

THESIS

THE EFFECTS OF ANTHROPOGENIC NOISE AND HUMAN  
ACTIVITIES ON UNGULATE BEHAVIOR

Submitted by

Casey L. Brown

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 2010

Master's Committee:

Director: N. Leroy Poff

Advisor: Lisa Angeloni

Co-Advisor: Kevin Crooks

Kurt Fristrup

Copyright by Casey L. Brown 2010

All Rights Reserved

## ABSTRACT

### THE EFFECTS OF ANTHROPOGENIC NOISE AND HUMAN ACTIVITIES ON UNGULATE BEHAVIOR

The effect of anthropogenic noise on terrestrial wildlife is a relatively new area of study with broad ranging management implications. Human activities may increase noise in protected areas, including U.S. National Parks. Grand Teton National Park (GTNP) draws nearly 4 million visitors a year to recreate on park roads, trails, and campgrounds. As visitors travel through the park and congregate around wildlife viewing locations, noise is one of the many disturbance stimuli introduced into the environment. This study investigated the potential impacts of human induced noise and human activities on the behavior of elk (*Cervus elaphus*) and pronghorn (*Antilocapra americana*) along a transportation corridor in GTNP. We conducted roadside scan surveys and focal observations of ungulate behavior while concurrently recording human activity and anthropogenic noise. Ungulates were less responsive (less likely to perform vigilant, flight and defensive behaviors) in noisy environments when more vehicles were passing and more responsive when pedestrians were present. These effects of noise on responsive behavior may have both positive and negative implications for wildlife conservation and management.

## ACKNOWLEDGMENTS

This project is the result of the assistance and advice from many individuals within Colorado State University and the National Park Service Sounds Lab. First, I would like to thank my co-advisers, Dr. Lisa Angeloni and Dr. Kevin Crooks, for their unwavering support throughout this project. I am grateful to my committee member, Dr. Kurt Fristrup, for his participation in this project, his willingness to provide equipment and support for the acoustical analysis, and his extensive knowledge of bioacoustics. I would like to thank Dr. Jesse Barber and Ms. Amanda Hardy, who helped with the initial study design and continued to give feedback and support throughout the duration of this project. I am also grateful for my field crew, Melinda Scott and Kristen Van Ort, for their diligent and organized work along with their great attitudes. I would like to thank Dr. Dan Mennitt and Damon Joyce, who have provided advice and support throughout the acoustical analysis. The scientists and personnel at the Cornell Ornithology Lab were all invaluable in their technical support. I am grateful for Dr. Jens Eickoff, Dr. Chris Burdett, and Dr. David Anderson for their statistical advice. Finally, I would like to thank my mom and dad for their support and love. Funding support was provided by the National Science Foundation's GK12 Fellowship, Rocky Mountain Goat Foundation Bill Burtress Fellowship, Math Science Partnership Fellowship, and my co-adviser, Dr. Lisa Angeloni.

## TABLE OF CONTENTS

CHAPTER 1: THE EFFECTS OF ANTHROPOGENIC NOISE AND HUMAN ACTIVITIES ON UNUGULATE BEHAVIOR.....	1
INTRODUCTION.....	1
METHODS.....	4
STUDY SITE.....	4
BEHAVIORAL OBSERVATION METHODS.....	5
Scan Sampling.....	5
Focal Animal Sampling.....	8
DATA ANALYSIS.....	10
Scan Sampling.....	10
Focal Animal Sampling.....	11
RESULTS.....	12
Scan Sampling.....	12
Focal Animal Sampling.....	14
DISCUSSION.....	15
ACKNOWLEDGMENTS.....	19
LITERATURE CITED.....	20

## LIST OF TABLES

### CHAPTER 1:

1.)	Summary of the relationships between acoustic, human activity, and covariate predictor variables and ungulate responsiveness for scan samples (nonlinear mixed model with herd ID as a random effect) and focal samples (linear regression).....	27
2)	AIC <sub>c</sub> model selection results where acoustic variables, human activity variables, and covariates were used to explain responsive behavior of ungulates during scan samples.....	28
3)	Top models predicting ungulate responsiveness selected with lowest AIC <sub>c</sub> values out of full model sets from scan and focal samples.....	29
4)	Relative variable importance weights for all variables within our full model sets for scan samples (64 total) and focal samples (32 total).....	30
5)	AIC <sub>c</sub> model selection results where human activity variables and covariates were used to explain responsive behavior of individual focal animals.....	31

# **CHAPTER 1**

## **THE EFFECTS OF ANTHROPOGENIC NOISE AND HUMAN ACTIVITIES ON UNGULATE BEHAVIOR**

### **INTRODUCTION**

The impact of anthropogenic noise on animals is a relatively new field of study with broad ranging conservation implications (Radle 1998, Rabin et al. 2006, Barber et al. 2010). Noise disturbances can be deleterious to an animal's physiology and behavior. If chronic, the noise may affect an animal's auditory system (Henderson 1976, Dooling & Popper 2007), increase cardiac and stress levels (Weisenberger et al. 1996, Krausman et al. 1998, Owen et al. 2004), and impair communication among individuals, groups and species (Erbe et al. 1999, Bee & Swanson 2007, Habib et al. 2007, Slabbekoorn & Ripmeester 2008). Noise has also been identified as a disturbance that could induce behavioral responses similar to those associated with predation risk (Dill 1974). The risk-disturbance hypothesis predicts that animals exposed to anthropogenic disturbances, such as noise, will exhibit antipredatory behavior that takes time and energy away from fitness-enhancing activities (Frid & Dill 2002). Indeed, prior studies have documented behavioral responses to anthropogenic noise for a variety of taxa, including mammals, birds, and amphibians (e.g., Quinn et al. 2006, Rabin et al. 2006, Bee & Swanson 2007, Nowacek et al. 2007, Habib et al. 2007, Bayne et al. 2008, Lengagne 2008, Francis et al. 2009). Specifically, noise disturbance has been shown to increase antipredatory

responses, such as vigilance and flight, in some species (Harrington & Veitch 1991, Weisenberger et al. 1996, Maier et al. 1998, Quinn et al. 2006). An increase in vigilance may be costly if it results in a decrease in maintenance activities such as foraging (Childress & Lung 2003, Fortin 2004), and flight may expend valuable amounts of energy (Ydenberg & Dill 1986). Thus, noise can affect habitat selection, foraging patterns, and overall energy budgets (Stockwell et al. 1991, Bradshaw et al. 1998), with potential population-level effects.

