32
	$\psi$	96.10			-13.40		-57.39								
Null	$p$	-1.74						NA	NA	0	2	-887.44	1779.28	41.39	0.00
	$\psi$	1.88													

**TABLE 4** Full model-averaged coefficients and 95% confidence intervals for subset of models <math>\Delta AIC</math> from top model for leporids

Covariate	Estimate	SE	95 CI lower	95 CI upper
$p$ (Intercept)	-1.79	0.06	-1.91	-1.66
$p$ (Facilities)	0.34	0.07	0.20	0.47
$p$ (Roads)	-0.28	0.08	-0.44	-0.12
$p$ (Wells)	-0.16	0.07	-0.30	-0.02
$\psi$ (Intercept)	51.82	77.03	-99.16	202.80
$\psi$ (Elevation)	-30.65	44.53	-117.94	56.63
$\psi$ (Roads)	-4.28	9.93	-40.17	13.37



**FIGURE 3** Effects of covariates predicted from averaged subset containing all models <math>\Delta AIC</math> on detection probability of leporids. Grey lines indicate 95% confidence interval

information: Results) and well pads (95% CI: -0.30 to -0.02; Table 4; Figure 3; Supporting information: Results). Both candidate models for leporids also contained covariates for occupancy, though 95% confidence intervals that overlapped 0 suggest poor fit of covariates on site occupancy (Table 3). Given predictors from Model 1 (Table 3), the overall probability of leporid daily detection was  $0.14 \pm 0.01$  and the overall probability of occupancy was  $1.00 \pm <0.01$ .

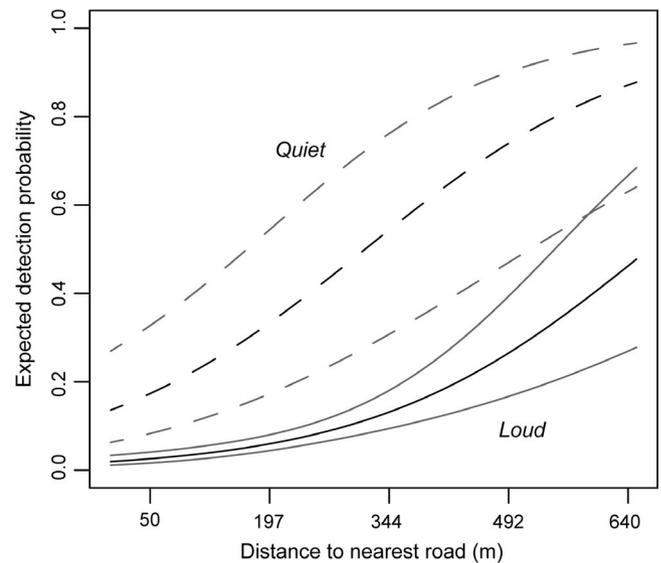
## 4 | DISCUSSION

Prior research suggests negative responses by wildlife to loud events such as encounters with aircraft, snowmobiles and vehicles (Shannon, Crooks, et al., 2016; Shannon, McKenna, et al., 2016). Often, however, studies were not structured to discern the relative impacts of acoustic stimuli or characterize the levels of noise exposure, particularly for large ungulates (Krausman et al., 1998; Laurian et al., 2008; Sawyer et al., 2009). We paired a continuous acoustic record with camera traps to incorporate anthropogenic noise with natural and anthropogenic landscape features into occupancy models of daily detections of mule deer and leporids. Mule deer were detected less frequently at sites with higher levels of daily anthropogenic noise, while leporid detection was not related to noise. Detection probabilities in both species were associated with proximity to anthropogenic landscape features including well pads, roads and facilities. For mule deer, this presents the potential for interactive effects of simultaneous acoustic and physical disturbance that may shape habitat use, particularly around roads. Our findings illustrate the importance of integrating

measures of the acoustic environment with known physical drivers of habitat use and represent a key development in our understanding of wild ungulate response to anthropogenic noise.

