# THE IMPACT OF ANTHROPOGENIC NOISE ON NORTHERN SAW-WHET OWL (*Aegolius acadius*) HUNTING BEHAVIOR

by

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# DEDICATION

This thesis is dedicated to my wife, Beth Mason, for her tireless support. And to the owls.

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# ABSTRACT

Anthropogenic noise has increased dramatically worldwide which has negatively impacted wildlife. The effect of noise on acoustically specialized predators has received limited attention. Here I demonstrate that noise generated by a natural gas compressor station degrades the ability of the northern saw-whet owl (*Aegolius acadius*) to detect and capture prey in the absence of light. The saw-whet owl is considered an acoustic specialist because it exhibits a high degree of ear asymmetry, an adaptation for precise three-dimensional sound localization in birds. I presented 31 wild-caught saw-whet owls with mice (*Mus musculus*) inside a flight tent under acoustic conditions ranging from control 29 dB(A) to 73 dB(A). By varying the noise treatments in intensity and spectral composition I recreated acoustic conditions corresponding with distances between 50 - 800 m from an active compressor station. I found that saw-whet owls were able to capture prey using hearing alone but were not able to capture mice at or above 61 dB(A), i.e., noise intensities found within 200 m of a compressor station. In order to assess the manner by which noise affected owl hunting, I postulated multiple hypotheses. First, the noise levels used in this experiment might affect owl hunting by the same amount, which I labeled the threshold hypothesis. Secondly, noise impacts might increase with increasing noise, which I labeled the dose-response hypothesis. I compared these hypotheses using a model selection framework. Hunting deficits increased with increasing noise lending support to the dose-response hypothesis. Each decibel increase in noise between 29-73 dB(A) resulted in an 11% decrease in the odds of the owl orienting toward its prey during a trial, a 7% decrease in the odds of a strike, and an 8% decrease in the odds of successfully capturing the mouse. These results suggest that unmitigated natural gas compressor station noise has the potential to decrease habitat suitability for acoustically specialized owls.

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| | |
|---|---|
| dB(A) | A-weighted decibel scale |
| fps | Frames per second |
| HD | High definition |
| IBO | Intermountain Bird Observatory |
| IDFG | Idaho Department of Fish and Game |
| IR | Infrared |
| USFWS | United States Fish and Wildlife Service |

# INTRODUCTION

Anthropogenic noise is widespread, pervasive, and increasing. Emanating from a multitude of sources including transportation networks (both road and air), urbanization, industry, and resource extraction projects, human-caused noise is now present over much of the globe. A common characteristic of anthropogenic noise is that it is dominated by low frequencies which attenuate slowly and can travel great distances (Berglund et al. 1996). The reach of noise is not limited by property lines or borders and can be detected deep into otherwise protected areas (Barber et al. 2011). A global rise in human population coupled with an increase in mechanization and a demand for natural resources is not expected to abate in the near future (McDonald 2008) and noise levels are likely to rise further.

A recent avenue of research has begun to explore the effects of anthropogenic noise on a broad range of taxa. The observed impacts to animal behavior have been roughly placed into four categories: 1) changes in temporal patterns, 2) alterations in distributions, 3) changes in mate attraction or territorial defense, and 4) decreases in foraging (Francis and Barber 2013). Temporal changes in behavior include night singing by European Robins (*Erithacus rubecula*), a behavioral adaptation that may reduce the impact of urban noise on communication but with unknown consequences to mate attraction and territoriality (Fuller et al. 2007). Changes to animal distributions in response to noise are well documented. For example, songbird densities (Bayne et al.

2008) and species richness (Francis et al. 2009) declined by one-third at noise sites compared to quiet sites in natural gas extraction fields. In a separate study of applied traffic noise to a road-less landscape, songbird abundance was found to decline by one-quarter and some species were shown to completely avoid the noise-exposed area (McClure et al. 2013). In the marine environment, Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) showed vertical and horizontal movements away from vessels, presumably in response to noise (Handegard et al. 2003;Vabǿ et al. 2002).

Changes to mate attraction and territoriality have been documented in a variety of species. In a playback study in Wyoming, researchers detected a one-third decrease in lek attendance by male greater sage-grouse (*Centrocenrcus urophasianus*) when natural gas drilling noise was experimentally applied and a three-quarter attendance decline when road noise was played (Blickley et al. 2012). Decreased attendance at sage-grouse leks in response to noise could hinder reproductive success. In a study of the reproductive behavior of ovenbirds (*Seiurus aurocapilla*), pairing success was reduced near noisy compressors compared to silent well pads (Habib et al. 2007).

Noise can affect foraging behavior by causing an increase in vigilance and/or anti-predator behavior. For example, chaffinches (*Fringilla coelebs*) spent more time in a head-up position when noise was played back when compared to foraging bouts in the absence of noise (Quinn et al. 2006). In a separate study, white-crowned sparrows (*Zonotrichia leucophrys*) spent more time in the vigilant, head-up position when foraging in road noise (Ware 2014). However, little is known about the effect of noise on the foraging behavior of acoustically specialized predators, which include many bats and owls. Two studies designed to investigate noise and predator-prey interactions used gleaning bats as a model species. Gleaning bats rely on echolocation for navigation but listen for prey-produced sounds when foraging (Barber et al. 2003). When the mouse-eared bat (*Myotis myotis*) was exposed to traffic noise researchers detected a decrease in hunting success of over 50% when bats foraged under acoustic conditions equivalent to 7.5 m from an active highway (Siemers and Schaub 2011). More recently researchers compared pallid bat (*Antrozous pallidus*) foraging times when exposed to highway traffic and natural gas compressor station noise (Bunkley 2013) and found a 300% increase in foraging times in noise conditions. Predator-prey interactions are an integral component of ecosystems and it is pertinent that the effect of noise on such relationships be examined. In particular, the effect of noise on the foraging behavior of an owl has yet to be examined.

The oldest known fossil of a *Strigiformes* owl was uncovered in Colorado, USA and is believed to be 58 million years old (Rich and Bohaska 1976). Since at least that time owls have successfully radiated across every continent except Antarctica, and they have evolved extraordinary adaptations for foraging at night. For example, owl wing and feather morphology has contributed to their ability to fly silently (Johnsgard 1988) which may improve the owl’s ability to hear prey while flying. The capacity to make in-flight corrections is important for owls because prey cues are often intermittent and moving. In a free-flight experiment, barn owls (*Tyto alba*) adjusted their in-flight trajectory in reaction to moving acoustic stimuli (Hausmann et al. 2008). Additionally, many owls are able to hear sounds below the minimum auditory threshold of humans (Dooling 2002; Dyson et al. 1998). The evolution of highly sensitive hearing in owls is likely a result of the routine challenge to detect faint prey-produced cues. Owls are further challenged to localize sounds instantaneously, a process that has driven the evolution of ear asymmetry in many owl species.

