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Original Article

Landscape and anthropogenic features influence the use of auditory vigilance by mule deer

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While visual forms of vigilance behavior and their relationship with predation risk have been broadly examined, animals also employ other vigilance modalities such as auditory vigilance by listening for the acoustic cues of predators. Similar to the tradeoffs associated with visual vigilance, auditory behavior potentially structures the energy budgets and behavior of animals. The cryptic nature of auditory vigilance makes it difficult to study, but on-animal acoustical monitoring has rapidly advanced our ability to investigate behaviors and conditions related to sound. We utilized this technique to investigate the ways external stimuli in an active natural gas development field affect periodic pausing by mule deer (*Odocoileus hemionus*) within bouts of rumination-based mastication. To better understand the ecological properties that structure this behavior, we investigate spatial and temporal factors related to these pauses to determine if results are consistent with our hypothesis that pausing is used for auditory vigilance. We found that deer paused more when in forested cover and at night, where visual vigilance was likely to be less effective. Additionally, deer paused more in areas of moderate background sound levels, though responses to anthropogenic features were less clear. Our results suggest that pauses during rumination represent a form of auditory vigilance that is responsive to landscape variables. Further exploration of this behavior can facilitate a more holistic understanding of risk perception and the costs associated with vigilance behavior.

Key words: **acoustic ecology, *odocoileus hemionus*, vigilance, mule deer**

INTRODUCTION

Vigilance is an important behavioral adaptation allowing early detection and evasion of predators, thereby increasing survival (Lind 2005). Vigilance manifests in several ways including neural mechanisms, behavioral strategies, and social strategies (Dimond and Lazarus 1974). Research on behavioral vigilance strategies has predominantly focused on the visual forms of vigilance behavior, such as scanning, alert behavior, or heightened awareness, which have been well documented across a wide range of animal taxa (Lima 1987; Quenette 1990; Frid 1997; Fortin et al. 2004). However, animals also employ other sensory cues such as smell (Muller-Schwarze 1994) or auditory vigilance by listening for the acoustic cues of predators (Barber et al. 2010), or the alarm calls of conspecifics (Randall and Rogovin 2002; Thompson and Hare 2010; Hare and Warkentin 2012). Such behavioral strategies may be particularly valuable when environmental conditions preclude the use of sight or for species where visual acuity is low.

The time invested in vigilance is considered a tradeoff to time invested in foraging, as the act of feeding is often incompatible with predator detection (Lima and Dill 1990). Foraging is expected to detract from the visual detection of predators, and it creates incidental noise that masks acoustic cues necessary for the auditory detection of predators (Molinari-Jobin et al. 2004). Thus, prey species are expected to modulate their investment in vigilance (both visual and auditory) with varying levels of predation risk in order to service metabolic requirements (maintain energy intake) while also evading predation (Brown 1999; Brown et al. 1999).

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Investment in antipredator behaviors such as vigilance is expected to vary with spatial changes in perceived predation risk, often referred to as the “landscape of fear” (Brown et al. 1999; Laundré et al. 2001; Laundré et al. 2010). Major landscape factors known to influence visual forms of vigilance behavior include food density (Beauchamp 2009), whether habitat is open or closed (Ebensperger and Hurtado 2005), distance to cover (Lima 1987), and level of human disturbance (Li et al. 2011), but the relationship between these factors is not always straightforward (Quenette 1990). Human disturbance, in particular, can have differing effects on risk perception and subsequently visual vigilance behavior, increasing perceived risk and scanning when it represents a form of predation risk (Frid and Dill 2002), or reducing perceived risk when it provides a spatial refuge from predators that avoid human activity (Berger 2007, Muhly et al. 2011; Rogala et al. 2011). However, little is known about the effect of landscape variables and human disturbance on auditory vigilance, or how this behavior may interact with visual vigilance to structure behavioral responses to predation risk. Employment of auditory vigilance may be coupled with visual vigilance, or these behaviors may trade off in relation to characteristics that make one or the other more effective (e.g., auditory vigilance may be prevalent where landscape characteristics preclude sight). In the case of a trade-off between auditory and visual vigilance, it is possible that the availability of visual cues themselves could impact the propensity to listen in addition to landscape features and acoustic stimuli. With respect to human activity, auditory vigilance may be affected in ways similar to visual vigilance, where animals potentially increase investment if an increase in risk is perceived; alternatively, human activity could reduce perceived risk by providing refuge from predators. Furthermore, anthropogenic noise could render auditory vigilance ineffective by masking sounds of interest, causing a decrease in its use.