Large mammals, such as ungulates, may be particularly sensitive to anthropogenic disturbances (Stankowich 2008, Bolger et al. 2008), including human activities associated with transportation and recreation (e.g., Gavin & Komers 2006, St. Clair & Forrest 2009, Fahrig & Rytwinski 2009). Noise is a common disturbance associated with such activities. Much of what is known about how transportation noise impacts ungulate behavior results from studies on aircraft disturbance (Harrington & Veitch 1991, Weisenberger et al. 1996, Maier et al. 1998, Radle 1998, Krausman 1998, Landon et al. 2003). Aircraft noise can alter ungulate behavior by increasing vigilance (Maier et al. 1998) and inducing flight response and habitat displacement (Harrington & Veitch 1991, Bleich et al. 1993, Krausman 1998). Energetic impacts on ungulates have also been reported as a result of aircraft disturbance. For example, Stockwell et al. (1991) noted a 43% reduction in foraging efficiency of desert bighorn sheep (*Ovis canadensis nelsoni*) in Grand Canyon National Park from helicopter disturbance.

Although road networks provide prevalent sources of noise (Barber et al. 2009, Manning et al. 2009) that may also modify behavior, few studies have examined the effects of road noise on ungulates. Vehicles and recreationists can produce noise at



ground level, and past research has indicated that snowmobile, biking and hiking in particular can alter the behavior of ungulates (Knight & Cole 1995, Taylor & Knight 2003, Borkowski et al. 2006), although the degree to which ungulates are responding to visual or acoustic disturbances generated from these activities is largely unknown. A growing number of studies have noted a range of behavioral responses in animal communities due to noise along road corridors. For example, birds sing at higher pitches, perhaps to reduce acoustic interference from low-frequency noises common along road systems (Slabbekoorn & Peet 2003, Slabbekoorn & den Boer-Visser 2006, Wood et al. 2006, Parris et al. 2009). Male frogs call less frequently (Lengagne 2008), and female frogs take longer to locate males in traffic noise (Bee & Swanson 2007). More generally, noise from roadways has been identified as an anthropogenic disturbance impacting abundance and distribution of a variety of taxa, with predominantly negative effects on large mammals (Fahrig & Rytwinski 2009).

Transportation networks have seen an increase in vehicle traffic throughout the United States during the past three decades (U.S. Federal Highway Administration 2009). This includes increased traffic along U.S. National Park Service (NPS) roads (Burson et al. 1999, National Park Service 2009). For many national park units, transportation on roads is the primary mode of travel to visit sites throughout the park. For example, Grand Teton National Park (GTNP) had 587,324 recreational visitors enter the park in approximately 217,527 vehicles just during the month of July, 2008 (National Park Service 2008). The NPS has been measuring both ambient and anthropogenic sounds for over 20 years (Pilcher et al. 2009), detecting a notable increase in ambient sound levels originating from transportation corridors (Barber et al. 2010).

The goal of our research was to quantify the behavioral response of ungulates to human induced noise and to different forms of human activity along a travel corridor in Grand Teton National Park. The corridor includes a scenic stretch of road and a multi-use pathway for non-motorized traffic that runs through predominantly open habitat where large ungulate species congregate, providing wildlife viewing opportunities for park visitors. If, according to the risk disturbance hypothesis (Frid & Dill 2002), activities of park visitors represent a form of predation risk to ungulates, then we predicted ungulates would display heightened levels of responsive behavior in the presence of anthropogenic stimuli, including both noise and human activity. Results from this study will provide novel information regarding wildlife responses to noise stimuli emanating from transportation corridors.

## **METHODS**

### **STUDY SITE**

Our study was conducted along Teton Park Road (TPR) in Grand Teton National Park in northwestern Wyoming, USA (43-50'00" N, 110-42'03" W). Park boundaries include approximately 1255 km<sup>2</sup> and host a wide range of ecosystem types, including alpine and subalpine environs at higher elevations and a sage-brush dominated community at lower elevations. TPR is located at the eastern base of the Teton Range and traverses the valley floor from north to south. In summer 2008, 12 km (7.7 miles) of a paved multi-use pathway for non-motorized travel was constructed parallel to TPR from the town of Moose at the southern two-thirds of our study area, to Jenny Lake at the northern end. This 22 km stretch of road and pathway was our study site. Our research

focused on the two ungulate species most prevalent along TPR, pronghorn (*Antilocapra americana*) and elk (*Cervus elaphus*), with elk the most abundant ungulate in the area.

## **BEHAVIORAL OBSERVATION METHODS**

### ***Scan sampling***

We conducted scan sampling from June to October 2008 to record the behavior of individuals within ungulate herds along TPR. We used 42 predetermined scan point locations to systematically scan for ungulates. Scan points were located every 160 to 650 meters alongside TPR and were selected to maximize visible area from the road and to standardize search efforts over each sampling bout throughout the entire study site. Scan sampling occurred during both daytime and crepuscular hours, with staggered starting times to balance sampling effort across dusk, dawn and daylight periods, allowing at least twelve hours between surveys.

To conduct scan sampling, we drove along TPR starting at either the northern or southern end of the study area and stopped at each scan point to scan for the presence of ungulate herds with binoculars and spotting scope. A herd was defined as  $\geq 1$  animal present, and a distance of 100 meters between groups of individuals was used to delineate different herds. We used binoculars and spotting scopes to scan for animals. Once a herd was sighted, initial data were recorded, including the time of observation; herd size; and whether the herd was clustered ( $\geq 50\%$  of individuals in herd  $< 25$  meters from nearest neighbor) or dispersed ( $\geq 50\%$  of individuals in herd  $\geq 25$  meters from nearest neighbor). We used laser rangefinders to measure the distance to the center of the herd from the road

(our vehicle) and the distance to closest vegetation cover, categorized as near (0-100 meters) or far (>100 meters) to cover.