In a prime example of convergent evolution, bilateral ear asymmetry has evolved independently in owls at least four times and is present in 6 owl genera (Norberg 1977). Ear asymmetry is critical for the instantaneous three-dimensional localization of sound and is prevalent in primarily nocturnal owls (Konishi 1973, Norberg 1977, Knudsen and Konishi 1979), harriers in the genus *Circus* (Rice 1982), and the nocturnal letter-winged kite (*Elanus scriptus*) (Negro et al. 2006). Ear asymmetry in birds allows for simultaneous readings of a sound location in both the horizontal and vertical planes (Knudsen and Konishi 1979). Approximately one third of all owl species worldwide exhibit some form of ear asymmetry, although species with this trait are not uniformly distributed. North of 35 degrees latitude half of all North American owl species and two thirds of European owls exhibit ear asymmetry (Johnsgard 1988). One explanation for this pattern is that owls hunting in northern latitudes are challenged with long, dark winters and the common presence of snow. Prey located in tunnels beneath snow, in vegetation, or in complete darkness may be difficult or impossible for owls to detect visually. Such circumstances would promote the evolution of highly sensitive, directional hearing to overcome the limitations of sight. However, acoustic specialization evolved in the absence of an additional challenge - anthropogenic noise.

The northern saw-whet owl (*Aegolious acadius*) is a forest dwelling species widely distributed across North America. It is largely migratory with variable movement patterns observed across its range (Stock et al. 2006; Whalen and Watts 2002). The saw-whet specializes on small mammals; Peromyscus and Microtus species comprised over

94% of their diet in Western Montana (Holt and Leroux 1996). Small mammals may be particularly challenging to capture due to the ease by which they can become obscured by snow or vegetation. However, the saw-whet owl is well adapted to using acoustic cues for hunting; it exhibits the highest degree of ear asymmetry recorded for any known species of owl (Norberg 1977).

Throughout a saw-whet's life cycle it is likely to be in contact with many types of anthropogenic noise. The owl occurs commonly in areas influenced by intense urbanization and resource extraction, as is the case in the northeastern United States. Resource development is also intense in the boreal forests of Canada, which comprises the northern range of the saw-whet. Therefore saw-whets are likely to come into frequent contact with drilling and compressor station noise. Highway traffic noise is also prevalent in saw-whet habitat. Eighty-three percent of the continental United States is within approximately 1 km of a primary road (Ritters and Wickham 2003), leaving few places untouched by road noise. It is possible that for many saw-whet owls exposure to human-caused noise is commonplace.

Anthropogenic noise has expanded due to an increase in human population and a coupled rise in demand for natural resources. In particular, energy extraction projects pose unique threats to quiet soundscapes. These projects are usually continuously active, as opposed to most transportation networks that have daily or seasonal activity patterns. Furthermore, resource extraction projects may be located in otherwise pristine landscapes, with noise broadcast over expansive areas otherwise devoid of human alteration. In an increasingly urban world, these remote areas might be crucial strongholds for some species. Natural gas extraction and its associated noise footprint have expanded dramatically in the last 50 years, with total domestic production in the United States reaching an all-time high in 2013 (USEIA 2014). In addition to domestic production, global demand for natural gas is high and will likely continue to rise as many countries around the world develop their resources. Compressor stations in natural gas extraction fields produce chronic broadband noise (Figure 1.1), and in areas of high compressor density background noise levels have been shown to be above ambient across an entire extraction field (Francis et al. 2011). However, compressors are not the only noise sources in extraction fields. Drilling rigs and road networks add to the overall acoustic footprint in these areas (Blickley et al. 2012). Moreover, noise from energy infrastructure commonly extends beyond the immediate extraction site and can reach into otherwise protected areas (Barber et al. 2011) with largely unknown consequences to ecological communities. Understanding the impacts of noise on wildlife will be a crucial step toward its effective management.

The degree to which noise affects animal behavior is thought to be dependent on the temporal, intensity, and frequency features of the noise (Francis and Barber 2013). Under this framework noise impacts are expected to increase when the amplitude above ambient is high and when the frequency of the noise stimulus overlaps with biologically relevant sounds. When this is the case, important acoustic cues can be masked by noise (Barber et al. 2010). Acoustic masking has been implicated as the reason for observed upward shifts in song frequency in both birds (Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008) and cetaceans (Au et al. 1985). By shifting song frequency out of the frequency range of noise the signal may be more easily perceived by the listener (Bermúdez-Cuamatzin et al. 2010; Nemeth and Brumm 2010). However, many species are not able to change the frequency of their vocalizations and the fitness consequences of doing so are largely unknown. Apart from acoustic masking, another mechanism for noise impacts has been posed. The distraction hypothesis posits that animals may redirect their finite attention in the presence of noise and thereby fail to respond appropriately to acoustic cues (Chan, Giraldo-Perez et al. 2010).

In communication animals strive to overcome signal transmission problems because the signal is mutually beneficial. However, there is no selective pressure for a prey item to become more acoustically conspicuous in noise. Therefore prey might be more likely to go undetected by a predator relying on hearing to detect faint movement cues. Acoustic specialists such as the northern saw-whet owl may be particularly affected. In order to independently examine the effect of noise on owls hunting acoustically, I had to control for the owls acute low-light vision (Martin 2010). In foundational studies of owl hearing, barn owls were shown to be insensitive to infrared light (IR) (Payne and Drury 1958; Konishi 1973). Furthermore, long-eared owls (*Asio otus*) did not show iris contraction (which would indicate sensitivity) when exposed to IR light (Hecht and Pirenne 1940). For these reasons I chose to film the free-flight hunting bouts with IR light. Northern saw-whet owls were not able to use IR light to detect prey or navigate as evidenced by their behavior; the owls did not fly back to the perch when only IR lights were illuminated though they would do this routinely when visible light was on inside the tent.

For an animal to capture prey each step in a predatory attack sequence must be successfully completed. First the predator must initially detect the prey, and then it must gather enough information to reach an attack decision. Lastly the predator must physically capture the prey. A breakdown at any step in this process would be expected to decrease hunting success for the predator. In this study I presented mice (*Mus musculus*) to wild-caught northern saw-whet owls inside a flight tent where sound and light levels were strictly controlled. The mouse footsteps on the arena floor produced broadband noise with intensities primarily between 0.5 – 20 kHz (Figure 1.2). In the absence of visible light, owls were challenged to hunt using only prey-produced sounds. Background noise levels were equivalent to those found between 50 and 800 m from an active compressor station (46 - 73 dB(A)). I hypothesized that owl hunting success would decrease in noise conditions found closer to a compressor station. I predicted that noise would negatively affect each step in the predatory attack sequence: the owls would (1) orient toward the prey less often (mouse detection), (2) be less likely to strike at prey, and (3) have lower prey capture rates as noise treatment level increased. This experiment was not designed to parse the distraction vs. masking hypotheses, which may not be mutually exclusive. Rather my objective was to assess the hunting behavior of owls in response to noise. Here I compare the dose-response hypothesis, where I predict that hunting deficits will increase with decreasing distance from a compressor station with the threshold hypothesis, where I predict an equal effect from all noise levels employed in the experiment. An evaluation of these hypotheses will provide a framework for mitigating noise impacts to owls.

# METHODS

## Owl Capture and Acclimation

Personnel from the Intermountain Bird Observatory at Boise State University have been monitoring owl migration in the Boise Mountains of SW Idaho since 1999 (Stock et al. 2006). Each autumn mist-nets are placed for owl capture in areas dominated by Douglas fir (*Pseudotsuga menzeisii*), mountain ninebark (*Physocarpus monogynus*), and chokecherry (*Prunus virginiana*). I used a subset of northern saw-whet owls caught at this banding station in my experiment. All captures and experimental trials took place in September and October of 2012 and 2013.