While there is extensive evidence that animals can hear and respond to the sounds of predators and conspecific alarm cues, studies that directly quantify investment in listening for predator cues are largely absent from the literature, perhaps because of the difficulty in observing listening behavior. We overcome this impediment through the use of recently developed acoustic recording collars (Lynch et al. 2013), applying this technology to evaluate the potential role of auditory vigilance for mule deer (*Odocoileus hemionus*). The mule deer is a prey species that is known to use vigilance as a form of antipredator behavior (Geist 1981; Altendorf et al. 2001; Lynch et al. 2013). The visual acuity of mule deer is well established, and potential dangers are often identified visually before they are close enough to be a concern (Geist 1981; Muller-Schwarze 1994; VerCauteren and Pipas 2003). However, mule deer spend up to 60% of their time resting (often in cover; Kie et al. 1991), requiring the use of other keen senses such as hearing to detect approaching animals (Muller-Schwarze 1994) and other changes in the environment. In fact, both the morphology and behavior of mule deer, including their oversized pinnae that amplify sounds (Calford and Pettigrew 1984), their sensitivity to wide ranging signals (250 Hz to 30 kHz, (Geist 1981), and their ability to detect animals as far away as 600 m in any direction using a combination of hearing, olfaction, and sight (Geist 1981); suggest that acoustic signals play important roles in their sensory ecology (Lingle et al. 2007; Teichroeb et al. 2013).

Mule deer periodically pause during rumination while masticating ingesta, and this behavior appears to be used for auditory vigilance (Lynch et al. 2013). In addition to increasing sound levels that could mask detection of auditory cues, the act of chewing autonomically engages the stapedius reflex, which reduces the sensitivity of the ear by damping the transmission of vibrations through the incus–malleus–stapes complex (Pang and Guinan 1997). This attenuation of acoustic signals inhibits an animal’s ability to survey the acoustic environment. However, in addition to serving a role in auditory surveillance, pauses during mastication also may reflect processes unrelated to listening, including physiological functions (e.g., the movement of ingesta, gut processing time, or jaw muscle relief), though pauses as defined in this study are bounded by and exclude regurgitation and swallowing. We assume physiological processes such as mastication and rumination would occur in a random pattern across the landscape, as the available forage species during the winter season in this pinyon juniper range are of universally poor quality (Bartmann et al. 1982). Therefore, if pauses are used for auditory vigilance, time invested in the behavior would be expected to vary with exposure to stimuli and changes in landscape properties, particularly those that influence perceived levels of risk and that impede visual vigilance.

To investigate spatial and temporal structuring in pause behavior, we conducted this study in the Piceance Basin area of northwestern Colorado, a topographically diverse region with heterogeneous vegetative communities that was actively undergoing natural gas production and extraction. This type of development has been shown to affect behavior in a range of ungulates (Northrup and Wittemyer 2013) and elicit changes in mule deer behavior consistent with an anti-predator response (Sawyer et al. 2006) and thus may be expected to cause an increase in their auditory vigilance. However, the human landscape features related to energy development (i.e., roads, drilling well pads, producing well pads, and facilities such as compressors) produce substantial noise, potentially masking other acoustic signals, degrading the efficacy of auditory vigilance, and ultimately causing a reduction in auditory vigilance. Additionally, these disturbed areas may offer a certain level of shelter by deterring predatory species, thereby reducing perceived risk and the use of auditory vigilance. Therefore, we examined the influence of proximity to these features on the proportion of time spent paused, our metric of auditory vigilance. We also assessed investment in pausing under conditions known to increase the perceived predation risk of ungulates (Altendorf et al. 2001; Stankowich 2008; Laundré et al. 2010), such as the presence of visual barriers that inhibit visual detection of predators (Hopewell et al. 2005). Specifically, we tested the predictions that pausing increased inside forested areas (relative to open regions), in rugged terrain, during nighttime hours (relative to daytime), and at closer distances to the edge of forested cover.

