



Evaluating the behavioural response of moose (*Alces alces*) to acoustic stimuli

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Abstract

Fear in animals is a motivational state that cause the animals to change their behaviour. Anti-predator behaviour is innate behaviours shown by prey species in situations where there is an increased risk of predation. This can be caused by the presence of the actual predator or by implied presence by acoustic, olfactory or visual cues. Such cues may provide a potential tool in management and can be used to elicit desired behavioural responses in animals such as moving away from the cue. Therefore, it is important to investigate what types of acoustic stimuli makes ungulates leave or increase their vigilance, in comparison to what acoustic stimuli will make them exhibit a non-disturbed behaviour such as feeding. In this study, I investigated how wild moose (*Alces alces*) that visited saltlick-stones in the forest responded to different acoustic stimuli: dog barking, human voice and bird calls (owl at night and woodpecker at daytime), compared to when moose are undisturbed by acoustic stimuli. The main research questions were: (1) Does any of the stimuli make moose leave the site more often than when undisturbed?; (2) How does the stimuli affect the amount of time moose spend vigilant or feeding?; and (3) After exposure to a stimuli, how long does it take before moose return to the site? I found that when exposed to human stimuli, moose left the attractive saltlick-stone in 75% of the events, which were significantly more often compared to when exposed to the sounds of (dog 39%, bird 24% and when undisturbed 11%). If moose did not leave the site, they spent more time vigilant and less time feeding, particularly when exposed to a dog or human stimuli. However, this response was also true for the non-threatening bird stimuli compared to when they were entirely undisturbed. When exposed to any of the three acoustic stimuli, moose took significantly longer to return to a site compared to when they were undisturbed. Longest time to return was after human stimuli. These results suggest that acoustic stimuli may be used in management situations where the aim is to evoke a quick flight response. Acoustic signals may hence serve as a potential measure to prevent ungulate-vehicle collisions.

Populärvetenskaplig sammanfattning

Rädsla är ett naturligt beteende som uppvisas av djur i situationer när de upplever någon typ av hot. De beteendemässiga förändringar djuren uppvisar när de känner sig hotade är ofta medfödda och har visat sig vara fördelaktiga genom evolutionen, optimala för att undkomma en hotfull situation. Bytesdjur uppvisar så kallade anti-predatorbeteenden, bland annat rädsla, vilka kan orsakas av den faktiska predatoren eller av något som antyder en predators närvaro orsakat av ljus, lukt eller ljud. Anti-predatorbeteenden är ofta studerat hos klövvilt, som till exempel hjortdjur, då dessa arter är vanliga bytesdjur och förekommer i de flesta miljöer. Vanliga beteenden när de upplever ett hot är att lämna platsen eller att öka sin vaksamhet. Att imitera ett hot kan potentiellt användas som ett verktyg i viltförvaltningen när syftet är att få djuret att lämna en specifik plats. Därför är det av intresse att undersöka vilken typ av ljud som skulle kunna vara användbara när målet är att få hjortdjur att lämna en plats eller öka dess vaksamhet. I denna studie undersökte jag hur vilda älgar som besökte uppsatta saltstenar reagerade på olika ljud som: hundskall, människoröst och fågelljud (uggla nattetid och hackspett dagtid), jämfört med när älgen var ostörd. Mina huvudsakliga frågor var: (1) Orsakar något av ljuden att älgarna väljer att lämna platsen, (2) Hur påverkar de olika ljuden den tid som älgarna ägnar åt att vara vaksam och åt att inta föda, samt (3) Hur lång tid tar det för en älg att komma tillbaka till platsen efter att den har hört ett ljud?

Jag fann att älgar som fått en människoröst uppspelad lämnade platsen i 75% av fallen, vilket var signifikant oftare i jämförelse med älg som upplevt hundskall (39%), fågelljud (24%) eller som varit ostörd (11%). Om älgen inte lämnade platsen ägnade den en längre tid åt att vara vaksam samt mindre tid åt att inta föda, särskilt när den hört en människoröst eller hundskall. Detta var dock också sant för fågelljud i jämförelse med när älgen var ostörd. Efter att ha fått de tre ljuden uppspelade dröjde det längre tid innan älgen kom tillbaka till platsen i jämförelse med när de var helt ostörda. Älgar som fått människorösten uppspelad tog dock längst tid på sig att komma tillbaka. Resultaten visar att ljud kan skapa beteendemässiga förändringar och att olika ljud kan ge olika stark respons. Ljuden kan därmed vara olika effektiva beroende på vilket sammanhang de används i. Dessa resultat antyder att ljud kan vara användbara i situationer där målet är att inducera en snabb flyktrespons. Ljud skulle därmed sannolikt kunna användas för att förhindra viltolyckor.