Upon capture, I transported the owls approximately 1 km inside a small pet carrier (70 cm x 30 cm x 30 cm) and released them inside a flight tent (description below) which served as the location for all experimental trials. I provided each owl a minimum of 1.5 hours inside the tent with a visible light on (Energizer blue LED headlamp) before presenting the owl with a mouse. In this way the owl could acclimate to hunting in this novel environment using both hearing and vision. If the owl hunted within 15 minutes after the release of a mouse, I retained the owl and used it in subsequent experimental trials on the following night(s). If an owl did not hunt, I released it and it was not used in the experiment. In this way I controlled for the owls’ hunger level, as each owl that participated in experimental trials had eaten just one mouse in the previous 19-24 hours.

The owls that participated in experimental trials were also familiar with the physical arrangement inside the tent through a successful hunting experience.

## Flight Tent

All experimental trials took place inside an 8 m x 7 m x 4 m light-proof flight tent. I placed two light sources inside the tent: a head lamp in the top corner of the tent illuminated the arena for acclimation trials (light visible to owls) and an array of 5 infrared lights illuminated the arena for the purpose of filming with IR sensitive cameras. I filmed all trials with two high definition (HD) cameras: a Canon (model XA-10) and Sony (model CX7) set to 30 frames per second (fps) and night mode.

I directed the cameras toward an owl perch that was 1.7 m high and 0.4 m wide. Around the perch, in view of the cameras, I placed a mouse runway that was 0.5 m wide and elevated 0.5 m above the ground. The mouse runway, constructed of plywood, was covered with thick carpet to provide a semi-soft striking surface and elevated with cinder blocks. On the carpet I scattered a thick layer of detritus gathered from under a Douglas fir tree which primarily consisted of fir needles and dirt. The nearest edge of the runway was 2.2 m and the furthest edge was 2.8 m from the perch (average 2.5 m). The runway served three purposes: 1) to keep the hunting arena in view of the cameras, 2) to control the distance between the owl and the mouse, and 3) to ensure the strike area was free of obstacles which could endanger the bird while hunting in the absence of light. I introduced the mice to the runway from outside the tent through one of two randomly chosen, insulated PVC tubes (3.8 cm diameter). The tubes were on opposite sides of the runway (Picture 1) which allowed me to randomize the mouse entry location.

## Experimental Trials

An experimental trial was a single hunting bout at a particular noise level. All owls participated in four consecutive experimental trials in the same night, including three noise trials and a control trial where I did not playback noise. I presented all trials in random order. The flight tent was not sound proof so the ambient noise conditions outside the tent were present during all experimental trials. I conducted trials during the owls' second night in captivity in 2012 and during both nights two and three during the 2013 season. In 2012 seven owls hunted in noise treatments which varied between 61 and 73 dB(A). Five additional owls hunted in noise treatments of lower intensity; however, due to an error in those particular sound files I retained only the control trials for use in the analysis. In 2013 nineteen owls hunted two times under three noise levels between 46 and 55 dB(A) and a control trial (see trial summary, Table 1.1).

When an owl captured a mouse during a trial I left the mouse with the owl for 15 minutes so as not to negatively associate the hunting behavior with a researcher entering the tent. When I entered the tent between trials I returned the owl to the perch either by approaching it, which would usually induce it to fly back to the perch, or by handling the owl and physically placing it on the perch. Provided the owl had killed a mouse during the previous trial, I would remove the mouse before leaving the tent and resume the experiment. After each hunting trial I employed a five minute noise free washout period to prevent carryover effects (Jones and Kenward 2003). I also included a five minute noise acclimation period prior to each trial so that owls would be acclimated to the noise before the trial began.

Upon completion of the first night of experimental trials (second night of captivity) I either released the owls near the flight tent (2012) or returned them to the hard-walled pet carrier that I placed in a protective structure near the flight tent (2013). This structure safeguarded the owls against potential predators. When owls were inside the pet carrier between trial nights I provided them with one mouse and water *ad libitum*. After completion of the experiment I released the owls near their point of capture.

## Playback Stimuli

In August of 2012 I recorded the Gobbler's Knob compressor station in the Jonah natural gas field in western Wyoming (N42 41.43 W109 48.66) using a Sennheiser shotgun microphone (ME-66) connected to a Roland (R0-5) WAV recorder sampling at a rate of 96 kHz. I made recordings from a variety of distances ranging from 50 to 500 m. At each distance I measured the sound pressure level using a Larsen-Davis 824 SPL meter. I made all recordings at night between the hours of 2100 – 0400, and the temperature between 10 - 12$^{o}$ C. Sound intensities were integrated over a three-minute time span. The intensities that I played back during the experiment were 73, 67, 61, 55, 49, and 46 dB(A) (see Table 1.2 for corresponding distances). I constructed the 49 and 46 dB(A) tracks by projecting the 73 dB(A) track to distances of 600 and 800 m respectively for each 1/3$^{rd}$ octave frequency band using the IHS ANSI Standard for Sound Attenuation (ISO 9613-2). At distances greater than 500 m (55 dB(A)) topography or the presence of other noise sources made obtaining a clear recording impractical.

Inside the flight tent I played back the noise treatments through Bose omni-directional speakers (model Freespace 51) powered by a Kicker amplifier (model IX500.2) or a Lepai amplifier (model LP-2020A). I mapped the sound intensity inside the flight tent using a Larsen Davis 824 SPL meter and placed the speakers as to produce an even sound field (+/- 2 dB) across the entire hunting area. The dB(A) sound integration made at the actual compressor station contained a broader frequency spectrum than could be accurately reproduced by the speakers inside the flight tent. Therefore I calibrated the stimulus files so that each 1/3$^{rd}$ octave frequency band within the relevant range of owl hearing (Dooling and Popper 2007) matched the original sound levels from the compressor station. This recalibration was done in MatLab with a custom program (D. Mennitt). During 2012 the sound system was powered off for the control trials. In 2013 I played a silent track through the sound system during control trials. The silent track was added to the experiment in 2013 to provide a negative control.

## Video Analysis

To quantify owl and mouse behavior I analyzed videos of the interactions using Adobe Premiere Pro (CS6). The trial began when the mouse was completely out of the tube and onto the runway. For each trial I recorded the cumulative number of seconds and the proportion of the trial that the mouse was physically moving. These variables were included in the analysis as covariates. I considered the mouse stopped when it did not move for five consecutive seconds. I also quantified the proportion of the trial that the owl was oriented toward the mouse. Correct orientation was defined by the owl pointing its facial ruff at or within one mouse length of the mouse. As these measurements were somewhat subjective, two researchers independently coded mouse movement and owl head orientation. In subsequent analyses I used an average of these scores. When an owl left the perch in direct pursuit of the mouse I tallied a strike and recorded the outcome of the strike as either a hit or miss.

## Data Analysis

I used logistic regression to determine for each treatment the odds of the owl orienting to the mouse (detection), striking at the mouse, and capturing the mouse. I conducted all data analyses in program R, version 3.1 (R Core Team 2014). For each dependent variable (odds of detection, strike, and capture) I compared the two hypotheses (dose-response vs. threshold) with each other, with models only containing covariates (described below), and with the null model. I represented all hypotheses with generalized mixed linear models and used the individual owl as a random intercept in order to account for inherent variability in owl behavior and to control for the repeated sampling of individual owls. I then ranked the models and compared them using Akaike’s Information Criterion (Akaike 1974). The covariates within all models $\Delta AIC<2$ were considered useful for inference if the 85% confidence intervals of their coefficients excluded zero. I used 85% confidence intervals instead of 95% because they are more appropriate under an AIC model selection framework (Arnold 2010).