Once the initial herd data were collected, behavior was recorded only if the herd was still visible within 500 meters of the scan point to ensure accuracy of behavioral observations. One observer scanned the herd from left to right recording behavior of each individual animal. Categorization of behavior followed definitions used by Childress and Lung (2005) and Borkowski et al. (2006) for elk in Yellowstone National Park, and included feeding, grooming (licking or scratching), bedded, mating (sparring or bugling), traveling (walking), flight (running), scanning (standing with head above shoulder level), vigilant (displaying alarm or acute attention toward stimuli), and defensive (kicking, biting, charging). Scan surveys lasted approximately 1 minute, allowing enough time to record the behavior of each individual in the herd.

While ungulate behavioral data were collected, a second observer simultaneously conducted a scan sample of all human activities within 200 meters of each scan point. Ungulates have been shown to be sensitive to the approach speed and direction of anthropogenic stimuli (Stankowich, 2008), thus stopped versus moving vehicles may elicit different responses; therefore vehicles were uniquely categorized as moving versus stopped. Ungulates may also be particularly responsive to the human form (Papouchis et al. 2001, Taylor and Knight 2003, Stankowich, 2008); therefore we also recorded the number of pedestrians along TPR. Human activities recorded during scan samples included the number of automobiles (autos) passing, the number of autos stopped (including our own vehicle), and the number of pedestrians at each scan point. Observers strived to remain in the vehicle to reduce potential observer effects, but on rare occasions

when it was necessary to exit the vehicle during a scan observation (e.g., to see a herd that was partially obscured from view), we recorded the observer as a pedestrian to account for our presence and potential influence. We also recorded whether motorcycles, trucks (including RV's and large commercial and construction vehicles), and bicycles were passing but rarely recorded these activities during our scan samples. Consequently, we did not analyze these three activities separately, but rather grouped passing motorcycles, RV's, and autos into an additional category (total vehicles passing) and omitted passing bicycles from the analyses.

Concurrent with the ungulate and human behavioral observations, a portable recording device was utilized to sample noise along the travel corridor. We found these devices to be an inexpensive option when compared to traditional recording equipment to capture anthropogenic noise. Our recorders provided uncalibrated sound files that provide a relative metric of sound that have been found to accurately capture sound pressure levels (Mennitt, unpublished data). The recorder (iAudio, Cowan America, Irvine, California) was attached to two funnel microphones mounted on our research vehicle approximately 1.5 meters off the ground and spaced 2 meters apart pointing in opposite directions. The close proximity of the recorder to the road allowed us to effectively record motorized vehicles, road noise, bicycles, and pedestrians (i.e., human voices). We used a sampling rate of 64 bits per second and recordings were saved as WMA files. We produced waveforms using SWITCH sound file converter (NCH Software, Canberra, Australia) and spectrograms using RAVEN PRO 1.4 (Cornell University, Ithaca, New York) to quantify sound measurements. We measured relative amplitude (peak and average power), peak frequency, and the inter-quartile range (IQR) for each observation

and provided summary statistics of these metrics to generally describe the acoustic characteristics recorded during our scan samples. Power is a measurement of amplitude over time, and peak power is the measurement of the maximum power of a recording. The interval over which peak power is defined is the spectrogram bin, which is one frame in time and one frequency bin. Average power is the mean power over the entire observation. The perception of loudness depends not only on the amplitude of a wave, but also on its frequency; sound travels in waves and the duration between waves per unit time is the frequency of a sound, measured in Hertz (Hz). Peak frequency is the frequency at which peak power occurs within the sample. The IQR divides a spectrogram into two frequency intervals that contain 25% and 75% of the energy in the sample, representing the 1<sup>st</sup> and 3<sup>rd</sup> quartile frequencies.

### ***Focal Animal Sampling***

In addition to scan sampling, we conducted extended behavioral observations of individual focal animals. Focal animal sampling was initiated opportunistically, between scan sampling events, as well as systematically, during scheduled daytime and crepuscular focal animal sessions. Observers drove the length of the study area searching for ungulate herds. When a herd was sighted within 500 meters of the road, sex classification (adult male, adult female and adult female with calf), dispersion, and location were recorded. A focal animal was randomly selected within a herd by counting individuals in the herd from left to right until reaching the chosen random number. The focal animal observer continuously recorded behavior (described above), including any changes in behavior, for up to 50 minutes or until the focal animal bedded or moved out

of view. Focal animal samples used in the analyses required a minimum 10-minute duration, with an average sample duration of 19.5 minutes (SE=0.19, range: 10-47 minutes;  $n = 100$ ). If a focal animal was lost from view during the early stages of a focal sample ( $n = 17$  instances), we selected a second focal animal with an identical sex classification to observe. If we were unable to increase our total observation time to 10 minutes with the second focal animal before it was lost from view ( $n = 10$  instances), we then selected a third focal animal. In these instances, we combined the behavioral data from the two or three multiple focal observations conducted on a single herd to produce a weighted average (weighted by the duration of each observation) response across individuals.

As with scan samples, we measured average power, peak power, peak frequency, and inter-quartile range (IQR) and provide summary statistics for these metrics to describe acoustic characteristics recorded during our focal samples. Acoustic recordings began with the start of a focal sample and continuously recorded sound for the duration of the sample. Simultaneously, a second observer alternated between conducting scan samples of behaviors for all individuals within the herd and then conducting scan samples of human activities in the vicinity (within 200 meters of the observers). The alternating herd and human activity scans continued throughout the duration of the focal animal sample, with repeated intervals of approximately 45 seconds to 3 minutes; the duration and frequency of scan samples were dependent on herd size and amount of human activity in the vicinity. The herd behavior scan data were collected for a concurrent study (Hardy, unpublished data); only the human activity data were used here. Anthropogenic

activities recorded and analyzed for focal samples included the number of autos, motorcycles, RV's, and bicycles passing; autos stopped; and pedestrians present.

## **DATA ANALYSIS**

### ***Scan sampling***

From our scan data, we determined the number of individuals in a herd that were exhibiting responsive behaviors, which included vigilant, flight, traveling, and defensive categories (Goldstein 2006, Borkowski 2006). We developed a candidate set of nonlinear mixed models with a binomial distribution (Proc NLMixed, SAS 9.1) to evaluate if and how acoustic variables and human activities predicted the probability that each individual within a herd was responding or not responding. We included the herd ID as a random effect to avoid statistical issues related to pseudoreplication, since it is reasonable to assume that an individual's behavior in a herd is correlated with the behavior of the other animals within the same herd.