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1. Introduction

Fear in animals is the degree of risk or threat animals perceive in a given situation (Stankowich & Blumstein, 2005) and can motivate change in their behaviour (Stankowich & Blumstein, 2005; Brown *et al.*, 2012). Behavioural responses as a result of fear are often innate and formed through evolution as optimal mechanisms for escaping the cause of fear in a specific situation (Sih *et al.*, 2004). Fear responses in situations with increased risk of predation result in prey displaying anti-predator behaviours (Frid & Dill, 2002; Stankowich & Blumstein, 2005; Kuijper *et al.*, 2014). Species under threat from a predator (e.g. preferred prey) may maintain innate anti-predator response even when this predator is absent and therefore still react to cues of this predator (Hettena *et al.*, 2014; Makin *et al.*, 2019).

1.1. What induces fear and how do ungulates respond?

Fear is commonly studied in ungulates, since this group of species are widespread and common prey (Prugh *et al.*, 2019). Thus, building the knowledge base on behavioural changes displayed by ungulates when they are exposed to a threat (Creel *et al.*, 2008; Creel & Christianson, 2008; Stankowich, 2008). For example, when ungulates detect the presence of a threat such as a predator, they tend to leave (Brown *et al.*, 2012) or increase vigilance (Stankowich, 2008; Brown *et al.*, 2012).

Besides the threat from a natural predator such as for example a wolf, ungulates feel threatened and change their behaviour with the presence of humans, in environments with human recreational activities or hunting (Stankowich & Blumstein, 2005; Brown *et al.*, 2012; Cromsigt *et al.*, 2013). While studies often focus on evaluating ungulate behavioural changes with the presence of different types of threats, emerging research suggest that by implying presence of a threat, the same type of behavioural changes such as leaving and increased vigilance are shown (Gilsdorf *et al.*, 2004; Hildreth *et al.*, 2013; Babińska-Werka *et al.*, 2015).

1.1.1. Inducing fear without the presence of the actual threat

Fear in ungulates may be induced by implying a predatory pressure through for example, lights and moving reflective objects (Koehler *et al.*, 1990), adding wolf

urine (Chamaillé-Jammes *et al.*, 2014) and by displaying acoustic stimuli such as the sound of a predator or the alarm calls of conspecifics (Babińska-Werka *et al.*, 2015; Shimura *et al.*, 2018). Of these methods, acoustic stimuli have been identified as a promising method when the aim is to induce a behavioural response in ungulates without the actual threat present, since the result from these studies show that the ungulates leave and increase their vigilance (Babińska-Werka *et al.*, 2015; Shimura *et al.*, 2018). To date, studies all focus on small, social ungulate species, such as sika-deer (*Cervus nippon*), the white-tailed deer (*Odocoileus virginianus*) and roe deer (*Capreolus capreolus*), (Gilsdorf *et al.*, 2004; Hildreth *et al.*, 2013; Babińska-Werka *et al.*, 2015; Honda, 2019). However, no studies have been conducted on large, solitary species such as moose (*Alces alces*).

1.2. What is the behavioural response of moose to acoustic stimuli?

Moose is one of the ungulate species that is solitary living and can be found in forests all over Sweden (Bergqvist *et al.*, 2002). In recent years, moose have received attention due to increased train accidents with moose (Seiler & Olsson, 2017) and due to causing costly damages to forestry production when browsing on especially young Scots pine (*Pinus sylvestris*), (Hörnberg, 2001; Härkönen *et al.*, 2008).

Even though several studies have been conducted on deer species regarding their behavioural responses to a threat, little is known about moose and their behavioural responses to different threats. Thus, in this project, I aimed to evaluate if moose display behavioural changes when exposed to acoustic stimuli and if there is a difference in response depending on the information in the acoustic stimuli. To achieve this, I compared how wild living and filmed moose responded to acoustic stimuli while visiting salt lick stones. I used and compared the responses to sounds expected to convey a potential threat: dog barking and human voice with an acoustic stimulus expected to be non-threatening: bird call, and with no acoustic stimuli displayed (silence i.e. no stimuli displayed). The anti-predatory behaviours I was interested in were leaving, vigilance and site avoidance. I was also interested in the behaviour feeding, since this is a natural behaviour indicating that the animals were not disturbed (Brown & Kotler, 2004), thus acting as a non-anti-predator behaviour.