In addition to the variables of interest, there were multiple covariates that I included in the models if they were independently determined to have had an effect on owl hunting behavior. These covariates were order of trial, night of trial, mouse movement, and year. Order of trial was the sequence of experimental trials (1-4) regardless of noise treatment. Night of trial was the first night of experimental trials or the second. Mouse movement was the proportion of the trial that the mouse was physically moving, and year pertained to the year that the trial took place, 2012 or 2013. I determined the independent effect of each of these covariates by regressing them against the hunting behaviors of interest (detection, strike, and capture odds) and I retained the variables where the 85% confidence intervals of the coefficients excluded zero.

# RESULTS

Each measure of owl hunting behavior was negatively impacted by noise. Detection rate, the proportion of the trial that the owl was correctly oriented to the mouse, decreased in response to increasing noise levels (Table 1.3, Figure 1.4). Similarly, strike and capture rates were highest in control conditions and trended downward as noise treatment levels increased (Table 1.4, Figure 1.5).

Logistic regression analysis revealed that order of trial, night of trial, mouse movement, and year all affected the odds of the owl detecting the mouse. Mouse movement was the only covariate that affected the odds of a strike. Night of trial and mouse movement both affected mouse capture odds. The coefficients for each covariate are summarized in Table 1.5.

The most parsimonious model for each measure of owl hunting (detection, strike, and capture) contained the dose-response parameter (Table 1.6). For this parameter noise was treated as a continuous variable and its inclusion in each top model indicates that as noise increased hunting success decreased (Figure 1.6). In all cases, the second model contained the threshold parameter but was $> 2$ $\Delta$AIC from the top model. Overwhelming model weight was assigned to the models containing the dose-response parameter (Table 1.6).

Upon examination of the dose-response coefficient, the odds of an owl detecting a mouse during a hunting bout was 0.89 for each decibel increase in noise (Table 1.7). This translates to an 11% decrease in the odds of a mouse being detected for each unit decibel increase in noise. Similarly, the odds of a strike was 0.93 for each decibel increase in noise, which corresponds to a 7% decrease in strike odds. Finally, the odds of a successful mouse capture was 0.92 for each decibel increase in noise, or an 8% decrease in capture odds. In each case, the 85% confidence intervals around the dB coefficient excluded zero (Table 1.7).

# DISCUSSION

Northern saw-whet owls hunted mice in noise treatments matching the frequency spectra and intensity conditions found 50 – 800 m from an active compressor station. The odds of the owls detecting, striking, and capturing mice decreased in response to increased noise, lending support to the dose-response hypothesis. The deficits were most pronounced at and above 61 dB(A), where the owls failed to capture any mice. The ability of owls to track mice was also severely curtailed at and above 61 dB(A). A general trend throughout the data was that the capture rate was lower than the strike rate and both were lower than the detection rate. This pattern held true in both treatment and control trials. An explanation for this trend is that simply detecting a prey item does not provide an owl with sufficient information to initiate an attack. Likewise, once an owl leaves the perch in pursuit of a mouse, capture is not guaranteed. Throughout the attack sequence the owl must assimilate a host of information about its prey; size, location, and prey movement patterns must be accurately determined for a hunting bout to be successful. The hunting deficits I observed likely resulted from the interference of noise on the gathering and processing of auditory information critical to successful prey detection and capture. According to the capture likelihood model (Table 1.7), each decibel increase in noise resulted in a 7% decrease in the odds of an owl capturing a mouse, which illustrates that small changes in noise intensity and/or frequency composition can have a profound effect on owl hunting behavior.

Though the hearing ability of the northern saw-whet owl has yet to be assessed, a composite from 13 owls from which audiograms have been obtained indicate that owl hearing is most sensitive between 0.5 – 8 kHz (Dooling 2002). Compressor noise is comprised of frequencies primarily below 10 kHz (Figure 1.1), which completely overlaps the functional range of owl hearing. However, higher frequencies attenuate faster than lower frequencies with increasing distance from a compressor. The owls in my experiment were attempting to detect the sounds of mouse footsteps on a forest floor substrate, which are fairly broad band with power ranging from 0.25 – 20 kHz (Figure 1.2). In all noise treatments, the intensity of the compressor station noise was higher than the intensity of the prey-produced sounds. Noise treatments equivalent to 50 – 200 m from a compressor station completely overlapped in frequency spectra with the noise produced by the mouse footsteps. Across this intensity range the owls did not successfully capture mice. From 500 – 800 m there was progressively less overlap in frequency with the mouse footsteps, which likely explains the hunting success observed at these intensities. When the frequency of the compressor noise did not completely overlap sound produced by prey, hunting success improved.

Acoustic masking of prey-produced sounds is a likely mechanism for the hunting deficits observed in my study; however, the results of my experiment do not allow for the dismissal of the distraction mechanism. Confounded with an increasing overlap in frequency spectra between playback stimuli and prey-produced sounds was an increase of noise amplitude. Increasing amplitude has been implicated with a rise in distraction for hermit crabs (*Coenobita clypeatus*) (Chan, Stahlman et al. 2010), and it is possible that rising noise levels increasingly distracted owls in my experiment. Regardless of mechanism, compressor noise caused hunting deficits for saw-whet owls. Compressors are increasingly common across the landscape and their noise should be considered as a pollutant capable of degrading owl habitat.

Compressor station noise could be substantially reduced by the use of sound attenuating walls. In addition to limiting the geographical extent of noise, acoustic barriers would reduce high frequency noise because such barriers readily deflect short sound wavelengths. Barrier walls around compressors in New Mexico reduced noise intensity by 10 dB(C) at 30 m (Francis et al. 2012). If these structures were placed around all compressors in this gas field the overall noise footprint would be reduced by approximately 70% (Francis et al. 2012). A compressor station that is 70 dB(A) at 30 m will be expected to naturally attenuate to 29 dB(A) in approximately 3 km. A barrier wall around this compressor station would allow the noise to reach 29 dB(A) in just 1 km, which highlights the potential effectiveness of sound attenuating walls. Moreover, the construction and installation of acoustic barrier walls are not likely to be prohibitively expensive (Bayne et al. 2008).

The spectral composition of compressor station noise, which is dominated by low frequencies, is similar to many other types of anthropogenic noise, including road noise. The acoustic properties of road noise depend on the level of traffic, the composition of vehicles on the road, the speed of the vehicles, and the road substrate. A 4-lane highway with 6,000 vehicles passing per hour at 65 mph is approximately 70 dB(A) at 200 m (Dooling and Popper 2007). In comparison, the Gobbler's Knob compressor station used in my experiment was 61 dB(A) at 200 m. Acoustically, highways with continuous traffic behave as a line source of sound whereas compressor stations produce a point source. Noise from line sources attenuate slower than noise from point sources. Specifically, noise from a line source attenuates at approximately 3 decibels per doubling of distance whereas noise from a point source attenuates at 6 decibels per doubling of distance. Despite these differences, road noise is spectrally similar to compressor station noise in that peak intensities are typically below 8 kHz (Dooling and Popper 2007). As with compressor station noise, road noise overlaps spectrally with the lower frequency bands produced by prey sounds (i.e. mouse footsteps) so the potential for acoustic masking near sources of road noise may be high. Thus, an important avenue of future research will be to determine whether road noise adversely affects the hunting efficiency of owls in a manner similar to compressor station noise.