Predictor variables included acoustic metrics (average power, peak power, peak frequency, and IQR) and human activities (automobiles passing, total vehicles passing, automobiles stopped, and pedestrians present). Predictor variables also included covariates that can influence ungulate responsive behavior, including distance to road, distance to cover, dispersion (clustered versus dispersed), Julian date, herd size, and time of day (Roberts 1996, Taylor & Knight 2003, Gavin & Komers 2006, Liley & Creel 2007). Species (pronghorn or elk) was also included as a predictor to investigate potential differences in responsiveness between species.



To yield a conservative number of final models, we first evaluated each single predictor variable separately (along with herd ID as a random effect) in a preliminary nonlinear mixed model to predict the probability that each individual ungulate was responding or not to the predictor. We then excluded all predictor variables with a  $p > 0.10$  from our final candidate model sets. We also calculated a correlation matrix of predictor variables using Spearman rank coefficients to avoid including correlated variables ( $r > |0.7|$ ) in the same candidate model (Tabachnick & Fidell, 1996).

We then included all possible combinations of this reduced set of acoustic, human activity, and covariate predictor variables to develop our final set of candidate models.  $AIC_c$  (Akaike Information Criterion adjusted for small sample size; Akaike, 1973, Burnham & Anderson, 2002) based on likelihood values were used to determine the best performing model of ungulate herd responsiveness. We reported  $AIC_c$  differences ( $\Delta$ ), measuring the information loss between models given the data. We also calculated model weights ( $w$ ) to compare model ranking, as well as relative variable importance weights (sum of model weights for all models containing that specific variable) to determine which variables are the strongest predictors of ungulate responsiveness.

### ***Focal animal sampling***

We used linear regressions (Proc Genmod, SAS 9.1) to evaluate the relationship between behavioral budgets of individual animals in the focal observations and acoustic and human activity. For this analysis our sampling unit was the focal animal and our response variable was the proportion of time spent responding (i.e., vigilant, traveling, flight). Proportionate data was square root arcsine transformed to achieve normality prior

to analyses. Human activity variables were measured as an overall rate, averaged across all human scans that occurred during a focal observation (i.e, mean number of activities per scan), to adjust for variation in the number of human activity scans conducted while observing focal animals.

We used the same approach as for the scan samples to achieve a final set of variables predicting focal animal responsiveness. We identified predictors with  $p < 0.10$  in a preliminary analysis of each separate acoustic and human activity variable and each covariate to include in a final model selection. We analyzed a similar set of acoustic and human activity predictors as for the scan samples, except that we also included passing motorcycles, RV's, and bicycles, which we recorded in sufficient frequency in our focal samples due to their longer duration. We used the same covariates as in the scan samples, including Julian date, distance to cover, distance to road, time of day, species, dispersion, and herd size. Past studies suggest the sex of an individual may also affect responsiveness (Lipetz & Beckoff 1999, Lima 1998), thus we additionally included a focal animal sex classification. As with the scan samples, after narrowing this list of predictor variables through preliminary analyses, all possible model combinations were analyzed to determine AIC<sub>c</sub> values, model weights, and variable importance weights.

## **RESULTS**

### ***Scan Sampling***

One hundred sixty-one scan samples were conducted between June 14 and October 15, 2008. We observed a total of 334 autos stopped, 265 total vehicles passing (including 245 autos, 11 RVs, 9 motorcycles), 135 pedestrians, and 4 bicycles passing

summed over 161 scans. During scan samples, peak power ranged between 64.0-110.0 dB (Mean = 99.3 dB; SE = 0.96), average power ranged between 37.8-80.9 dB (Mean = 64.9; SE=0.91); peak frequency ranged between 172.3-4306.6 Hz (Mean=957.6; SE=40.6); and IQR ranged from 172.3-5168 Hz (Mean=604.5; SE=58.2).

The preliminary analyses of acoustic and human activity variables using nonlinear mixed models revealed that peak power, average power, total vehicles passing, and pedestrians were each separately predictive of ungulate responsiveness during scan samples (Table 1). Peak power and average power are highly correlated variables ( $r=0.96$ ,  $p<.0001$ ), thus we only included peak power given its stronger relationship with ungulate responsiveness. Dispersion, distance to road, and species covariates also predicted ungulate responsiveness (Table 1). The final set of acoustic, human activity, and covariate predictors were not highly correlated (all  $r < |0.7|$ ), hence all 6 variables (peak power, total vehicles passing, pedestrians, dispersion, distance to road, species) were included in the final model selection.

When comparing all possible combinations of final predictor variables, model selection found the global model to be the top model, including variables for peak power, total vehicles passing, pedestrians, dispersion, distance to road, and species (Tables 2, 3). However, considerable model selection uncertainty was evident based on the  $\Delta$  AIC and model weights for the competing models (Table 2). For the acoustic and human activity predictors, ungulates were more likely to respond when there were more pedestrians present and less likely to respond with high levels of sound and traffic (Tables 3, 4). For the covariates, ungulates were more likely to respond when herds were dispersed, closer to TPR, and composed of pronghorn (Tables 3, 4). Dispersion was the most important

predictor variable, followed by pedestrians, total vehicles passing, species, peak power, and distance to road (Table 4). The relative importance weight of peak power (0.49) suggests that it still retains some explanatory power in comparison to human activity predictors and covariates (Burnham & Anderson 2002).

### ***Focal Animal Sampling***

Ninety-nine focal samples were recorded throughout the field season generating 2,000 minutes of individual focal observations. We observed 3,751 autos stopped, 3,321 vehicles passing (including 3,035 autos, 183 RV's, 103 motorcycles), 1,241 pedestrians, and 45 bicycles passing summed over 1,700 human activity scans that were concurrent with the 99 focal observations. During focal samples, peak power ranged between 101.7-111.1 dB (Mean=109; SE=0.14); average power ranged from 57.0-77.0 dB (Mean=69.2; SE=0.40); peak frequency ranged from 172.3-11886.5 Hz (Mean=957.8; SE=74.1) and IQR ranged from 172.3-3445.3 Hz (Mean=789.8; SE=96.3).