I predicted that:

1. When moose are exposed to dog stimuli or human stimuli a significantly greater proportion will leave a site compared to when they are undisturbed, while moose exposed to bird stimuli will not leave significantly more often compared to being undisturbed.
2. When exposed to dog or human stimuli, moose increase their vigilance and decrease their time spent feeding. When moose are exposed to bird stimuli, they will not significantly change these two behaviours.
3. When moose are exposed to dog or human stimuli, they will spend more time out of frame compared to being undisturbed, while moose exposed to bird stimuli will not spend more time out of frame compared to being undisturbed.
4. After being exposed to dog or human stimuli, the time before moose return will be significantly longer compared to being undisturbed, while moose will not take significant longer time to return after being exposed to bird stimuli.

2. Method

2.1. Study area

The study was conducted in the Grimsö wildlife research area (GWRA) in south-central Sweden. The current moose density in the area was 11 moose/1 000 ha (ÄSO, 2020). In the GWRA, saltlick stones have been used since decades to attract and monitor moose. The landscape is dominated by forest consisting of mostly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), 18% of the area consist of boggy wetlands (Faber, 1998).

Saltlick stones are an artificial resource, highly attractive to moose. Especially during spring and early summer when moose feed intake requires a higher sodium concentration (Laurian *et al.*, 2008). Attractant sites with saltlick stones were used to be able to conduct the experiment in a controlled environment. After monitoring 19 sites, 8 sites were selected for conducting the experiment: The sites were selected based on visit rate by moose and because I wanted a minimum distance of 1 km between the sites (fig 1; Appendix 1).

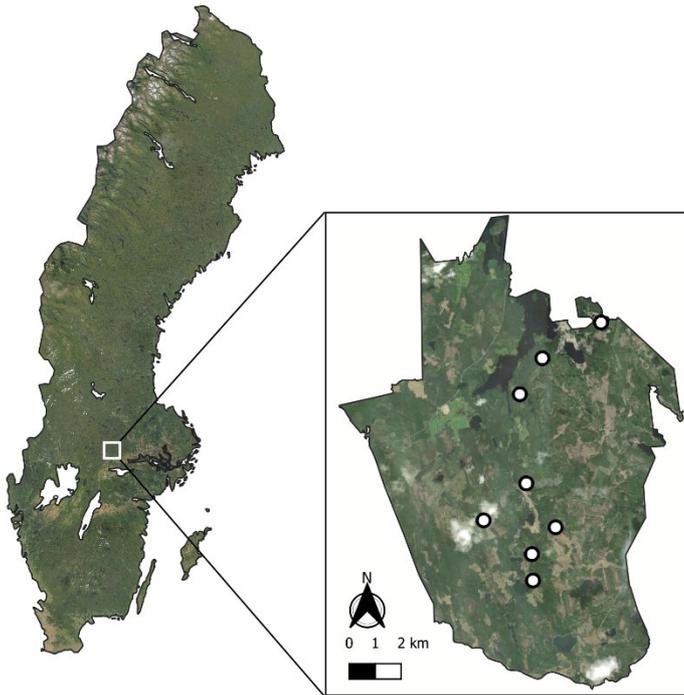


Figure 1. Locality of the Grimsö wildlife research area in Sweden (left) and the 8 sites in the area where the experiment were conducted (right; Source Esri, 2020).

2.1.1. Site setup

At each site, I conducted an experiment to evaluate moose response to different acoustic stimuli. This was done using a technical equipment especially developed for this purpose. The motion activated scaring system (MASS) were activated by motion, for example by an animal. The system was connected to a Reconyx hyperfire 2 (RECONYX INC, 2015), set on recording video. Recording started immediately when activated, acoustic stimuli or a silent control were displayed after a 20 sec delay and for a period of 20 sec, while the camera continued recording for another 20 sec. Each trial thus consisted of a 60 second video. The MASS unit and the camera were placed 10 meters from the saltlick stone at each site.