Our method isolates the effects of noise on mule deer by accounting for conditional exposure to natural and anthropogenic landscape features. Although the exact mechanism driving avoidance of noisy habitats is unknown, we provide evidence that noise directly underlies such a response. Masking of critical acoustic cues by anthropogenic noise is one potential mechanism explaining mule deer behaviour in response to noise. Acoustic masking can reduce an animal's knowledge of its immediate surroundings—leading to reduced environmental awareness and avoidance of impacted habitats (Lohr et al., 2003). Previously, researchers in the Piceance Basin explored this idea by fitting mule deer with on-animal acoustical monitors to analyse trends between acoustic vigilance and anthropogenic disturbance (Lynch et al., 2015). Mule deer acoustic vigilance rates increased with background noise levels (up to moderate levels) as well as factors that dictate effectiveness of visual vigilance such as light conditions and vegetation density. At high noise levels, deer decreased acoustic vigilance (Lynch et al., 2015). As such, high average daily power of anthropogenic noise appeared to reduce the effectiveness of acoustic vigilance. Such an effect could drive avoidance and reduce the estimates of detection probability. When sound stimuli are frequent or long-lasting, they are more likely to mask acoustic cues. However, loud, acute noise stimuli can elicit a startle response that may contribute to reduced detection at a site (Francis & Barber, 2013). Following a startle response to approaching humans, mule deer are known to relocate an average distance of over 800 m from the initiation point (Krausman et al., 2006), and the cumulative effects for sites exposed to increased noise could be reduced detections. Regardless of the mechanism, our results suggest that human noise changes mule deer behaviour and reduces habitat use.

In addition to anthropogenic noise, mule deer were influenced by anthropogenic landscape features associated with habitat alteration from oil and gas development. The strongest driver of mule deer detection in our study was the avoidance of sites near roads, which corresponds with previous results from this system that report avoidance of roads (Lendrum et al., 2013; Northrup et al., 2015) and is thought to be linked to increased rates of predation (Lendrum et al., 2018). In a post hoc analysis, we explored the interactive effects of noise and distance to road under contrasting loud and quiet noise conditions. The lowest recorded daily power of anthropogenic noise from our study was 57.26 dB. If we extend these quiet conditions to all possible sites while keeping other covariates at their mean and overstorey type as 'forest', mule deer detection estimates ranged from a low of  $0.14 \pm 0.05$  when roads were near to a high of  $0.88 \pm 0.08$  when roads were distant (Figure 4, dashed lines). Under high noise conditions (77.74 dB), predicted detection estimates ranged from a low of  $0.02 \pm 0.01$  when roads were near to a high of  $0.48 \pm 0.11$  when roads were distant (Figure 4, solid lines). Overall, under high noise conditions there is a 10% reduction in probability of detection when roads are near and a 44% reduction in the probability of detection when



**FIGURE 4** Predicted effects of distance to road on mule deer detection under high (dashed lines) and low (solid lines) noise conditions. Grey lines indicate 95% confidence interval

roads are far. This implies that both noise and fragmentation could drive habitat loss for mule deer and suggests that compounded effects of noise and physical landscape features could further reduce habitat selection.

Mule deer habitat use was less influenced by other anthropogenic landscape variables, including the distance to nearest natural gas facility and well pads. After controlling for the negative relationship between noise and detections, mule deer were more likely to use habitats near natural gas facilities and well pads, though effect sizes were small. This contrasts with previous results found in this system, where mule deer were found to strongly avoid well pads in the active drilling and production phase, particularly during the day (Northrup et al., 2015). Energy development activity during our study was markedly lower than during previous work in the system, with the system currently in a post-drilling, production phase—a period with relatively low human activity and associated noise. Given the avoidance of noise and the attraction of pads in this study, our results suggest that noise might be a key contributor to the strong aversion to pads found previously. Under quiet conditions, the large swaths of cleared land surrounding well pads may provide improved predator detection for prey and reduced cover for predators (Lendrum et al., 2018). Additionally, well pad reclamation techniques may provide seasonal foraging opportunities for mule deer that were not available when previous studies were conducted (Webb et al., 2011). These distinct responses further strengthen our assertion that future assessments of habitat use impacts on wildlife carefully account for levels of anthropogenic noise on the landscape.

The leporid community also responded to physical landscape features associated with shale gas development, but leporid detection trends did not support an effect of noise. Leporid detection was higher at sites closer to roads and well pads and further from natural gas facilities. These results are somewhat surprising given a previously reported increase in predation rate by carnivores near

roadways in this system (Lendrum et al., 2018). The lack of road and well pad avoidance may indicate that habitat modifications associated with these features, such as vegetative growth resulting from disturbance or restoration efforts, are attractive to leporids, and further illustrates how natural history differences can drive habitat use patterns in the context of anthropogenic noise.