Univariate regression analyses of acoustic and human activity predictors indicated that focal animal responsiveness was predicted by the rates of motorcycles passing and autos passing, as well as the species and sex of the focal animal and distance to cover (Table 1). The final set of human activity and covariate predictors were not highly correlated (all  $r < |0.7|$ ), and hence all 5 variables (motorcycles passing, autos passing, species, sex, distance to cover) were included in the final model selection.

When comparing all possible combinations of selected human activity variables and covariates, autos passing, motorcycles passing, and species were present in the top model (Table 3, 5). Although there was again considerable model selection uncertainty

(Table 5), the top four models (out of 32), which also contained sex and distance to cover as covariates, were within 2.0  $\Delta$ AIC and considered competitive models (Burnham & Anderson 2002). Focal animals increased their responsiveness with increased motorcycle traffic and decreased their responsiveness with increased auto traffic, and pronghorn spent a greater proportion of time responsive than elk (Tables 3, 4). Individuals also spent a greater proportion of time responsive when further from cover, and cows with a calf were more responsive than males or females without a calf (Table 4). Autos passing and motorcycles passing were the most important predictors of ungulate responsiveness, followed by species, distance to cover, and sex (Table 4).

## **DISCUSSION**

The risk-disturbance hypothesis states that anthropogenic disturbances such as human-related presence, objects, or sounds will elicit antipredatory behavior (Frid & Dill 2002). Thus, we expected heightened levels of responsive behavior of ungulates in the presence of anthropogenic noise pollution along Teton Park Road in Grand Teton National Park. Our results suggest that noise can alter responsive behaviors in ungulates. Contrary to our predictions, however, ungulates were not more likely to respond, but rather less likely to respond to increased noise levels, as well as vehicle traffic, in our scan samples. In our focal observations we did not find a relationship between responsiveness and our noise measurements; this difference from the scan samples could be due to the decrease in variation of vehicle noise averaged over longer sampling bouts in the focal samples. However, similar to the scan samples, ungulates were less responsive with increasing rates of automobiles passing.

One possible explanation for these findings is that ungulates in Grand Teton National Park do not perceive noise and traffic stimuli as a form of predation risk, perhaps because frequent exposure to these stimuli has led to habituation. Habituation occurs when wildlife responses to stimuli decrease over time after repeated exposure without subsequent consequence (Thorpe 1963). Predictable human activities that do not harm wildlife may condition animals to these disturbances (Thompson & Henderson 1998). Ungulates have been known to habituate to regular exposure of non-lethal human activities (Stankowich 2008). Elk in particular have shown habituation patterns along roads and other areas disturbed by human activities (Lyon & Ward 1982, Morrison et al. 1995, Thompson & Henderson 1998).

An alternative explanation for our results is that ungulates still perceive anthropogenic noise and vehicle traffic as a form of predation risk, but cannot afford to maintain high levels of responsiveness to such a continuous and pervasive form of disturbance. Specifically, the risk allocation hypothesis (Lima & Bednakoff 1999) suggests that investment in antipredator behavior depends on the temporal variation in risk; when periods of risk are brief and infrequent, animals may devote a larger proportion of those risky intervals to antipredator behavior, reserving the majority of feeding effort for low risk situations. In contrast, when periods of risk are lengthy and more frequent, animals may devote a reduced proportion of those risky intervals to antipredator behavior in order to avoid the high cost of lost foraging. In the context of anthropogenic disturbance, Miller et al. (2001) found certain human activities, when infrequent and unpredictable, were related to heightened levels of flush distance in ungulates. In our study, automobile traffic, with its associated noise, was the most

prevalent anthropogenic disturbance; thus, high traffic levels may have elicited reduced responsiveness due to risk allocation decisions. Interestingly, scan samples revealed that pedestrians, a less frequent form of disturbance than vehicle traffic, were more likely to elicit responsive behaviors such as vigilance and flight in ungulates, a result consistent with prior studies implicating the human form as an importance source of disturbance for ungulates (Papouchis et al. 2001, Taylor and Knight 2003, Stankowich, 2008). Further, focal observations revealed that ungulates spent a greater proportion of time responsive with an increase in motorcycle traffic, the least common form of disturbance, as would be predicted by the risk allocation hypothesis.

Separating the visual and auditory components of disturbances on wildlife has been a common challenge for acoustic field studies (Pater 2001). Our study attempted to isolate the effects of noise through multivariate modeling, and some interesting insights can also be inferred by contrasting the behavioral effects of motorcycles and bicycles. Although motorcycles represent a loud disturbance that evoked responsive behavior in ungulates, bicycles, with a similar shape visually, were quieter and not associated with responsive behavior. This might suggest that the loud noise generated from motorcycles, more so than the visual stimulus, may indeed evoke responsiveness and detract from fitness-enhancing behavior. Future experimental work will help to clearly separate the effects of visual and auditory components of human disturbance.

In addition to anthropogenic disturbances, a variety of biological covariates impacted ungulate responsiveness. Ungulates were more responsive closer to roads, further away from vegetative cover, and when herds were dispersed rather than clustered, consistent with past studies of ungulate behavior (Frid 1997, Gavin & Komers 2006,

Stankowich 2008). Females with young were more responsive than adult males and adult females without young, again consistent with prior studies (Lipetz & Beckoff 1999, Childress & Lung 2003, Wolff & Van Horn 2003). Finally, pronghorn were more likely to respond than elk. Pronghorn are often considered particularly sensitive to human disturbances and studies have documented pronghorn risk-avoidance behavior in proximity to roads with traffic (Berger et al. 1983, Gavin & Komers 2006).

Understanding the behavioral responses of wildlife to anthropogenic disturbance can have important conservation and management implications (Buccholz 2007, Caro 2007, Angeloni et al. 2008). Our results highlight an interesting effect of disturbance on behavior. Except in the case of motorcycles, which are relatively infrequent disturbance events, ungulates spent less time responding with increased noise levels and vehicle traffic, allowing more time for maintenance activities such as feeding. Presumably, increased levels of energy enhancing activities can positively affect fitness, suggesting a possible benefit of reduced responsiveness to loud noise and automobiles. However, unresponsive behavior could have negative implications as well. For example, decreased responsiveness in ungulates may reduce their ability to visually detect predators and other cues in the environment. This could add to the reduced detection of acoustic cues potentially caused by the noise itself; past studies have shown anthropogenic sounds can impact animals by masking important auditory cues (Barber et al. 2010), which in this case might include predator sounds, bugling, and calf-cow calls. Reduced responsiveness of ungulates to road traffic could also lead to increased levels of human-wildlife conflict such as negative direct encounters with recreationists or collisions with vehicles (Conover 2002). Road impacts and direct encounters with wildlife are major concerns for



NPS managers (Olliff & Caslick 2003, Amendt 2008). Managers could use a variety of strategies, including signs, interpretive materials, and education programs, to communicate to park visitors the potential impacts of noise on wildlife.