2.1.2. Acoustic samples

One and the same sound file were used for representing one acoustic stimuli. The barking dog were recorded from a dog used for moose hunt and the human voice was a male talking in a normal conversational tone. During night (hour 22-03), the bird stimuli was represented by the territorial song of a Boreal owl (*Aegolius funereus*) and during daytime it was represented by the drumming of a Black woodpecker (*Dryocopus martius*). The decibel ranged between 60-70 dB for all three acoustic stimuli. The research area is a hunting and recreational area,

therefore, the sound of a barking dog or a human likely have a threatening context for moose in this area, while the two bird species, commonly occurring in the area and as such the two bird sounds are so called informative and non-threatening. The silent acted as a control for displaying moose behaviour when they are not disturbed by an acoustic stimulus, and for detecting possible behavioural changes due to electronic sounds that could not be detected with the human ear.

During one hour, the system was set to display three acoustic stimuli at most. The first acoustic stimuli of the hour were randomized. In order to ensure all acoustic stimuli (dog, human and bird) was represented in each hour and to reduce the repeatability of the order of the sound files, the two subsequent stimuli were organized.

The system was set to a delay, meaning that after it was activated, it could not be activated again until 3 minutes after. The sound file setup was organized in an order, always having 4 silent controls after an acoustic sound file. This to ensure a gap between the exposure to acoustic stimulus within the hour.

The acoustic stimuli were displayed during the hour's when moose are most active, 18h-10h. The remaining hours, the system was set to only display the silent control. This enabled to avoid a large number of false activations by wind but in the same time still receive the information if a moose was visiting a site. Every time the system was activated, the event was logged in a text file. Every log entry had a corresponding 60 second video.

2.2. Data collection

Monitoring of 19 sites started 10 March 2020. The experiment with the acoustic stimuli at the 8 chosen sites started 21 May 2020, data was collected until 10 July 2020 (50 nights of data collection). I visited sites every third day, when I changed memory cards and batteries. At each visit, I also took three measurements of the decibel levels: twice during setup – 1 m from the speakers and at the saltlick stone – and once when collecting data three days later – 1m from the speakers. I took measurements during setup and before changing batteries in order to ensure the decibel levels kept the same level throughout the sampling period. The decibel was measured using the app Decibel X (SkyPaw, 2019).

2.3. Video analysis

Using the software program BORIS, I quantified individual behavioural data from the videos, BORIS is created for analysing videos by using time-constrained event

logging (Friard & Gamba, 2016). I analysed the videos by quantifying seconds spent on displayed behaviour by every individual in the video separately (full ethogram in table 1) and rounded time spent on a behaviour to the nearest second. I separated the seconds spent for each behaviour into three 20 second time periods: “before”, “during” and “after”. Where “during” was displaying moose behaviour while being exposed to either an acoustic stimulus or the silent control.

65 videos captured were too dark to analyse. Thus, I edited these videos using Clideo (Clideo, 2014), an online tool in which one can increase brightness of the videos. Five videos were still too dark to analyse even after brightness editing or due to moose only displaying parts of the head in the video.

For the silent control videos ($n = 402$), 279 videos were analysed. This large number of videos was due to the file setup with 4 silent controls between sound files. For every hour containing silent control videos, a minimum of 1 was analysed.

I analysed up to two silent control videos after each acoustic stimulus: 1 within 6 minutes and 1 more than 6 minutes after. The 6 minutes were chosen due to the setup of a 3 minute delay of the system, meaning if moose were exposed to an acoustic stimulus and stayed at the site, the next time the system could be activated and display a silent control was after 3 minutes, if moose still stayed at the site after this, next activation was after another 3 minutes, which were 6 minutes since the acoustic stimuli were displayed. This was to see if there was a lag effect of the acoustic stimuli (e.g. prolonged vigilance behaviour even after the acoustic stimuli has been off for some minutes). After 6 minutes I assumed that moose would have gone back to being undisturbed. I compared these two types of silent control videos as a control of moose undisturbed behaviour at the site and found no difference between the videos, thus combined them into a single category (see section 3.1 Descriptive results).

To explore if the owl song and woodpecker drumming could be combined into the category bird, to fit the initial hypothesis, I compared the likelihood to leaving the site, amount of time spent vigilant and amount of time spent feeding and found no difference (see section 3.1 Descriptive results).

Table 1. Ethogram of the behaviours quantified in BORIS for each individual moose in video.