Predation risk in mammals is largely based on body size, which dictates the type and quantity of predators for a species as well as availability of refugia (Cooper & Blumstein, 2015). Leporids may select habitats that have higher densities of rocky areas and abandoned burrows and may not travel far from their home range (Naughton, 2012). Mule deer rely on forested areas and the natural topography of the Piceance to provide safety from predators (Lynch et al., 2015; Northrup et al., 2015). In addition to habitat differences, Leporids reliance on smaller ranges may mean they are detected by cameras more quickly after disturbance, while the larger range of mule deer may mean they can more easily avoid sites associated with anthropogenic noise. Thus, daily detections in response to noise could be driven by body size and the scale of refugia rather than a lack of response to human noise. While we did not assess the effects of micro-site characteristics in this study, it may be warranted in future studies to further disentangle the effects of acoustic disturbances and habitat use. The juxtaposition of responses by two mammal groups provides insight into species-specific differences in response to noise that can inform management decisions among species.

Our results suggest a negative effect of anthropogenic noise on mule deer habitat use that is discernible in the context of other anthropogenic landscape features and extends well beyond the physical footprint of habitat alteration. However, our results indicate that physical and acoustic habitat factors do not act in isolation. To provide greater clarity, future studies should also use experimental approaches that control for levels of noise exposure and human activity across a gradient of fragmentation to determine relative contribution of each driver to habitat use. Understanding how noise interacts with the effects of habitat alteration and fragmentation is a fundamental issue for integration of acoustics into existing conservation frameworks (Piggott et al., 2015; Shannon, Crooks, et al., 2016; Shannon, McKenna, et al., 2016). For example, a species' threshold for persistence within human-altered environments may be driven by the relationship between degree of habitat fragmentation and vulnerability to predation (Haapakoski et al., 2013). Exposing fragmented habitats to anthropogenic noise further impacts behaviour and could exacerbate species loss by compounding the negative effects of fragmentation for prey species. Such cumulative impacts of noise and human alterations to the landscape are evident in our results.

## ACKNOWLEDGEMENTS

This research was supported by the National Park Service Natural Sounds and Night Skies Division, Colorado Parks and Wildlife (CPW), US Bureau of Land Management and ExxonMobil Production/XTO Energy, and the Sophie Danforth Conservation Biology Fund through the Roger Williams Park Zoo. T. Hawkins helped place song

meters. C. Garsha and M. McKenna helped prepare song meters and field gear.

## AUTHORS' CONTRIBUTIONS

R.T.B., P.E.L. and C.L. collected the data; N.J.K., R.T.B. and P.E.L. analysed the data; N.J.K. led the writing of the manuscript. All the authors conceived the ideas, designed the methodology, contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available from figshare <https://doi.org/10.6084/m9.figshare.12965945.v1> (Kleist et al., 2020).

## ORCID

Nathan J. Kleist  <https://orcid.org/0000-0002-2468-4318>

Rachel T. Buxton  <https://orcid.org/0000-0002-2772-8435>

George Wittemyer  <https://orcid.org/0000-0003-1640-5355>

## REFERENCES

- Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, 25(3), 180–189. <https://doi.org/10.1016/j.tree.2009.08.002>
- Bartmann, R. M., White, G. C., & Carpenter, L. H. (1992). Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs*, 121, 1–39.
- Barton, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Bayne, E. M., Habib, L., & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, 22(5), 1186–1193. <https://doi.org/10.1111/j.1523-1739.2008.00973.x>
- Borkowski, J. J., White, P. J., Garrott, R. A., Davis, T., Hardy, A. R., & Reinhart, D. J. (2006). Behavioral responses of bison and elk in Yellowstone to snowmobiles and snow coaches. *Ecological Applications*, 16(5), 1911–1925. [https://doi.org/10.1890/1051-0761\(2006\)016\[1911:BROBAE\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1911:BROBAE]2.0.CO;2)
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32. <https://doi.org/10.3390/rs10060911>
- Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R., & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. *PLoS ONE*, 7(7), 38–40. <https://doi.org/10.1371/journal.pone.0040505>
- Bureau of Land Management. (2016). *Record of Decision and Approved Resource Management Plan Amendment for the Bureau of Land Management Roan Plateau Planning Area Colorado River Valley Field Office and White River Field Office*. U.S. Department of the Interior Bureau of Land Management. [https://eplanning.blm.gov/public\\_projects/lup/65892/91073/109538/ROD\\_RMPA\\_Only.pdf](https://eplanning.blm.gov/public_projects/lup/65892/91073/109538/ROD_RMPA_Only.pdf)
- Buxton, R. T., Lendrum, P. E., Crooks, K. R., & Wittemyer, G. (2018). Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. *Global Ecology and Conservation*, 16, e00493. <https://doi.org/10.1016/j.gecco.2018.e00493>
- Buxton, R. T., McKenna, M. F., Brown, E., Ohms, R., Hammesfahr, A., Angeloni, L. M., Crooks, K. R., & Wittemyer, G. (2020). Varying behavioral responses of wildlife to motorcycle traffic. *Global Ecology and Conservation*, 21, e00844. <https://doi.org/10.1016/j.gecco.2019.e00844>
- Buxton, R. T., McKenna, M. F., Clapp, M., Meyer, E., Stabenau, E., Angeloni, L. M., Crooks, K., & Wittemyer, G. (2018). Efficacy of extracting indices from large-scale acoustic recordings to monitor