METHODS

Study area

The study took place in the Piceance Basin of Northwestern Colorado, in an area that serves as winter range for mule deer from October through May. The area consists of both mixed mountain shrub and pinyon-juniper woodlands at an elevation of approximately 2000 m. This landscape naturally provides topographical relief and a diverse range of habitats, from dense cover to open, exposed regions (Bartmann et al. 1992). The landscape is also shaped by human activities associated with energy development, largely in the form of road networks servicing natural gas wells that are in varied phases of production or development. Human activity levels are high in this area, with several wells and natural gas facilities running 24 h a day, 7 days a week.

Acoustic data collection

Ten wild adult female mule deer (aged 4.5–11.5 years) were randomly selected from a multi-year global positioning system (GPS) radio tracking study (Lendrum et al. 2012, 2013) and wore collar-mounted acoustic recording devices for approximately 2 weeks during the winter to track audible behaviors and ambient environmental sounds (Lynch et al. 2013). The microphones contained within the acoustic recording collars were mounted such that they were positioned against the throats of the deer. This positioning, along with their sensitivity, allowed capture of the sounds of footfalls, vocalizations, foraging, rumination (regurgitation, mastication, and swallowing), and even respirations when the deer were otherwise inactive. Prior to collar deployment, the technique was validated on captive individuals. During this testing period, we verified, through comparison of direct observations and concurrent audio files, that the collars clearly documented sounds produced by deer. During the study period, deer also wore GPS radio collars to track their movements. Protocol and procedures employed for capture were reviewed and approved under the Colorado State University Institutional Animal Care and Use Committee (IACUC) protocol 10-2350A. Once recovered, the acoustic recording devices provided continuous date-time stamped MPEG-2 Audio Layer III recordings. Following protocols detailed in Mennitt and Fristrup (2012), the acoustic recording collar was calibrated using a Type-1 (American National Standards Institute [ANSI] S 1.4-1983 [R 2006]) sound level meter (Larson Davis 831, Larson Davis, Depew, NY). This calibration was necessary to acquire broadband background sound levels from the collar.

Detection of auditory vigilance behavior

Previous research revealed that mule deer frequently pause during mastication bouts, creating brief periods of relative quiet that would allow for auditory vigilance (Lynch et al. 2013). Mastication bouts are part of the rumination process during which deer are stationary and are regurgitating and breaking down ingesta. For the purpose of this study, bouts were defined as continuous periods of mastication, bounded by continuous periods of other behaviors such as browsing or walking. Pauses during bouts occurred periodically, typically bounded by swallowing and regurgitation, but it should be noted that we could not acoustically identify any other digestive activity during the pauses. The pauses analyzed in this study were completely distinct from the swallowing and regurgitation portions of the mastication process (see electronic Supplementary Material for a recording of the focal behavior).

Periods of mastication during rumination and the pauses included within them were identified by examining recorded acoustic data, displayed as spectrograms with 1-s, one-third octave band resolution using the Sound Pressure Level Annotation Tool (U.S. National Park Service Natural Sounds and Night Skies Division, Fort Collins, CO). In the spectrograms, these periods were visually distinct from other behaviors (Figure 1), verified aurally, and then annotated manually. During these mastication bouts, deer were typically stationary (as indicated by audio and GPS data), and steadily processing ingesta (as indicated by acoustic data).

Using custom software developed in Matlab (Mathworks v. 2012b, Natick, MA), the waveforms of manually selected mastication bouts, described above, were further processed to automatically detect the start and end of pauses. The pause detector software worked on the time series data by first performing a full-wave rectification of the acoustic signal, essentially transforming the amplitude values to positive numbers. Then, the detector stepped through the data at 45-s intervals marking pauses as instances where levels remained below a 14th percentile threshold for a minimum of 1.4 s (selection of optimal automatic pause detection parameters are described in electronic Supplementary Material). This dynamic threshold approach was selected because it promoted consistent detection across varying signal levels from individual collars. Figure 2 displays a detected pause, marked on the original signal (a) and the rectified signal (b).

To identify all pauses, we applied a set of parameter values to all mastication bouts from all individual deer (see electronic Supplementary Material). Relevant metrics for each pause such as begin time, end time, and duration were logged, and a 1-s one-third octave wideband sound pressure level (SPL) extracted from the center of each pause event was used to represent the background ambient SPL during the pause. Anthropogenic noise tends to occur on the lower end of the frequency spectrum (<2 kHz) (Francis et al. 2009; Barber et al. 2010), so to better assess the potential impacts of anthropogenic sounds on pause length, we calculated a truncated wideband SPL (dBT) that focused on low frequency sound (20–1250 Hz) in addition to the dBW wideband SPL (25–6300 Hz).