Behaviour	Description
Feeding	Moose browsed on vegetation in the surrounding area around the saltlick stone or licked at the saltlick stone.
Fleeing	Moose moved in a fast pace, seemingly disturbed by something
Leaving the site	Moose left the site. Moose were considered left the site when they were out of camera frame.
Standing	Moose stood by the saltlick stone or in the surrounding, seemingly undisturbed
Social interaction	Moose displayed social interaction with another moose, either cooperative or competitive
Vigilant	Moose displayed a clear alert behaviour, listened and were observant to the surrounding. If feeding, moose stopped completely and displayed an alert behaviour such as ears up and looked in few directions
Walking	Moose walked in a slow pace, seemingly not stressed or disturbed

2.4. Data variables

To study moose response to acoustic stimuli, behavioural response variables (table 2) and explanatory variables (table 3) of interest were chosen from the dataset.

Table 2. Chosen response variables for the analysis.

Variable	Description
Leaving the site	Binary variable quantifying if moose left the site during the video. Yes=1, No=0
Vigilant	The time moose spent vigilant divided by time in frame to account for if moose left frame. Giving a proportional variable with binomial distribution, ranging from 0-1
Feeding	The time moose spent feeding divided by time in frame to account for if moose left frame. Giving a proportional variable with binomial distribution, ranging from 0-1
Time out of frame	The time moose spent out of frame divided by total time. Giving a proportional variable with binomial distribution, ranging from 0-1
Time to return	Minutes elapsed since the last visit by moose at a site

Table 3. Chosen explanatory variables for the analysis.

Variable	Description
Trial day	Trial day ranging from day 1 until day 50
Period	Factor with three levels: before, during and after. Giving the 20 second periods divided into: before exposure to acoustic stimuli or silent control, exposure to acoustic stimuli or silent control and after exposure to acoustic stimuli or silent control
Stimuli	Factor with four levels, one for each acoustic stimulus: dog, human, bird or the silent control
Rain	Amount of precipitation (mm/hour)
Wind	Strength of wind measured in m/s
Site	Site ID number 1-8
Previous stimuli	The stimuli played at the previous moose visit.

Ecological variables of interest for the analysis was the meteorological parameters rain and wind, since these could possibly cause refraction, scattering and absorption of sound waves, leading to influence on sound propagation (Ziemann *et al.*, 2016; Trikootam & Hornikx, 2019). They have also been shown to cause changes in ungulate behaviour and distribution (Herfindal *et al.*, 2019). This data was obtained from Lantmet (LantMet, 2020).

2.4.1. Leaving the site

To explore changes in the likelihood to leave the site, I fitted a binomial regression model, using the variable leaving the site (yes=1; no=0), as a response (table 2). Since I was interested in exploring if moose left more if exposed to a certain stimulus, moose that left the site within the first 20 seconds and did not return within the 60 second video were excluded. Among my explanatory variables (table 3), I included trial day to explore if the likelihood to leave changed over the trial period. To explore if the likelihood to leave differed depending on the acoustic stimuli, I added a categorical variable, ‘stimuli’ which could be one of the four (dog, human,

bird or silent control). To detect any signs of habituation to a certain stimulus, I included an interaction term between trial day and stimuli. I also included rain and wind to account for possible changes in behavioural response due to weather. Finally, I included site as a random effect to account for site-level variation.

2.4.2. Behaviours: Vigilant, Feeding and Time out of Frame

I fitted a binomial regression model using time spent vigilant, time spent feeding and time spent out of frame as the response variables (table 2). Three separate models were used for the three response variables. For each model, I included trial day, stimuli, period, the interaction between stimuli and period, rain and wind (table 3). Trial day were included to detect signs of habituation, stimuli to compare the time spent on behaviour depending on which stimuli moose were exposed to, period to compare difference before, during and after exposure. I included an interaction term between period and stimuli to distinguish if the amount of time moose spent on the behaviour differed before, during and after exposure to a certain acoustic stimulus or compared to silent control. I included rain and wind to account for difference in shown behaviours due to weather and finally site as a random effect to account for site-level variation.

2.4.3. Time to return

To explore if the time until next visit by moose changed, I fitted a gamma regression model using time to return as a response (table 2). Of the explanatory variables (table 3), I added previous stimuli since I was interested in if moose took longer time to return to a site depending on what stimuli previous moose were exposed to. I included trial day to explore if the time to return changed over the trial period. I included rain and wind to account for difference due to weather and site as a random effect to account for site-level variation.