Finally, it is important to emphasize that noise can have negative impacts on fitness and population persistence in ways that may not be reflected by individual behavioral responses (Gill et al. 2001). For example, noise might increase stress, mask acoustic cues, and affect population distribution and demography without necessarily dramatically altering the types of behavior we recorded in this study. Conversely, animals may behaviorally respond to a disturbance without notable population consequences (Gill et al. 2001). Continued research of noise effects on animal behavior, along with assessment of possible population-level impacts, will provide further insight regarding transportation networks through natural areas and their associated disturbances on wildlife.

## **ACKNOWLEDGMENTS**

A.R. Hardy, Dr. J.R. Barber, Dr. K.M. Fristrup, Dr. K.R. Crooks, and Dr. L. Angeloni are the co-authors of the journal publication of this chapter. We would especially like to thank the National Park Service Sounds Lab for providing sound recording equipment and assisting with acoustical analysis and the Cornell Ornithology Lab for providing software assistance. We also thank the technicians for the collection and organization of data. We are grateful to Dr. J. Eickoff for providing statistical help. Colorado State University, the National Science Foundation, and the Rocky Mountain Goat Foundation supported this project.

## LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In Second international symposium on information theory: 267-281. Petrov, B.N. & Csaki, F. (Eds). Budapest: Akademiai Kiado.
- Ament, R., A. P. Clevenger, O. Yu, and A. Hardy. 2008. An assessment of road impacts on wildlife populations in US National Parks. *Environmental Management* **42**:480-496.
- Angeloni, L., M. A. Schlaepfer, J. J. Lawler, and K. R. Crooks. 2008. A reassessment of the interface between conservation and behaviour. *Animal Behaviour* **75**:731-737.
- Barber, J. R., K. M. Fristrup, C. L. Brown, A. R. Hardy, L. M. Angeloni, and K. R. Crooks. 2009. Protecting the wildlife therein: Protecting park fauna from anthropogenic noise. *Park Science* **26(3)**:26-31.
- Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution* **25(3)**:180-189.
- Bayne, E.M., L. Habib, and S. Boutin. 2008. Impacts of Chronic Anthropogenic Noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology* **22(5)**:1186-1193.
- Bee, M. A., and E. M. Swanson. 2007. Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour* **74**:1765-1776.
- Berger, J. D. Daneke, J. Johnson, and S. H. Berwick. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: Implications for the conservation of large mammalian herbivores. *Biological Conservation* **25(3)**:193-208.
- Bleich, V. C., R. T. Bowyer, A. M. Pauli, M. C. Nicholson, and R. W. Anthes. 1994. Mountain sheep *Ovis canadensis* and helicopter surveys: ramifications for the conservation of large mammals. *Biological Conservation* **70**:1-7.
- Bolger, T. D., D. Newmark, T. A. Morrison, D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* **11**: 63-77.
- Borkowski, J. J., P. J. White, R. A. Garrott, T. Davis, A. R. Hardy, and D. J. Reinhart. 2006. Behavioral responses of bison and elk in Yellowstone to snowmobiles and snow coaches. *Ecological Applications* **16**:1911-1925.

- Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1998. Energetic implications of disturbance caused by petroleum exploration to woodland caribou. *Canadian Journal of Zoology* **76**:1319-1324.
- Buccholz, R. 2007. Behavioural biology: an effective and relevant conservation tool. *Trends in Ecology & Evolution* **22**:401-407.
- Burnham, K. P., and D. R. Anderson 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag, New York.
- Burson, S. L., J. L. Belant, K. A. Fortier, and W. C. Tomkiewicz III. 2000. The effect of vehicle traffic on wildlife in Denali National Park. *Arctic* **53**:146-151.
- Caro, T. 2007. Behavior and conservation: a bridge too far? *Trends in Ecology & Evolution* **22**:394-400.
- Childress, M. J., and M. A. Lung. 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour* **66**:389-398.
- Conover, M. R. 2002. Resolving human-wildlife conflicts: the science of wildlife damage management. CRC Press LLC, Florida.
- Dill, L. M. 1974. The escape response of the zebra danio (*Brachydanio rerio*). I. The stimulus for escape. *Animal Behaviour* **22**:711-722.
- Dooling, R. J., A. N. Popper, and E. B. A. Llc. 2007. The effects of highway noise on birds. Report prepared for the California Department of Transportation. Sacramento, California.
- Erbe, C., A. R. King, M. Yedlin, and D. M. Farmer. 1999. Computer models for masked hearing experiments with beluga whales (*Delphinapterus leucas*). *The Journal of the Acoustical Society of America* **105**:2967.
- Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* **14**(1):21.
- Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. *Oikos* **107**:172-180.
- Francis, C.D., C.P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. *Current Biology* **19**:1415-1419.
- Frid, A. 1997. Vigilance by female Dall's sheep: Interactions between predation risk factors. *Animal Behaviour* **53**:799-808.

- Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**:11.
- Gavin, S. D., and P. E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology* **84**:1775-1780.
- Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* **97**:265-268.
- Goldstein, M. I., A. J. Poe, E. Cooper, D. Youkey, B. A. Brown, and T. L. McDonald. 2005. Mountain goat response to helicopter overflights in Alaska. *Wildlife Society Bulletin* **33**:688-699.
- Habib, L., E. M. Bayne, and S. Boutin. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology* **44**:176-184.
- Harrington, F. H., and A. M. Veitch. 1991. Short-term impacts of low-level jet fighter training on caribou in Labrador. *Arctic* **44**:318-327.
- Henderson, D., R. P. Hamernik, D. S. Dosanjh, and J. H. Mills 1976. Effects of noise on hearing. Raven Press, New York.
- Knight, R. L., and D. N. Cole. 1995. Wildlife responses to recreationists. *Wildlife and Recreationists: Coexistence through management and research*: 51-70. Island Press, Washington D. C.
- Krausman, P. R., M. C. Wallace, C. L. Hayes, and D. W. DeYoung. 1998. Effects of jet aircraft on mountain sheep. *The Journal of Wildlife Management* **62**:1246-1254.
- Landon, D. M., P. R. Krausman, K. K. G. Koenen, and L. K. Harris. 2003. Pronghorn use of areas with varying sound pressure levels. *Southwestern Naturalist* **48**:725-728.
- Lengagne, T. 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation* **141**:2023-2031.
- Liley, S., and S. Creel. 2007. What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology* **19**(2):245-254.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* **27**:215-290.

- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* **153**:649-659.
- Lipetz, V. E., and M. Bekoff. 1982. Group-size and vigilance in pronghorns. *Journal of Comparative Ethology* **58**:203-216.
- Lyon, L. J., A. L. Ward. 1982. Elk and land management. Pages 442-477 in J. W. Thomas and D. E. Toweill, editors. *Elk of North America: ecology and management*. Stackpole Books, Pennsylvania.
- Maier, J. A. K., S. M. Murphy, R. G. White, and M. D. Smith. 1998. Responses of caribou to overflights by low-altitude jet aircraft. *Journal of Wildlife Management* **62**:752-766.
- Manning, R., P. Newman, K. Fristrup, D. Stack, and E. Pilcher. 2009. A program of research to support management of visitor-caused noise on Muir Woods National Monument. *Park Science* **26(3)**: 54-58.
- McCourt, K. H., J. D. Feist, D. Doll, and J.J. Russell. 1974. Disturbance studies of caribou, A. G. B. R. and other mammals in the Yukon and Alaska, V. P. B. R. R. C. S. L. F. Series, and S. Canadian Arctic Gas Study Ltd. and Alaskan Arctic Gas Study Co., BC.
- Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin* **29**:124-132.
- Morrison, J. R., W. J. De Vergie, A. W. Alldredge, A. E. Byrne, and W. W. Andree. 1995. The effects of ski area expansion on elk. *Wildlife Society Bulletin* **23**:481-489.
- Nowacek, D. P., L. H. Thorne, D. W. Johnston, and P. L. Tyack. 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review* **37**:81-115.
- Olliff, T., and J. Caslick. 2003. Wildlife–Human Conflicts in Yellowstone. *Yellowstone Science* **11**:18-21.
- Owen, M. A., R. R. Swaisgood, N. M. Czekala, K. Steinman, and D. G. Lindburg. 2004. Monitoring stress in captive giant pandas (*Ailuropoda melanoleuca*): behavioral and hormonal responses to ambient noise. *Zoo Biology* **23**:147-164.
- Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. *The Journal of Wildlife Management* **65**:573-582.
- Parris, K. M., M. Velik-Lord, and J. M. A. North. 2009. Frogs Call at a Higher Pitch in Traffic Noise. *Ecology and Society* **14(1)**: 25.

- Pater, L. 2001. Defining auditory thresholds for animal species. In Proceedings of the Effects of Noise on Wildlife Conference, Happy Valley-Goose Bay, Labrador. Institute for Environmental Monitoring and Research **2**:22-25.
- Pilcher, E. J., P. Newman, and R. E. Manning. 2009. Understanding and Managing Experiential Aspects of Soundscapes at Muir Woods National Monument. *Environmental Management* **43**:425-435.
- Quinn, J. L., M. J. Whittingham, S. J. Butler, and W. Cresswell. 2006. Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *Journal of Avian Biology* **37**:601-608.
- Rabin, L. A., R. G. Coss, and D. H. Owings. 2006. The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). *Biological Conservation* **131**:410-420.
- Radle, L. A. 1998. "The Effect of Noise on Wildlife: A Literature Review" World Forum for Acoustic Ecology Online Reader.
- Slabbekoorn, H., and A. den Boer-Visser. 2006. Cities change the songs of birds. *Current Biology* **16**:2326-2331.
- Slabbekoorn, H., and M. Peet. 2003. Birds sing at a higher pitch in urban noise. *Nature* **424**:267.
- Slabbekoorn, H., and E. A. P. Ripmeester. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology* **17**:72-83.
- Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation* **141**:2159-2173.
- St Clair, C. C., and A. Forrest. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, *Cervus elaphus*. *Behaviour* **146**:393-413.
- Stockwell, C. A., G. C. Bateman, and J. Berger. 1991. Conflicts in national parks: a case study of helicopters and bighorn sheep time budgets at the Grand Canyon. *Biological Conservation* **56**:317-328.
- Tabachnick, B. G. , and L. S. Fidell. 1996. Using multivariate statistics, Third edition. HarperCollins College Publishers. New York.
- Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications* **13**:951-963.

- Thompson, M. J., and R. E. Henderson. 1998. Elk habituation as a credibility challenge for wildlife professionals. *Wildlife Society Bulletin* **26**:477–483.
- Thorpe, W. H. 1963. *Learning and instinct in animals*. Methuen. London.
- U.S. Federal Highway Administration. 2008. U.S. Department of Transportation. Washington, DC. Accessed 1 April 2010.  
<http://www.fhwa.dot.gov/ohim/tvtw.tvtpage.cfm>.
- U.S. Park Service. 2008. U.S. Department of Interior, Washington, DC. Accessed 15 March 2010 from <http://www.nature.nps.gov/stats/park.cfm>.
- U.S. Park Service. 2009. U.S. Department of Interior, Washington, DC. Accessed 15 March 2010 from <http://www.nature.nps.gov/stats/park.cfm>.
- Weisenberger, M. E., P. R. Krausman, M. C. Wallace, D. W. De Young, and O. E. Maughan. 1996. Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. *The Journal of Wildlife Management* **60**:52-61.
- Wolff, J. O., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* **81**:266-271.
- Wood, W. E., and S. M. Yezerinac. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *The Auk* **123**:650-659.
- Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. *Advanced Studies in Behavior* **16**:229-249.

**Table 1** Summary of the relationships between acoustic, human activity, and covariate predictor variables and ungulate responsiveness for scan samples (nonlinear mixed model with herd ID as a random effect) and focal samples (linear regression). Predictors with  $p < 0.10$  were included in a final model selection process. For scan samples, peak power and average power were highly correlated variables; thus only peak power was included because of its stronger relationship with ungulate responsiveness.