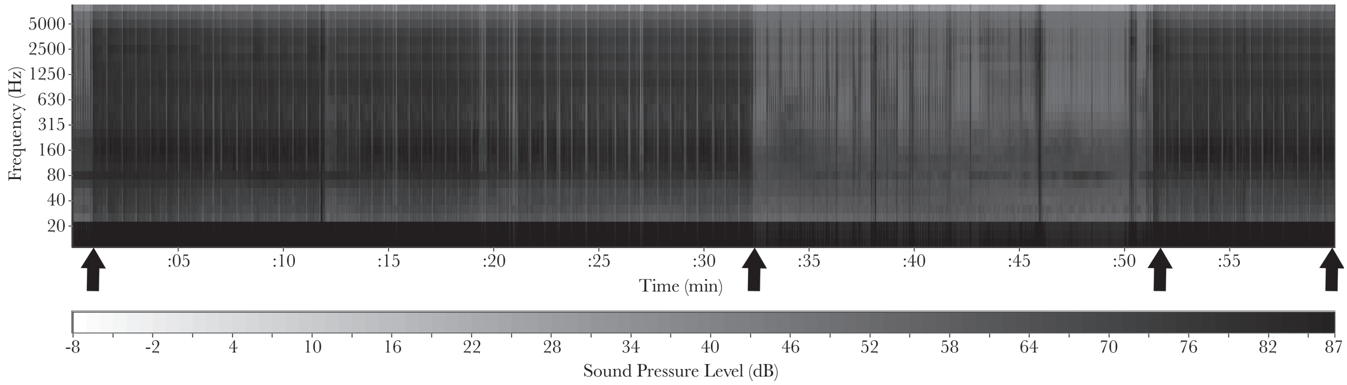

Figure 1

Hour-long spectrogram of mule deer behavior. High sound pressure levels are indicated by darker shades, low sound pressure levels are indicated by lighter shades. Two mastication bouts are distinguishable from 01 to 33 min, and again from 51 to 59 min as areas of higher sound levels (as bounded by arrows). Pauses are located within each bout, and are represented by lighter shaded vertical stripes of varying width. Between mastication bouts, the deer was stationary, intermittently inhaling, exhaling, and eructating. The dark horizontal stripe seen throughout the hour at 80 Hz corresponds to the sound of mechanized equipment (such as a generator or compressor station).