All analyses were conducted using R (R Development Core team, 2020). The GLMMs were run using the ‘glmer’ function in the lme4 package (Bates *et al.*, 2015). To ensure I was using the most parsimonious models, I selected the models based on the lowest AIC (Akaike, 1973) corrected for small sample sizes (AICc). I conducted model selection on every model described above using the ‘dredge’ function in the MuMIN package (Bartoń, 2013). Top models ($\Delta\text{AICc} < 2$) were averaged using the ‘mod.avg’ function, also in the MuMIN package. The results I present are the conditional model averages.

3. Result

3.1. Descriptive results

I collected 4308 videos, of which 824 displayed moose. The results from the early analysis of the silent control videos showed no difference for the silent control videos recorded < 6 minutes after an acoustic stimulus or > 6 minutes after an acoustic stimulus ($p = 0.189$). The result from the analysis of the two bird sounds showed no difference between the two ($p = 0.109$). Therefore, the final dataset consisted of four final categories; dog stimuli, human stimuli, bird stimuli and silent control. The analysed dataset consisted of 696 events which displayed 761 individuals (table 4).

Table 4. The number of video-events displaying moose exposed to an acoustic stimuli: dog, human, bird or to a silent control and the number of individuals in the events. Shown divided to periods: before, during and after to account for moose leaving the site.

	N _{Events}		N _{Individuals}	
Dog	142		158	
	Before	142	Before	158
	During	124	During	138
	After	98	After	110
Human	143		154	
	Before	143	Before	154
	During	127	During	137
	After	48	After	48
Bird	132		147	
	Before	132	Before	147
	During	112	During	125
	After	106	After	120
Silent	270		302	
	Before	279	Before	302
	During	239	During	257
	After	228	After	248
Total	696		761	

Moose spend a most of their time displaying the behaviours Vigilant, Feeding or Out of frame in the three time periods (table 5; fig 2-5).

Table 5. Average time in seconds \pm standard deviation for the different behaviours, in the three periods: before, during and after.

	Before	During	After
Feeding			
Dog	8.37 \pm 8.56	2.41 \pm 4.37	4.47 \pm 7.31
Human	7.87 \pm 8.42	1.40 \pm 2.77	1.59 \pm 4.95
Bird	8.72 \pm 8.53	5.28 \pm 7.36	7.55 \pm 8.74
Silent	10.33 \pm 8.91	12.05 \pm 8.87	11.90 \pm 8.95
Fleeing			
Dog	0.06 \pm 0.53	1.78 \pm 3.18	0.45 \pm 1.53
Human	0.06 \pm 0.37	3.31 \pm 3.35	0.44 \pm 1.74
Bird	0.16 \pm 0.87	0.50 \pm 1.69	0.22 \pm 1.09
Silent	0.11 \pm 0.75	0.04 \pm 0.45	0.01 \pm 0.23
Social interaction			
Dog	0.00 \pm 0.00	0.01 \pm 0.16	0.00 \pm 0.00
Human	0.23 \pm 2.06	0.02 \pm 0.24	0.00 \pm 0.00
Bird	0.20 \pm 1.42	0.02 \pm 0.18	0.00 \pm 0.00
Silent	0.00 \pm 0.00	0.02 \pm 0.21	0.02 \pm 0.26
Standing			
Dog	3.25 \pm 5.37	0.65 \pm 2.39	0.83 \pm 3.05
Human	3.10 \pm 5.51	0.49 \pm 1.75	0.21 \pm 1.47
Bird	2.74 \pm 4.85	1.01 \pm 3.41	0.81 \pm 2.91
Silent	2.78 \pm 5.71	2.21 \pm 5.27	1.46 \pm 4.28
Time out of frame			
Dog	2.03 \pm 4.93	4.56 \pm 7.51	7.97 \pm 9.24
Human	2.06 \pm 4.85	7.70 \pm 6.91	15.07 \pm 8.37
Bird	2.22 \pm 5.14	3.46 \pm 7.31	5.87 \pm 8.53
Silent	2.36 \pm 5.42	3.55 \pm 7.34	4.07 \pm 7.81
Vigilant			
Dog	2.14 \pm 4.97	9.93 \pm 7.35	4.65 \pm 6.82
Human	2.68 \pm 5.46	6.55 \pm 6.61	2.28 \pm 6.62
Bird	2.07 \pm 5.27	8.18 \pm 7.72	3.41 \pm 5.82
Silent	1.81 \pm 4.74	1.17 \pm 3.46	1.51 \pm 4.35
Walking			
Dog	4.16 \pm 4.95	0.65 \pm 1.89	1.63 \pm 3.82
Human	4.00 \pm 5.04	0.53 \pm 1.97	0.42 \pm 1.87
Bird	3.88 \pm 5.22	1.55 \pm 3.25	2.14 \pm 4.20
Silent	2.61 \pm 4.29	0.96 \pm 2.73	1.02 \pm 3.19