Analysis	Model Set	Variable	Coefficient	SE	P-value
Scan Samples	Acoustic	Peak power	-0.0266	0.014	0.064
		Average power	-0.0255	0.010	0.090
		Peak frequency	0.0002	0.000	0.950
		IQR	0.0001	0.000	0.960
	Human activities	Total vehicles passing	-0.1644	0.080	0.060
		Pedestrians	0.0930	0.050	0.080
		Autos passing	-0.1317	0.090	0.130
		Autos stopped	0.0732	0.070	0.330
	Covariates	Dispersion	1.0800	0.360	0.003
		Distance to Road	-0.0021	0.009	0.024
		Species	-0.6000	0.350	0.091
		Time	0.5800	0.390	0.138
		Herd size	-0.0100	0.012	0.393
		Distance to Cover	-0.3000	0.550	0.600
		Julian date	0.0010	0.004	0.760
Focal Samples	Acoustic	Average power	-0.0015	0.005	0.777
		IQR	0.0004	0.000	0.850
		Peak power	-0.0025	0.015	0.864
		Peak frequency	0.0005	0.000	0.900
	Human activities	Motorcycles passing	0.4169	0.169	0.014
		Autos passing	-0.0365	0.019	0.056
		Total vehicles passing	-0.0266	0.017	0.123
		Autos stopped	-0.0154	0.012	0.199
		Bicycles passing	-0.3127	0.330	0.344
		Pedestrians	-0.0100	0.013	0.431
		RV's passing	-0.0931	0.015	0.529



<b>Covariates</b>	Species	0.0952	0.042	0.024
	Sex	0.5300	0.050	0.033
	Distance to Cover	-0.0900	0.040	0.036
	Julian date	-0.0008	-0.001	0.151
	Herd size	-0.0027	0.002	0.187
	Time	-0.0302	-0.030	0.476
	Dispersion	0.0300	0.040	0.498
	Distance to Road	-0.0008	0.000	0.962

**Table 2** AIC<sub>c</sub> model selection results where acoustic variables, human activity variables, and covariates were used to explain responsive behavior of ungulates during scan samples. The top 12 models (out of 64) holding 70% of the total model weight are presented. Intercept, variance, and random effect (Herd ID) are also included in the final parameter count (K).

Model	K	$\Delta AIC_c$	$w$
dispersion, pedestrians, total vehicles passing, species, peak power, distance to road	9	0.00	0.10
dispersion, pedestrians, total vehicles passing, species,	7	0.07	0.10
dispersion, pedestrians, total vehicles passing, distance to road	7	0.21	0.09
dispersion, pedestrians, species, peak power, distance to road	8	0.57	0.07
dispersion, pedestrians, total vehicles passing, species, peak power	8	1.09	0.06
dispersion, pedestrians, total vehicles passing, species, distance to road	8	1.42	0.05
dispersion, total vehicles passing, species, distance to road	7	1.56	0.05
dispersion, total vehicles passing, distance to road	7	1.48	0.05
dispersion, pedestrians, total vehicles passing, peak power, distance to road	8	1.72	0.04
dispersion, pedestrians, species, distance to road	7	1.70	0.04
dispersion, species, peak power, distance to road	7	2.22	0.03
dispersion, pedestrians, species, peak power	7	2.24	0.03

**Table 3** Top models predicting ungulate responsiveness selected with lowest AICc values out of full model sets from scan and focal samples.

Top Model	Variable	Estimate	SE	Lower 95% CL	Upper 95% CL
<b>Scan Samples</b>	Intercept	0.53	1.47	-2.38	3.44
	Herd ID	1.83	0.49	0.86	2.79
	Dispersion	1.14	0.35	0.45	1.84
	Pedestrians	0.12	0.05	0.01	0.22
	Total vehicles passing	-0.15	0.09	0.09	0.03
	Species	-0.69	0.35	-1.38	0.003
	Peak power	-0.01	0.01	-0.04	0.01
	Distance to Road	-0.001	0.0008	-0.003	0.0002
<b>Focal samples</b>	Intercept	0.57	0.05	0.47	0.67
	Autos passing	-0.06	0.02	-0.09	-0.03
	Motorcycles passing	0.45	0.17	0.12	0.79
	Species	0.19	0.01	0.16	0.22

**Table 4** Relative variable importance weights for all variables within our full model sets for scan samples (64 total) and focal samples (32 total). The ‘direction’ column notes whether the variable is positively or negatively related to ungulate responsiveness. Dispersion, species, cover distance, and sex are discrete variables so ‘direction’ reports the term associated with greater responsiveness.

<b>Analysis</b>	<b>Variable</b>	<b>Weight</b>	<b>Direction</b>
<b>Scan Samples</b>	Dispersion	0.98	Dispersed
	Pedestrians	0.73	Positive
	Total vehicles passing	0.66	Negative
	Species	0.61	Pronghorn
	Peak power	0.49	Negative
	Distance to road	0.40	Negative
<b>Focal Samples</b>	Autos passing	0.95	Negative
	Motorcycles passing	0.89	Positive
	Species	0.62	Pronghorn
	Distance to cover	0.45	Far
	Sex	0.39	Female w/calf

**Table 5** AIC<sub>c</sub> model selection results where human activity variables and covariates were used to explain responsive behavior of individual focal animals. The top 12 models (out of 32) holding 93% of the total model weight are presented. Intercept is also included in the final parameter count (K).

Model	K	$\Delta AIC_c$	w
autos passing, motorcycles passing, species	4	0.00	0.22
autos passing, motorcycles passing, species, distance to cover	5	0.93	0.14
autos passing, motorcycles passing, distance to cover	4	1.25	0.12
autos passing, motorcycles passing, sex, species	6	1.38	0.11
autos passing, motorcycles passing, sex	5	2.15	0.08
autos passing, motorcycles passing, distance to cover, sex	6	2.24	0.07
autos passing, motorcycles passing	3	2.68	0.06
autos passing, motorcycles passing, species, distance to cover, sex	7	2.73	0.06
autos passing, sex, species	5	4.45	0.02
autos passing, species	3	4.66	0.02
autos passing, species, distance to cover	4	5.26	0.02
autos passing, species, distance to cover, sex	6	5.51	0.01