Much of what we know about sound localization and information processing in owls comes from free-flight experiments with trained barn owls (Knudsen 2002; Knudsen et al. 1984; Konishi 1973). Like the saw-whet, barn owls exhibit ear asymmetry and are able to localize prey in the absence of light. A common thread in many sound localization experiments is that the owls are hand-reared and tame. The use of trained owls has proven beneficial because once owls learn an experimental paradigm, conditions can be manipulated in ways that reveal underlying processes. However, there are limitations to using trained owls. First, tame owls are often kept in captivity for the duration of their lives and the husbandry and training process is time and labor intensive. This effort may be worthwhile if multiple experiments are planned over many years, but is impractical for short-term projects. Secondly, the applicability of an experiment to wild animal populations is questionable if the experimental subjects are not wild. The owls used in my experiment had no known experience with humans and were therefore more likely to behave in a way representative of wild saw-whet owls.

Northern saw-whet owls are not the only owl species that routinely use acoustic cues for hunting. For example, the great gray owl (*Strix nebulosa*) often plunges through snow to capture prey items outside of its visual reach (Godfrey 1967). The same is true for boreal owls (*Aegolious funereus*) (Korpimaki and Hakkarainen 2012). For such behavior to be successful, the owl must complete the entire predatory attack sequence aurally. Although the degree to which owls use hearing to initially detect prey is not well documented, it is likely to be high and it follows that extraneous noise may interfere with this process. A crucial consideration when interpreting the effect of noise on owl hunting behavior is the distance between the owl and its prey when the owl initiates its attack. Boreal owls, a congener of the saw-whet owl, attacked their prey in the wild from an average distance of 5.6 m (Bye et al. 1992). Though similar data do not exist for the saw-whet, it is unlikely that their attack distance in the wild is less than the 2.5 m average distance between owl and mouse in my experiment. Furthermore, it may be common for an owl to initially detect its prey aurally because hearing is omni-directional and effective through physical obstacles such as vegetation or snow. Although the distance from which an owl initially detects its prey is unknown, it is reasonable to assume that the distance will usually exceed 2.5 m.

Despite the general conclusions of my study, there are cases of acoustically specialized predators hunting successfully in the presence of anthropogenic noise. For example, tawny owls (*Strix aluco*) consumed a higher proportion of rodents in suburban areas and switched to birds in urban areas (Zalewski 1994). One explanation for this switch in prey is that while auditory cues are important for the detection of inconspicuous prey such as mice, visual cues are sufficient to detect birds in areas where the acoustic cues of potential prey are masked by anthropogenic noise. The high levels of light in urban environments may make visual detection of conspicuous prey such as birds an effective foraging strategy. In the present experiment, saw-whet owls (n=2) captured mice in five of six trials conducted in conditions of both light and noise.  This result indicates that when a saw-whet owl is able to use its vision, noise does not prevent hunting success.

The degree to which noise drives habitat use patterns in owls has not been investigated. If owls in the wild experience hunting deficits around areas of high noise, it is possible they will move to areas better suited to hunting. The acoustic degradation of otherwise functional owl habitat is likely to manifest at multiple trophic levels. In the marine environment a reduction in predatory fish resulted in an increase in starfish (*Asteroidea*) that increasingly preyed upon reef building corals, thereby altering reef community structure (Dulvy et al. 2004). In another study, noise from compressor stations resulted in an increase in flower pollination by black-chinned hummingbirds (*Archilochus alexandri*) and concomitant decreases in pinyon pine (*Pinus edulis*) seedling recruitment (Francis et al. 2012). It is possible that distributional changes to a top-level predator such as an owl could result in changes through a trophic cascade. If hunting pressure by owls were relieved around noisy compressor stations, unchecked rodent populations would be expected to increase. From an ecological perspective it is important to know if the hunting deficits observed in my experiment manifest in wild owls. If they do, the broader ecosystem implications should be explored.

Profound transformation is occurring across many landscapes due to a myriad of anthropogenic activities including but not limited to resource extraction (Copeland et al. 2009; Schneider et al. 2003). Because the potential for continued habitat alteration caused by industrial activities will remain high for the foreseeable future, resource managers will be challenged to mitigate impacts to a host of wildlife species (Akani et al. 2004). In an era of complex environmental problems associated with wide scale habitat alteration and global climate change, managing anthropogenic noise may be a relatively easy way to increase resiliency in a variety of species. Because environmental perturbations have a cumulative impact on ecosystem integrity (Spaling and Smit 1993), the maintenance of natural acoustic environments could lessen the overall burden faced by many species. By fundamentally altering soundscapes across the planet we may be changing predator–prey dynamics with largely unknown consequences. Anthropogenic noise is a widespread and as yet underappreciated pollutant, the effects of which are starting to come to light. Fortunately noise mitigation techniques are readily available. The effective management of noise will be an important step to maintaining ecological balance in the face of pervasive anthropogenic change.

**Table 1.1.** **A summary of the noise treatments and sample sizes from northern saw-whet owl hunting trials which took place in 2012 and 2013. Each owl hunted once per treatment level in 2012 and twice per treatment level in 2013.**

| 2012 | | | 2013 | | |
|---|---|---|---|---|---|
| Treatment | # owls | # trials | Treatment | # owls | # trials |
| Control | 12 | 12 | Control | 18 | 39 |
| 61 | 7 | 7 | 46 | 18 | 39 |
| 67 | 7 | 7 | 49 | 18 | 39 |
| 73 | 6 | 6 | 55 | 18 | 39 |

**Table 1.2.** **A summary of the noise intensity levels played back to northern saw-whet owls inside a flight tent while they hunted mice in 2012 and 2013. The noise intensities were measured and recorded from distances ranging from 50 – 500 m from an active compressor station (Gobbler's Knob compressor station, Jonah Field, Wyoming). As I did not make recordings from beyond 500 m, the 49 and 46 dB(A) tracks were projected for each 1/3rd octave band according to the ANSI standard for sound attenuation (ISO 9613-2).**

| Year | Noise Intensity dB(A) | Distance (m) |
|---|---|---|
| 2012 | 73 | 50 |
| 2012 | 67 | 100 |
| 2012 | 61 | 200 |
| 2013 | 55 | 500 |
| 2013 | 49 | 600 |
| 2013 | 46 | 800 |

**Table 1.3. Northern saw-whet owls hunted mice under noise treatment levels ranging from control (no added noise) to 73 dB(A). The number of trials that an owl correctly oriented its facial ruff toward a mouse during a trial is compared between treatment levels. Number of owls and total trials for each treatment level are also indicated. The detection rate is the proportion of trials that an owl oriented toward the mouse at least once. All hunting trials took place in 2012 and 2013.**

| Treatment dB(A) | Owls | Trials | Trials with a detection | Detection Rate |
|---|---|---|---|---|
| Control | 31 | 50 | 49 | 0.98 |
| 46 | 19 | 38 | 32 | 0.84 |
| 49 | 19 | 38 | 28 | 0.74 |
| 55 | 19 | 38 | 25 | 0.66 |
| 61 | 7 | 7 | 5 | 0.71 |
| 67 | 7 | 7 | 4 | 0.57 |
| 73 | 6 | 6 | 4 | 0.67 |