- biodiversity. *Conservation Biology*, 32(5), 1174–1184. <https://doi.org/10.1111/cobi.13119>
- Buxton, R. T., McKenna, M. F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L., & Wittemyer, G. (2017). Noise pollution is pervasive in U.S. protected areas. *Science*, 356(6337), 531–533. <https://doi.org/10.1126/science.aah4783>
- Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise affects risk assessment and attention: The distracted prey hypothesis. *Biology Letters*, 6(4), 458–461. <https://doi.org/10.1098/rsbl.2009.1081>
- Cooper, W. E., & Blumstein, D. T. (2015). *Escaping from predators: An integrative view of escape decisions and refuge use* (W. E. Cooper Jr. & D. T. Blumstein, Eds.). Cambridge University Press.
- Drolet, A., Dussault, C., & Côté, S. D. (2016). Simulated drilling noise affects the space use of a large terrestrial mammal. *Wildlife Biology*, 22(6), 284–293. <https://doi.org/10.2981/wlb.00225>
- Dyer, S. J., O'Neill, J. P., Wasel, S. M., & Boutin, S. (2001). Avoidance of industrial development by woodland caribou. *The Journal of Wildlife Management*, 65(3), 531. <https://doi.org/10.2307/3803106>
- Fiske, I., & Chandler, R. (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10). <https://doi.org/10.18637/jss.v043.i10>
- Fiske, I., & Chandler, R. (2019). Overview of unmarked: An R package for the analysis of data from unmarked animals. CRAN. <https://doi.org/10.1002/wics.10>
- Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: An urgent conservation priority. *Frontiers in Ecology and the Environment*, 11(6), 305–313. <https://doi.org/10.1890/120183>
- Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Current Biology*, 19(16), 1415–1419. <https://doi.org/10.1016/j.cub.2009.06.052>
- Franklin, D. J., Lonsbury-Martin, B. L., Stagner, B. B., & Martin, G. K. (1991). Altered susceptibility of 2f1-f2 acoustic-distortion products to the effects of repeated noise exposure in rabbits. *Hearing Research*, 53(2), 185–208. [https://doi.org/10.1016/0378-5955\(91\)90053-C](https://doi.org/10.1016/0378-5955(91)90053-C)
- Geist, V. (1981). *Behavior: Adaptive strategies. Mule and black-tailed deer of North America*. University of Nebraska Press.
- Griffiths, M., Calaby, J., & McIntosh, D. (1960). The stress syndrome in the rabbit. *CSIRO Wildlife Research*, 5(2), 134. <https://doi.org/10.1071/cwr9600134>
- Haapakoski, M., Sundell, J., & Ylönen, H. (2013). Mammalian predator-prey interaction in a fragmented landscape: Weasels and voles. *Oecologia*, 173(4), 1227–1235. <https://doi.org/10.1007/s00442-013-2691-y>
- Hawkins, S. J., Charpentier, R. R., Schenk, C. J., Leathers-Miller, H. M., Klett, T. R., Brownfield, M. E., Finn, T. M., Gaswirth, S. B., Marra, K. R., Le, P. A., Mercier, T. J., Pitman, J. K., & Tennyson, M. E. (2016). Assessment of Continuous (Unconventional) Oil and Gas Resources in the Late Cretaceous Mancos Shale of the Piceance Basin, Uinta-Piceance Province, Colorado and Utah, 2016. In *U.S. Geological Survey Fact Sheet 2016–3030*. <https://doi.org/10.3133/fs20163030>
- Holt, D. E., & Johnston, C. E. (2014). Evidence of the Lombard effect in fishes. *Behavioral Ecology*, 25(4), 819–826. <https://doi.org/10.1093/beheco/aru028>
- Injaian, A. S., Taff, C. C., & Patricelli, G. L. (2018). Experimental anthropogenic noise impacts avian parental behaviour, nestling growth and nestling oxidative stress. *Animal Behaviour*, 136, 31–39. <https://doi.org/10.1016/j.anbehav.2017.12.003>
- International Energy Agency. (2018). 2018 World Energy Outlook: Executive Summary. In *Oecd/lea*. Retrieved from [www.iea.org](http://www.iea.org)
- Ivan, J. S., & Newkirk, E. S. (2016). Cpw Photo Warehouse: A custom database to facilitate archiving, identifying, summarizing and managing photo data collected from camera traps. *Methods in Ecology and Evolution*, 7(4), 499–504. <https://doi.org/10.1111/2041-210X.12503>