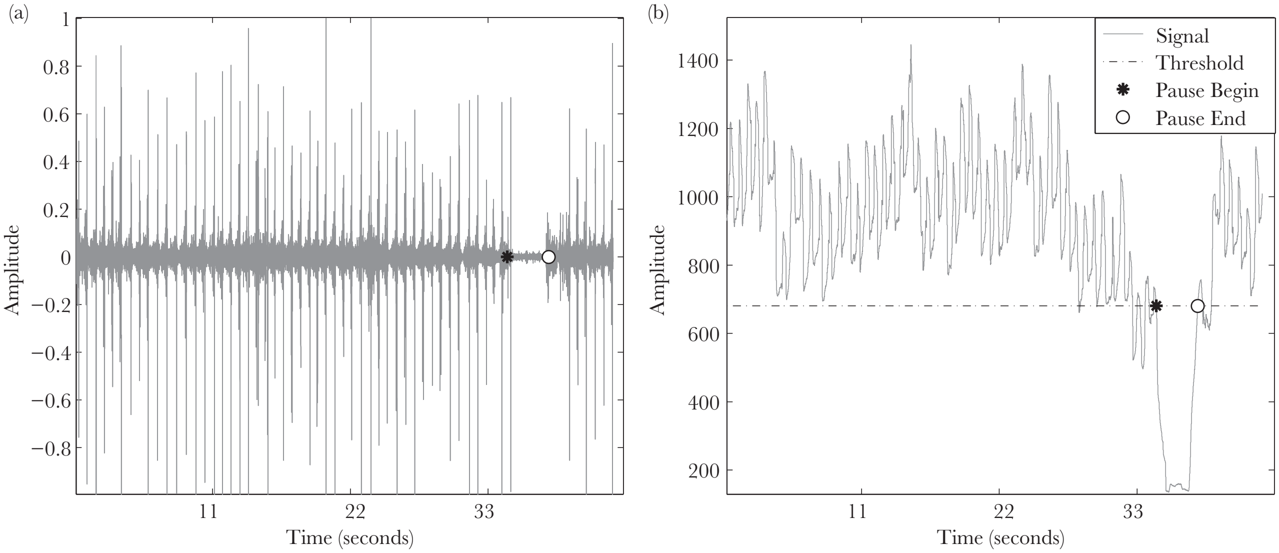

Figure 2

Example of automatic pause detection. Begin (*) and end (○) times of a single pause are marked in the original time series data (a) and on the rectified signal (b). Detection percentile threshold is marked by dotted line on the right panel. Detector was triggered to mark a pause when the signal dropped below this percentile for at least 1.4 s. The signal before and after the pause represents chewing during mastication.

The detector code and detailed information on detector performance are provided in electronic Supplementary Material.

Modeling natural and anthropogenic effects

To examine factors influencing variation in pause characteristics, we fit models of pause behavior during rumination in a Bayesian hierarchical framework. Our dependent variable was the proportion of the mastication bout spent paused (calculated as the sum of the duration of all pauses within a bout divided by the duration of the bout to standardize for bout length). For this variable, we fit beta regression models with intercepts varying by individual to account for the nested structure of the data (multiple bouts for each individual). The model structure is provided in electronic Supplementary Material.

To extract landscape covariates for each mastication bout, we matched the time of the midpoint of each mastication bout to the GPS location for that deer that was closest in time. Deer locations were taken every 30 min using a GPS collar (Model G30C, Advanced Telemetry Systems, Isanti, MN). Where GPS fix failure did not make this possible, the location closest in time to the start or end of the bout was assigned to the bout if the location was taken within 1 h of the bout midpoint. Bouts not associated with a successful GPS fix according to this definition were dropped from the analysis. Consecutive bouts that occurred in spatially overlapping and temporally adjacent locations were combined into a single bout, assuming the short period of activity by the deer (e.g., brief movements and foraging) separating the bouts did not merit independent treatment. All covariates, described below, were extracted using the "raster" package (Hijmans and van Etten 2013) in the R statistical software version 3.0.1 (R Core Team 2013).

The natural covariates expected to influence auditory vigilance (Table 1) included the distance of the deer to the edge of forested land cover (Edge), a binary covariate for whether it was located in forested (0) or open (1) land cover (Open), a terrain ruggedness index measuring the change in slope between the cell of interest and those surrounding it (TR), and a binary covariate for whether the bout occurred during the day (0) or between sunset and sunrise (1) (Night). Each of the spatial data layers was displayed with 30 m resolution. These factors were selected because they were expected to influence perceived predation risk and the ability to detect predators visually by influencing the line of sight distance. The anthropogenic factors expected to influence auditory vigilance (Table 1) included distance to the center of the nearest well pad with wells that were being actively drilled (D drill), distance to the center of the nearest well pad with only wells that were producing gas (D prod), distance to the center of the nearest natural gas facility (D fac), distance to the nearest road (D rd), and median wideband sound level (dBW.med) during the pause. These anthropogenic factors were selected because they might increase perceived predation risk (by presenting a disturbance), or they might decrease perceived predation risk (by deterring predators); further, sound levels have the potential to influence the ability to detect predators aurally. Following definitions of the Colorado Oil and Gas Conservation Commission, a well pad was considered a drilling well pad between the time that drilling began until product began to be extracted; it was considered a producing well pad once product began to be extracted. For well pads on which multiple wells existed, a pad was considered a drilling pad as long as at least one well was being drilled. A natural gas facility was defined as either a gas plant or compressor station.