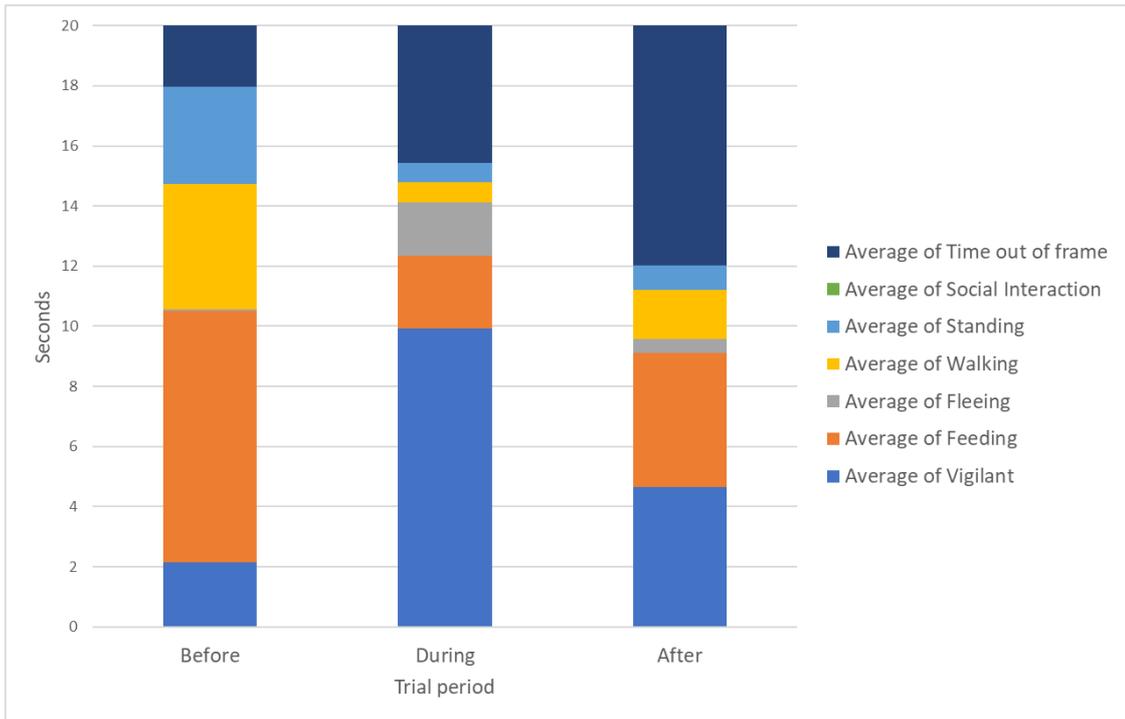


Figure 2. Average amount of time in seconds moose spent out of frame or displaying behaviours in ethogram when exposed to dog stimuli. Divided into periods: before, during and after.