- Kleist, N. J., Buxton, R. T., Lendrum, P. E., Linares, C., Crooks, K. R., & Wittemyer, G. (2020). Data from: Noise and landscape features influence habitat use of mammalian herbivores in a natural gas field. *Figshare*. <https://doi.org/10.6084/m9.figshare.12965945.v1>
- Kleist, N. J., Guralnick, R. P., Cruz, A., & Francis, C. D. (2016). Anthropogenic noise weakens territorial response to intruder's songs. *Ecosphere*, 7(3), 1–11. <https://doi.org/10.1002/ecs2.1259>
- Kleist, N. J., Guralnick, R. P., Cruz, A., Lowry, C. A., & Francis, C. D. (2018). Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proceedings of the National Academy of Sciences of the United States of America*, 115(4), E648–E657. <https://doi.org/10.1073/pnas.1709200115>
- Knick, S. T., Dobkin, D. S., Rotenberry, J. T., Schroeder, M. A., Vander Haegen, W. M., & van Riper, C. (2003). Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *The Condor*, 105(4), 611. <https://doi.org/10.1650/7329>
- Krausman, P. R., Avey, J., Brown, C. F., Devers, P. K., Tull, J. C., Jansen, B. D., & Cain, J. W. (2006). Distances moved by startled desert mule deer. *The Southwestern Naturalist*, 51(3), 436–439. [https://doi.org/10.1894/0038-4909\(2006\)51\[436:dmsdm\]2.0.co;2](https://doi.org/10.1894/0038-4909(2006)51[436:dmsdm]2.0.co;2)
- Krausman, P. R., Wallace, M. C., Hayes, C. L., & DeYoung, D. W. (1998). Effects of Jet Aircraft on mountain sheep. *The Journal of Wildlife Management*, 62(4), 1246–1254. <https://doi.org/10.2307/3801988>
- Landon, D. M., Krausman, P. R., Koenen, K. K. G., & Harris, L. K. (2003). Pronghorn use of areas with varying sound pressure levels. *The Southwestern Naturalist*, 48(4), 725–728. [https://doi.org/10.1894/0038-4909\(2003\)048<0725:puoawv>2.0.co;2](https://doi.org/10.1894/0038-4909(2003)048<0725:puoawv>2.0.co;2)
- Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M., & Breton, L. (2008). Behavior of moose relative to a road network. *Journal of Wildlife Management*, 72(7), 1550. <https://doi.org/10.2193/2008-063>
- Lendrum, P. E., Anderson, C. R., Long, R. A., Kie, J. G., & Bowyer, R. T. (2012). Habitat selection by mule deer during migration: Effects of landscape structure and natural-gas development. *Ecosphere*, 3(9), <https://doi.org/10.1890/ES12-00165.1>
- Lendrum, P. E., Anderson, C. R., Monteith, K. L., Jenks, J. A., & Bowyer, R. T. (2013). Migrating mule deer: Effects of anthropogenically altered landscapes. *PLoS ONE*, 8(5). <https://doi.org/10.1371/journal.pone.0064548>
- Lendrum, P. E., Crooks, K. R., & Wittemyer, G. (2017). Changes in circadian activity patterns of a wildlife community post high-intensity energy development. *Journal of Mammalogy*, 98(5), 1265–1271. <https://doi.org/10.1093/jmammal/gyx097>
- Lendrum, P. E., Northrup, J. M., Anderson, C. R., Liston, G. E., Aldridge, C. L., Crooks, K. R., & Wittemyer, G. (2018). Predation risk across a dynamic landscape: Effects of anthropogenic land use, natural landscape features, and prey distribution. *Landscape Ecology*, 33(1), 157–170. <https://doi.org/10.1007/s10980-017-0590-z>
- Liaw, A., & Wiener, M. (2002). Classification and regression by random forest. *R News*, 2(3), 18–22.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68(4), 619–640. <https://doi.org/10.1139/z90-092>
- Lohr, B., Wright, T. F., & Dooling, R. J. (2003). Detection and discrimination of natural calls in masking noise by birds: Estimating the active space of a signal. *Animal Behaviour*, 65(4), 763–777. <https://doi.org/10.1006/anbe.2003.2093>
- Lynch, E., Northrup, J. M., McKenna, M. F., Anderson, C. R., Angeloni, L., & Wittemyer, G. (2015). Landscape and anthropogenic features influence the use of auditory vigilance by mule deer. *Behavioral Ecology*, 26(1), 75–82. <https://doi.org/10.1093/beheco/aru158>
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)