**Table 1.4. Northern saw-whet owls hunted mice under noise treatment levels ranging from control (no noise added) to 73 dB(A). Owl strikes and captures are compared between treatment levels. Strikes were the number of trials where the owl left the perch in pursuit of the mouse (regardless of outcome), captures were successful strikes. All hunting trials took place in 2012 and 2013.**

| Treatment dB(A) | Owls | Trials | Strikes | Strike Rate | Captures | Capture Rate |
|---|---|---|---|---|---|---|
| Control | 31 | 50 | 24 | 0.48 | 16 | 0.37 |
| 46 | 19 | 38 | 11 | 0.29 | 6 | 0.29 |
| 49 | 19 | 38 | 10 | 0.26 | 7 | 0.26 |
| 55 | 19 | 38 | 7 | 0.18 | 4 | 0.18 |
| 61 | 7 | 7 | 1 | 0.14 | 0 | 0.00 |
| 67 | 7 | 7 | 0 | 0.00 | 0 | 0.00 |
| 73 | 6 | 6 | 1 | 0.17 | 0 | 0.00 |

**Table 1.5. Coefficients for covariates: order of trial (order), night of trial (night), mouse movement (movement), and year. Each covariate was regressed independently (logistic regression) against three measures of owl hunting behavior: detection, strike and capture likelihood. Variables were included in the subsequent analyses of noise on owl hunting behavior when the 85% confidence interval of their coefficients excluded zero (indicated in bold type).**

| | Covariate | Coefficient | SE | CI - | CI + |
|---|---|---|---|---|---|
| Detection | **Order** | 0.19 | 0.003 | 0.19 | 0.20 |
| | **Night** | 0.85 | 0.421 | 0.25 | 1.46 |
| | **Movement** | 1.38 | 0.723 | 0.34 | 2.42 |
| | **Year** | 0.15 | 0.003 | 0.15 | 0.16 |
| Strike | Order | -0.15 | 0.154 | -0.38 | 0.07 |
| | Night | -0.06 | 0.352 | -0.56 | 0.45 |
| | **Movement** | 2.67 | 0.810 | 1.50 | 3.83 |
| | Year | -0.67 | 0.473 | -1.35 | 0.01 |
| Capture | Order | -0.06 | 0.186 | -0.33 | 0.21 |
| | **Night** | 0.71 | 0.427 | 0.10 | 1.33 |
| | **Movement** | 1.33 | 0.878 | 0.06 | 2.59 |
| | Year | 0.38 | 0.651 | -0.56 | 1.32 |

**Table 1.6. Model results for three measures of northern saw-whet owl hunting behavior: the odds of the owl orienting toward (detection), striking, and capturing the mouse. For the 'dose-response' parameter noise was treated as a continuous variable, for the 'threshold' parameter noise was categorized as 'on' or 'off'. Covariates were mouse movement (movement), night of trial (night), order of trial (order), and year.**

**Detection**

| Model | AIC | ΔAIC | k | wi |
|---|---|---|---|---|
| dose-response + movement + night + order + year | 165.58 | 0 | 6 | 0.97 |
| threshold + movement + night + order + year | 172.53 | 6.95 | 5 | 0.03 |
| mouse movement + night + order + year | 189.30 | 23.72 | 5 | 0.00 |
| Null | 191.13 | 25.55 | 1 | 0.00 |

**Strike**

| Model | AIC | ΔAIC | k | wi |
|---|---|---|---|---|
| dose-response + movement | 187.72 | 0 | 3 | 0.92 |
| threshold + movement | 192.64 | 4.92 | 3 | 0.08 |
| movement | 205.28 | 17.56 | 2 | 0.00 |
| null | 219.04 | 31.32 | 1 | 0.00 |

**Capture**

| Model | AIC | ΔAIC | k | wi |
|---|---|---|---|---|
| dose-response + movement + night | 149.38 | 0 | 4 | 0.84 |
| threshold + movement + night | 152.68 | 3.30 | 4 | 0.16 |
| movement + night | 163.05 | 13.67 | 3 | 0.00 |
| null | 167.48 | 18.10 | 1 | 0.00 |

**Table 1.7. The most parsimonious model for each measure of owl hunting behavior (detection, strike, and capture odds) included the parameter 'dose-response'. The coefficients for this parameter are reported along with their standard errors. The odds column includes the change in probability of each reported hunting behavior for each decibel increase in noise from 29 dB(A) to 73 dB(A). Confidence intervals (85%) around the odds are also reported.**

| | Parameter | Coefficient | SE | Odds | CI - | CI + |
|---|---|---|---|---|---|---|
| Detection | Dose-response | -0.12 | 0.03 | 0.89 | 0.84 | 0.93 |
| Strike | Dose-response | -0.07 | 0.02 | 0.93 | 0.90 | 0.95 |
| Capture | Dose-response | -0.08 | 0.02 | 0.92 | 0.89 | 0.96 |

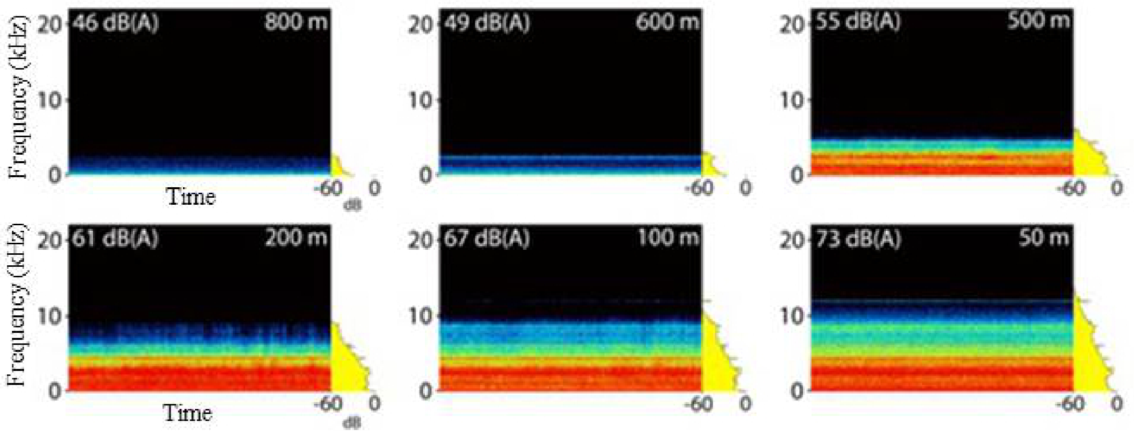


**Figure 1.1.** **Spectrograms of the noise stimuli presented to northern saw-whet owls while they hunted mice inside of a flight tent. Within each spectrogram the x-axis depicts time and the y-axis is frequency (kHz). The noise intensity is indicated in the top left of each spectrogram (dB(A)) and the distance that the file was recorded from a compressor station is indicated in the upper right (m). The colors represent relative intensity, with warmer colors indicating more power. The power spectra attached to the right of each spectrogram display the relative intensities for the range of frequencies comprising the noise. In the power spectra, relative intensity (dB(A)) is on the x-axis and frequency is on the y-axis.**

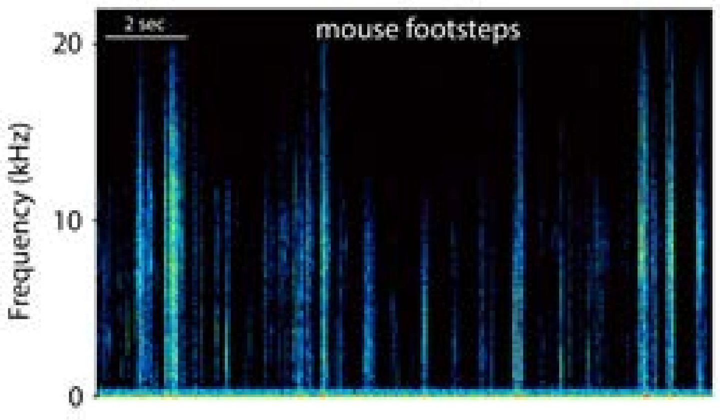


**Figure 1.2.** **A spectrogram of mouse footsteps on the arena floor, recorded inside the flight tent from a distance of 10 cm. Time is on the x-axis and frequency in on the y-axis. Sound intensity is indicated by the color spectrum, with warmer colors indicating more power. Northern saw-whet owls were challenged to hunt mice in the absence of light by keying in on the noise produced by mice walking on the floor of the hunting arena.**