After all covariates were extracted, we fit 4 separate models to the dependent variable (Table 2). All models contained all covariates described above, but the structure of each was organized to explore the functional form (linear vs. non-linear) of the anthropogenic covariates. Interaction effects (between night and landcover, and between night and sound level) were considered, but no evidence for interaction effects was found (i.e., coefficients for interaction terms were not different from 0). The 4 models without interaction terms were compared using deviance information criteria (DIC; Spiegelhalter et al. 2002; but as formulated by Plummer 2012), with the best fit model used to reveal which factors were significant in predicting proportion of the mastication bout spent paused. Though we calculated multiple measures of background

Table 1

Names, descriptions, and predicted effect (+/− indicates possible influence in either direction; see explanation in Introduction section) on the proportion of bout paused for covariates used in Bayesian hierarchical models

	Description	Predicted effect
Natural covariates		
Edge	Distance to the edge of forested land cover[a]	−
Open	Binary covariate for being in forested land cover (0) or not (1)[a]	−
TR	Terrain ruggedness index–measure of change in slope between the cell of interest and those surrounding it[b]	+
Night	Binary covariate for whether the bout was between sunsxet and sunrise (1) or not (0)[c]	+
Anthropogenic covariates		
D prod	Distance to center of producing well pad[d]	+/−
D drill	Distance to center of drilling well pad[d]	+/−
D fac	Distance to center of natural gas facility[e]	+/−
D rd	Distance to nearest road[f]	+/−
dbW.med	Median wideband sound pressure level (25–6300 Hz)[g]	+/−

Sources for covariates are indicated in the following footnotes.

[a] Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/)

[b] Calculated from digital elevation model obtained from United States Geological Survey seamless data warehouse (http://nationalmap.gov/viewer.html).

[c] The United States Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

[d] Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/).

[e] Obtained via ground truthing.

[f] United States Geological Survey seamless data warehouse (http://nationalmap.gov/viewer.html) and validated through ground truthing.

[g] Calculated from on-deer recording devices.

Table 2

Model structure and deviance information criteria (DIC) values for models predicting the proportion of a mastication bout during which a deer was silent (paused)

Model	Structure	DIC
1	Edge + Open + TR + Night + log(D prod) + log(D drill) + log(D fac) + log(D rd) + dbW.med + dbW.med^2	−1884
2	Edge + Open + TR + Night + D prod + D drill + D fac + D rd + dbW.med + dbW.med^2	−1882
3	Edge + Open + TR + Night + D prod + D drill + D fac + D rd + dbW.med	−1882
4	Edge + Open + TR + Night + D prod + D prod^2 + D drill + D drill^2 + D fac + D fac^2 + D rd + D rd^2 + dbW.med + dbW.med^2	−1878

sound level, we only report on models fit with the median dBW values because they provided a better fit (lower DIC) than models with mean dBW, mean dBT, and median dBT values (assessed separately from the 4 presented models). All models were fit in the R statistical software (R Core Team 2013) using the "rjags" package (Plummer 2013). We ran 2 chains for 8 000 000 iterations, discarding the first 4 000 000 as burn-in and thinning the chains to every 10th sample. We used starting values for all parameters that were expected to be overdispersed relative to the posterior distributions and assessed convergence to the posterior distribution using the Gelman–Rubin diagnostic (Gelman and Rubin 1992) and by examining trace plots of the resulting chains.

RESULTS

The automatic acoustic detector yielded 53 856 pause detections (with a median of 86.0 pauses per bout per individual, interquartile range [IQR] lower and upper: 42.0, 133.3) during 500 mastication bouts. The median duration of a mastication bout was 1.38 h (IQR: 0.57, 2.21). The median pause duration was 2.29 s (IQR: 1.79, 2.90), though a number of long pauses (up to 6.3 s) were also noted in the dataset. A median of 3.8% (IQR: 3.4%, 4.4%) of the time spent masticating was allocated to pausing.

All models converged to the posterior distribution (Gelman–Rubin diagnostic for all parameters < 1.1; Gelman and Rubin 1992). Aside from Model 4 (Table 2), which had quadratic terms on all distance and sound covariates, all models had similar DIC values, indicating little difference among models (Table 2). Because it provided the best fit for the data according to DIC, we report coefficients for each covariate from Model 1 (Table 3), which were similar to and representative of the other models. As predicted, after accounting for other covariates, deer paused for a greater proportion of bouts during the night than during the day (Figure 3), and for smaller proportions of bouts when in open areas (Figure 3). Contrary to predictions, deer paused for a greater proportion of bouts when they were further from natural gas facilities (Table 3). Lastly, there was a quadratic relationship between dBW and pause behavior, whereby deer paused for a greater proportion of bouts in areas of intermediate sound level (Figure 4). The other covariates analyzed, such as distance to a road, distance to producing and drilling well pads, terrain ruggedness index and distance to the edge of forested land cover, were not significant predictors in models (<95% of posterior distribution on one side of 0; Table 3).