- Maier, J. A. K., Murphy, S. M., White, R. G., & Smith, M. D. (1998). Responses of caribou to overflights by low-altitude Jet Aircraft. *The Journal of Wildlife Management*, 62(2), 752. <https://doi.org/10.2307/3802352>
- Marai, I. F. M., & Rashwan, A. A. (2004). Rabbits behavioural response to climatic and managerial conditions – A review. *Archives Animal Breeding*, 47(5), 469–482. <https://doi.org/10.5194/aab-47-469-2004>
- Martinez, C., & Preston, T. M. (2018). Oil and gas development footprint in the Piceance Basin, western Colorado. *Science of the Total Environment*, 616–617, 355–362. <https://doi.org/10.1016/j.scitotenv.2017.10.280>
- Meisingset, E. L., Loe, L. E., Brekkum, Ø., Van Moorter, B., & Mysterud, A. (2013). Red deer habitat selection and movements in relation to roads. *Journal of Wildlife Management*, 77(1), 181–191. <https://doi.org/10.1002/jwmg.469>
- Merchant, N. D., Fristrup, K. M., Johnson, M. P., Tyack, P. L., Witt, M. J., Blondel, P., & Parks, S. E. (2015). Measuring acoustic habitats. *Methods in Ecology and Evolution*, 6(3), 257–265. <https://doi.org/10.1111/2041-210X.12330>
- Murphy, M. A., Evans, J. S., & Storfer, A. (2010). Quantifying Bufo boreas connectivity in Yellowstone National Park with landscape genetics. *Ecology*, 91(1), 252–261. <https://doi.org/10.1890/08-0879.1>
- Naughton, D. (2012). The natural history of Canadian mammals. *The Natural History of Canadian Mammals*, <https://doi.org/10.5860/choice.50-6766>
- Northrup, J. M., Anderson, C. R., & Wittemyer, G. (2015). Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. *Global Change Biology*, 21(11), 3961–3970. <https://doi.org/10.1111/gcb.13037>
- Northrup, J. M., & Wittemyer, G. (2013). Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters*, 16(1), 112–125. <https://doi.org/10.1111/ele.12009>
- Olaya, V. (2009). Basic land-surface parameters. *Developments in Soil Science*, 33, 141–169. [https://doi.org/10.1016/S0166-2481\(08\)00006-8](https://doi.org/10.1016/S0166-2481(08)00006-8)
- Parks, S. E., Johnson, M., Nowacek, D., & Tyack, P. L. (2011). Individual right whales call louder in increased environmental noise. *Biology Letters*, 7(1), 33–35. <https://doi.org/10.1098/rsbl.2010.0451>
- Parris, K. M., & McCarthy, M. A. (2013). Predicting the effect of urban noise on the active space of avian vocal signals. *The American Naturalist*, 182(4), 452–464. <https://doi.org/10.1086/671906>
- Phillips, J. N., & Derryberry, E. P. (2018). Urban sparrows respond to a sexually selected trait with increased aggression in noise. *Scientific Reports*, 8(1), 1–10. <https://doi.org/10.1038/s41598-018-25834-6>
- Piggott, J. J., Townsend, C. R., & Matthaei, C. D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution*, 5(7), 1538–1547. <https://doi.org/10.1002/ece3.1465>
- Sawyer, H., Kauffman, M. J., & Nielson, R. M. (2009). Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, 73(7), 1052–1061. <https://doi.org/10.2193/2008-478>
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113. <https://doi.org/10.1111/j.2041-210x.2010.00012.x>
- Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS ONE*, 9(4), <https://doi.org/10.1371/journal.pone.0094630>
- Shannon, G., Crooks, K. R., Wittemyer, G., Fristrup, K. M., & Angeloni, L. M. (2016). Road noise causes earlier predator detection and flight response in a free-ranging mammal. *Behavioral Ecology*, 27(5), 1370–1375. <https://doi.org/10.1093/beheco/arw058>