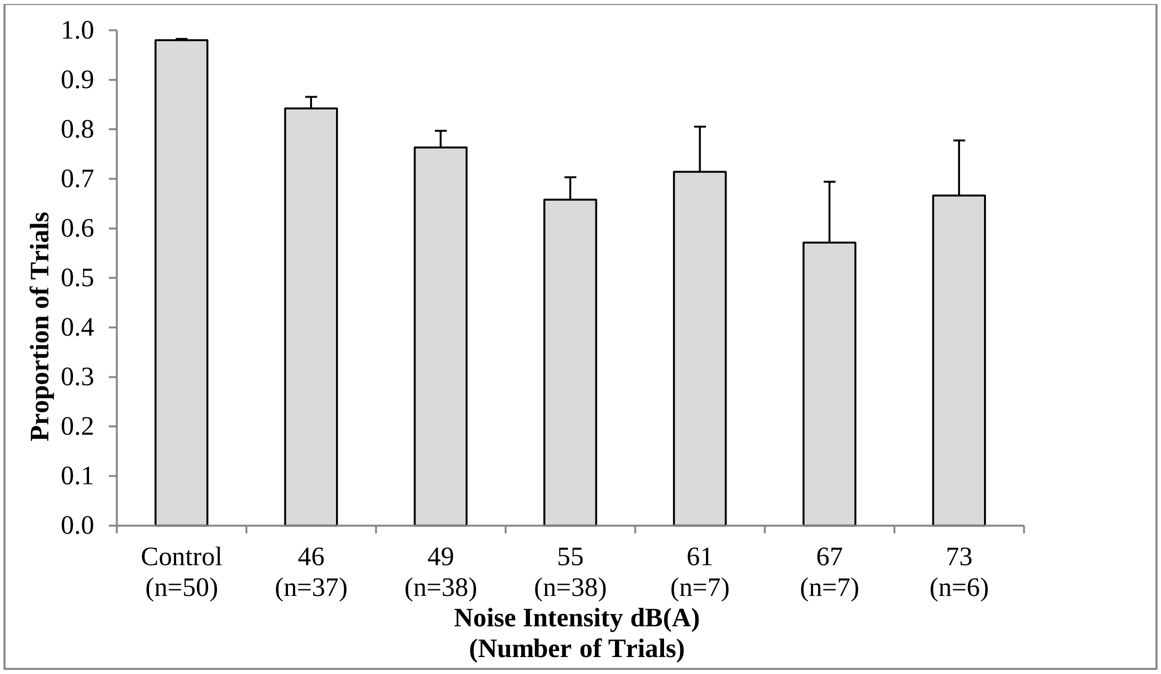


**Figure 1.3 The mean (±SE) proportion of trials that the owls detected a mouse. A detection was defined by the owl orienting its facial ruff directly toward the mouse during an experimental trial. Noise treatment intensities varied from control (no noise added) to 73 dB(A). The number of trials at each noise level is indicated in parentheses on the x-axis.**

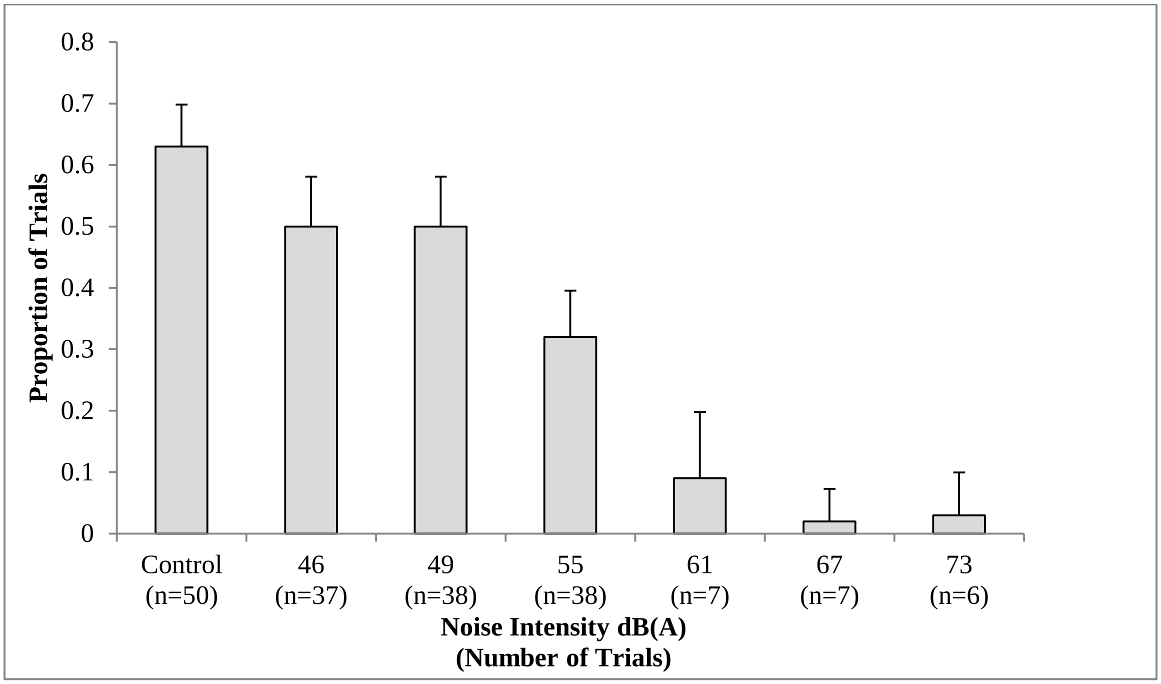


**Figure 1.4. The mean (±SE) proportion of trials that the owls were oriented toward the mouse is compared for each treatment level (control – 73 dB(A)). Number of trials are indicated in parentheses on the x-axis.**