DISCUSSION

Although vigilance is an important antipredator strategy, the mechanisms driving the use of auditory vigilance behavior are not well studied. Here, we present one of the first detailed assessments of this potentially critical behavior, and demonstrate how acoustic technology can change what we understand about how the landscape influences behavioral decision making. Our results demonstrated that pauses during mastication bouts were structured by landscape properties that are expected to influence perceived

Table 3

Representative model (Model 1) for the proportion of bout paused with median coefficient values and 95% credible intervals (CI) for each covariate

Covariate	Median coefficient	95% CI	
Edge	0.035	−0.022	0.09
Open	**−0.119**	**−0.23**	**−0.009**
TR	0	−0.002	0.002
Night	**0.377**	**0.272**	**0.483**
log(D drill)	−0.009	−0.1	0.083
log(D fac)	**0.194**	**0.097**	**0.292**
log(D rds)	0.067	0.006	0.13
log(D prod)	−0.03	−0.1	0.042
dbW.med	0.079	−0.032	0.191
dbW.med^2	**−0.055**	**−0.104**	**−0.006**

Significance is indicated with bold font.

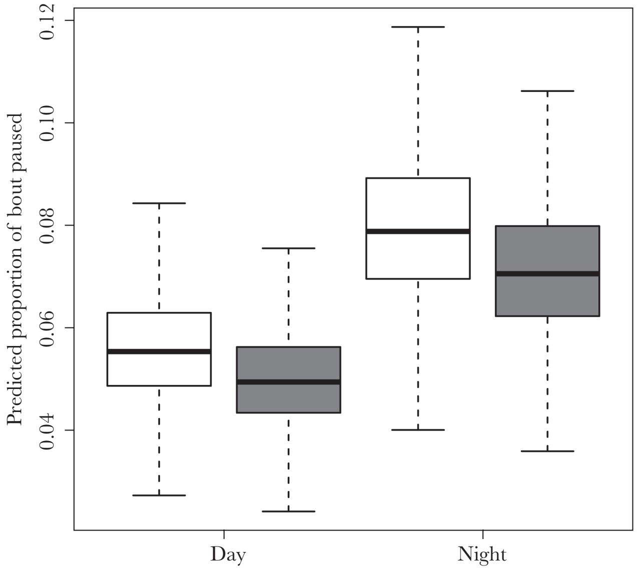

Figure 3

The median and interquartile range (IQR) for predicted proportion of bout paused for day and night time periods (derived from fitted model), where predicted proportion is standardized by bout length. Dashed lines extend to 95% credible interval. Forested landcover is represented by white boxes and open areas are represented by gray boxes.

risk and impede visual vigilance. Consistent with predictions, we found that deer paused more extensively where concealment cover abounded and thus where visual vigilance was likely to be less effective. In addition, deer allocated a larger proportion of time to pausing during mastication bouts at night, implying that auditory vigilance is an important defense mechanism when darkness reduces the effectiveness of visual scanning. Previous research on vigilance behavior in wild species (Lima 1987; Altendorf et al. 2001; Lind 2010) has overlooked the importance of auditory vigilance, potentially because this behavior is not easily seen during behavioral observations and may be obscured when it is predominantly employed. Our results suggest that exploring this behavior allows deeper understanding of an animal's perception of risk and the costs associated with vigilance behavior. Furthermore, identification of landscape characteristics associated with increased auditory vigilance provides an additional way to behaviorally identify properties that can augment more typical assessments of perceived predation risk (e.g., giving up densities or measures of visual vigilance).