- Shannon, G., Lewis, J. S., & Gerber, B. D. (2014). Recommended survey designs for occupancy modelling using motion-activated cameras: Insights from empirical wildlife data. *PeerJ*, 2014(1), 1–20. <https://doi.org/10.7717/peerj.532>
- Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., Warner, K. A., Nelson, M. D., White, C., Briggs, J., McFarland, S., & Wittemyer, G. (2016). A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews*, 91(4), 982–1005. <https://doi.org/10.1111/brv.12207>
- Slabbekoorn, H. (2013). Songs of the city: Noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Animal Behaviour*, 85(5), 1089–1099. <https://doi.org/10.1016/j.anbehav.2013.01.021>
- Sleeter, B. M., Wilson, T. S., & Acevedo, W. (Eds.), (2012). Status and trends of land change in the Western United States—1973 to 2000: U.S. Geological Survey Professional Paper 1794–A. 324 pp. <https://pubs.usgs.gov/pp/1794/a/>
- Souther, S., Tingley, M. W., Popescu, V. D., Hayman, D. T. S., Ryan, M. E., Graves, T. A., Hartl, B., & Terrell, K. (2014). Biotic impacts of energy development from shale: Research priorities and knowledge gaps. *Frontiers in Ecology and the Environment*, 12(6), 330–338. <https://doi.org/10.1890/130324>
- Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C. M., Dominoni, D. M., Shannon, G., Aschehoug, E., Goodwin, S. E., Kawahara, A. Y., Luther, D., Spoelstra, K., Voss, M., & Longcore, T. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. *Trends in Ecology & Evolution*, 30(9), 550–560. <https://doi.org/10.1016/j.tree.2015.06.009>
- Trainor, A. M., McDonald, R. I., & Fargione, J. (2016). Energy sprawl is the largest driver of land use change in United States. *PLoS ONE*, 11(9), 1–16. <https://doi.org/10.1371/journal.pone.0162269>
- Ware, H. E., McClure, C. J. W., Carlisle, J. D., & Barber, J. R. (2015). A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proceedings of the National Academy of Sciences of the United States of America*, 112(39), 12105–12109. <https://doi.org/10.1073/pnas.1504710112>
- Webb, S. L., Dzialak, M. R., Osborn, R. G., Harju, S. M., Wondzell, J. J., Hayden-Wing, L. D., & Winstead, J. B. (2011). Using pellet groups to assess response of elk and deer to roads and energy development. *Wildlife Biology in Practice*, 7(1), 32–40. <https://doi.org/10.2461/wbp.2011.7.3>
- Weller, C., Thomson, J., Morton, P., & Aplet, G. (2002). *Fragmenting our lands: The ecological footprint from oil and gas development*. The Wilderness Society.
- Wellington, K., Bottom, C., Merrill, C., & Litvaitis, J. A. (2014). Identifying performance differences among trail cameras used to monitor forest mammals. *Wildlife Society Bulletin*, 38(3), 634–638. <https://doi.org/10.1002/wsb.425>
- White, G. C., & Lubow, B. C. (2007). Fitting population models to multiple sources of observed data. *The Journal of Wildlife Management*, 66(2), 300. <https://doi.org/10.2307/3803162>
- Wisdom, M. J., Rowland, M. M., & Suring, L. H. (2005). *Habitat threats in the sagebrush ecosystem*. Alliance Communications Group.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Kleist NJ, Buxton RT, Lendrum PE, Linares C, Crooks KR, Wittemyer G. Noise and landscape features influence habitat use of mammalian herbivores in a natural gas field. *J Anim Ecol*. 2021;00:1–11. <https://doi.org/10.1111/1365-2656.13416>