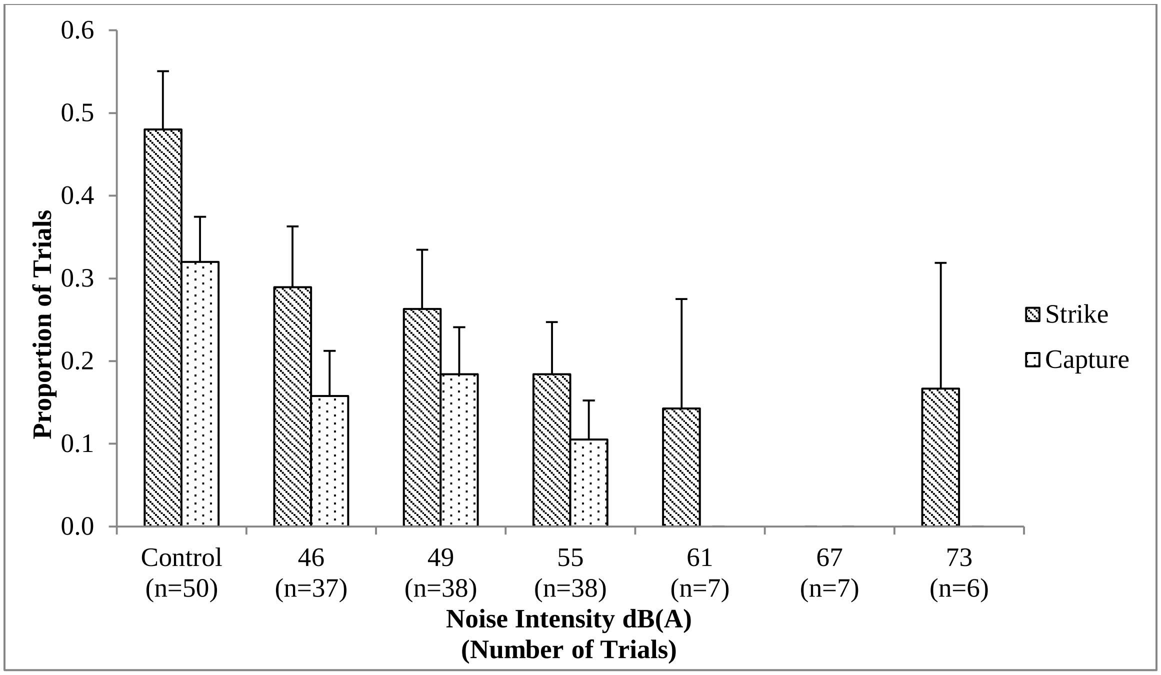


**Figure 1.5. A summary of strike and capture success for northern saw-whet owls hunting mice in noise conditions which ranged from control (no noise added) to 73 dB(A). The strike rate is the proportion of trials that the owl left the perch in pursuit of the mouse regardless of the outcome. Capture rate is the proportion of trials that the owl successfully captured the mouse. There were no strikes at 67 dB(A) and there were no mouse captures at or above 61 dB(A). The number of trials for each treatment level is indicated in parentheses. Error bars are SE.**

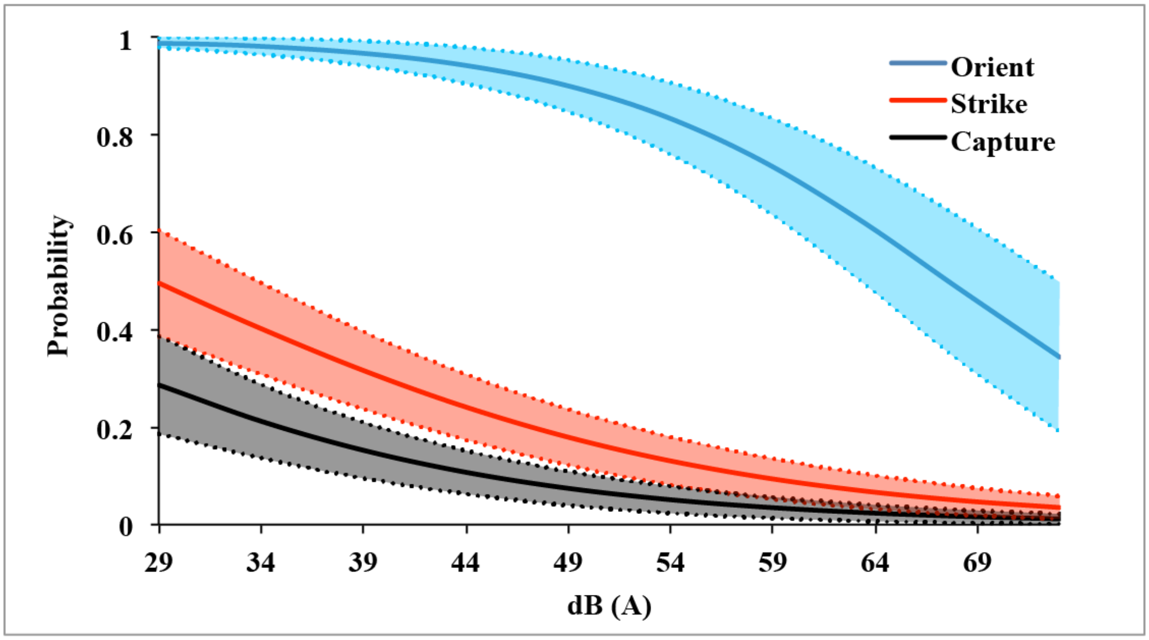
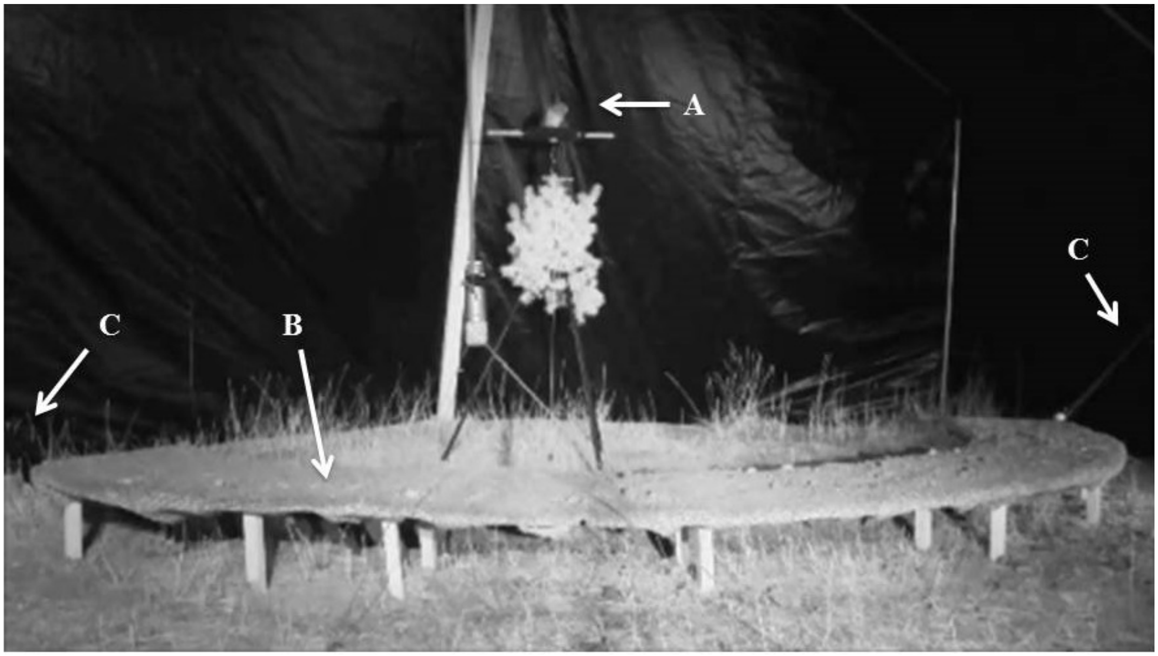


**Figure 1.6. The probability of an owl orienting toward (detection), striking, and capturing a mouse for the range of noise levels used in the experiment. The control (absence of added noise) averaged 29 dB(A) and the loudest treatment was 73 dB(A). Curves were determined by plotting the most parsimonious model for each measure of owl hunting. Shaded areas represent standard errors.**



**Picture 1.** **Hunting arena inside flight tent as seen from Canon video camera. The owl is on the perch (A) around which is an elevated mouse runway (B). The mouse delivery tubes are on the far left and right of the picture (C). A mouse can be seen at the base of the tube on the right side.**

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