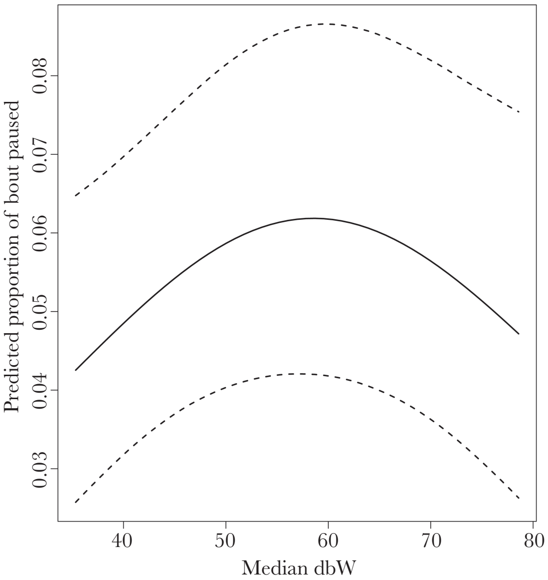

Figure 4

Predicted proportion of bout paused by median dBW (25–6300 Hz) values (solid line) with 95% credible interval (dotted lines). Predicted proportion is standardized by bout length.

It is important to note that our findings do not preclude additional explanations for pausing behavior; for example, pausing may allow deer to be quiet to reduce detection when predators are near or it may be involved in physiological processes (though we note that pauses in our analysis excluded any audible activity including swallowing and regurgitation). As such, pausing during mastication likely serves multiple, simultaneous purposes. It is notable that in our analysis, the role of auditory vigilance, as evident from the increase in pausing at night and in cover, was strong enough to overcome the confounding influence of other modalities of pausing. Our pause identification procedure excluded all pauses less than 1.4 s in length, which may have reduced the influence of strictly biophysical activity from the behaviorally oriented listening pauses. Anecdotally, we noted that extended pauses were influenced by ecological stimuli (e.g., coyote calls occurred in conjunction with longer pauses), suggesting that longer pauses play a greater role in listening. A more efficient procedure for separating biophysical activity from behaviorally motivated pause categories would provide stronger inference and merits further investigation. For instance, future studies could experimentally manipulate perceived predation risk or disturbance in a controlled setting to identify the extent to which pauses are adjusted for listening.

One of the negative consequences of increasing vigilance due to perceived risk is time taken away from other fitness enhancing behaviors (Frid and Dill 2002; Lind 2005). Therefore, an increase in auditory vigilance could result in a reduction in time spent invested in other behaviors. It has been argued that vigilance can be cost-free when anti-predator vigilance is conducted during spare time (Illius and Fitzgibbon 1994), such as the interval of time between cropping and bringing a mouthful of forage fully into the mouth (Blanchard and Fritz 2007). However, unlike visual scanning, auditory vigilance cannot be conducted during the act of chewing, both because the sound of chewing itself masks auditory cues of interest in certain frequency bands, and because chewing triggers the stapedius reflex, an involuntary muscular contraction which limits the transmission of acoustic signals (Pang and Guinan 1997). This trade off is emphasized by a study that reported 58% of roe deer were preyed upon whilst ruminating, perhaps because the act of chewing hindered the deer's ability to hear approaching predators (Molinari-Jobin et al. 2004). As such, trade-offs between noise-producing behaviors and auditory vigilance may be as pertinent to animal ecology and behavior as other, more commonly studied behaviors.

In summary, the investigation of auditory vigilance provides novel insight to animal time budgets and perceptions of risk, augmenting the more frequently studied visual vigilance behaviors, and offers a new lens through which to view the landscape of fear. Mule deer allocated a substantial amount of time to pausing in the midst of mastication bouts during the study period, with both natural and anthropogenic landscape features differentially impacting the use of this behavior. However, further research is necessary to understand the relationship between vigilance modalities (visual, olfactory, and auditory), and how these different behaviors compliment, tradeoff, or supersede one another. Such studies might employ either simultaneous visual and auditory inspection of vigilance behavior, or accelerometry or magnetometry sensors (to gather fine scale information about head movements and orientations) to better understand interactions between these behaviors and their landscape context. Studies assessing different contexts where these behaviors are utilized and their relative roles across species also would further increase understanding. Additional research is also needed to gain a better understanding of the relationship between behavioral measures of vigilance, concomitant brain and sensory processing requirements, and the direct fitness consequences of investment in this activity, a critical component to determine the cost-benefit ratio of these behaviors. Finally, although the bout-level data acquired from this study did not allow us to investigate the immediate factors that influenced individual pauses, we identified a number of long pauses that closely followed significant acoustic events (such as coyote calls or vehicles passing nearby). The biologic import of these hyper-vigilant events is likely significant, and points to an exciting new approach for identifying specific predator-prey interactions.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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