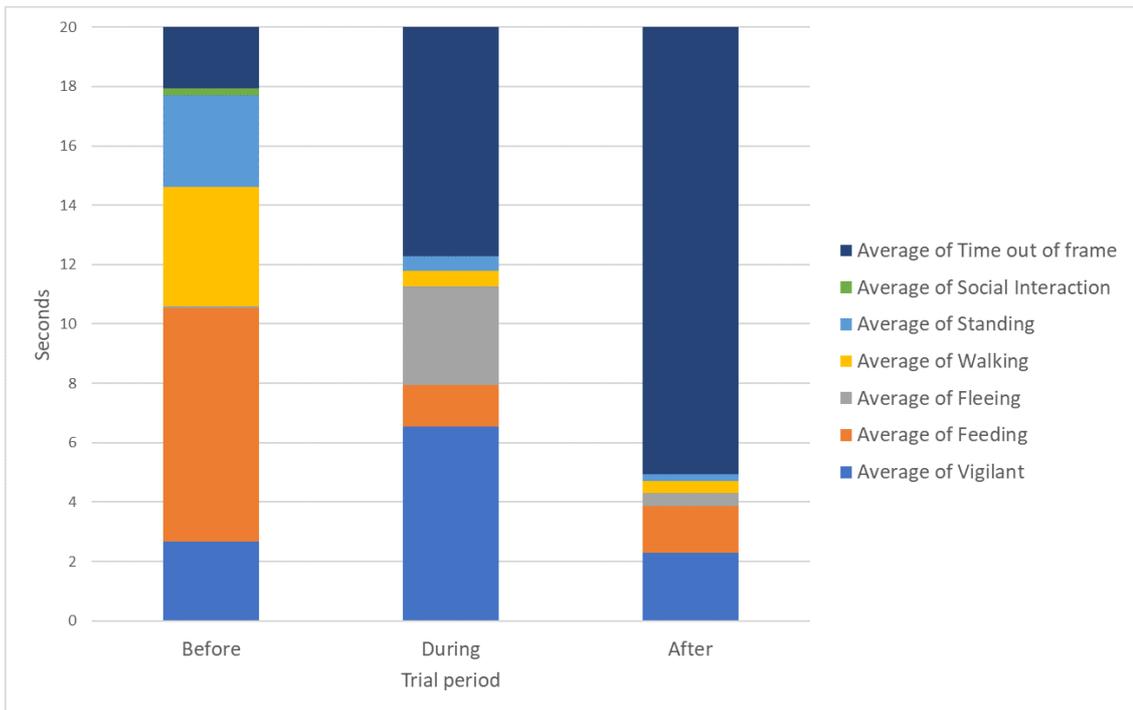


Figure 3. Average amount of time in seconds moose spent out of frame or displaying behaviours in ethogram when exposed to human stimuli. Divided into periods: before, during and after.

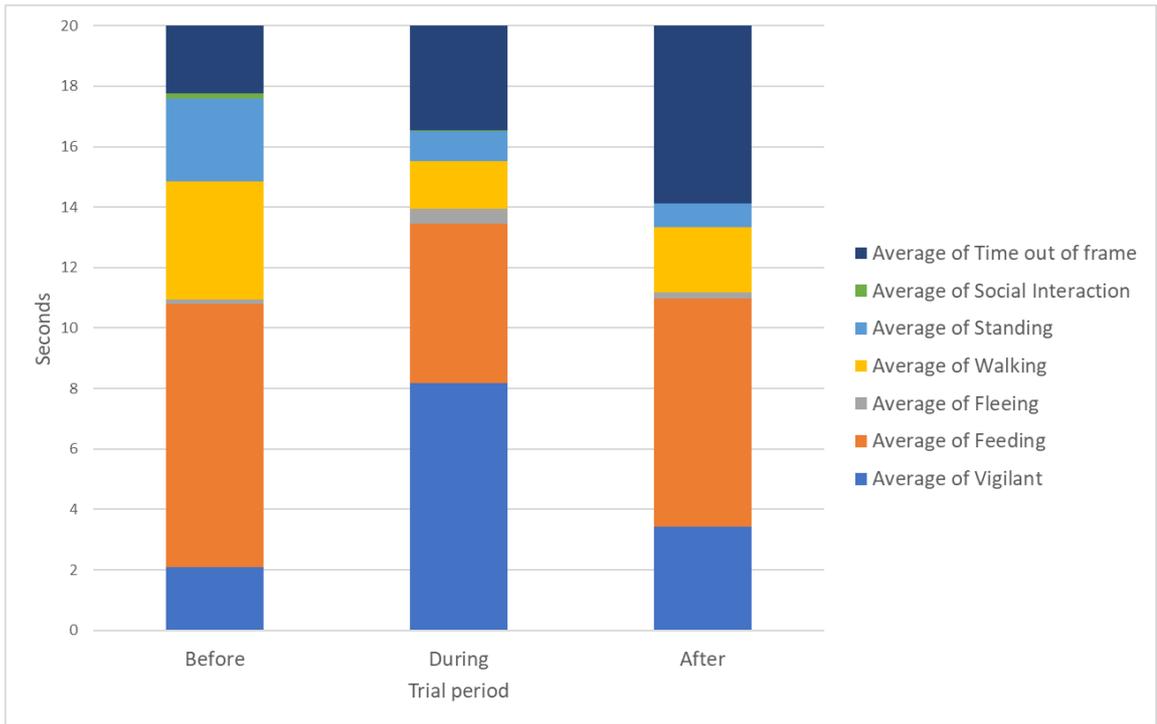


Figure 4. Average amount of time in seconds moose spent out of frame or displaying behaviours in ethogram when exposed to bird stimuli. Divided into periods: before, during and after.

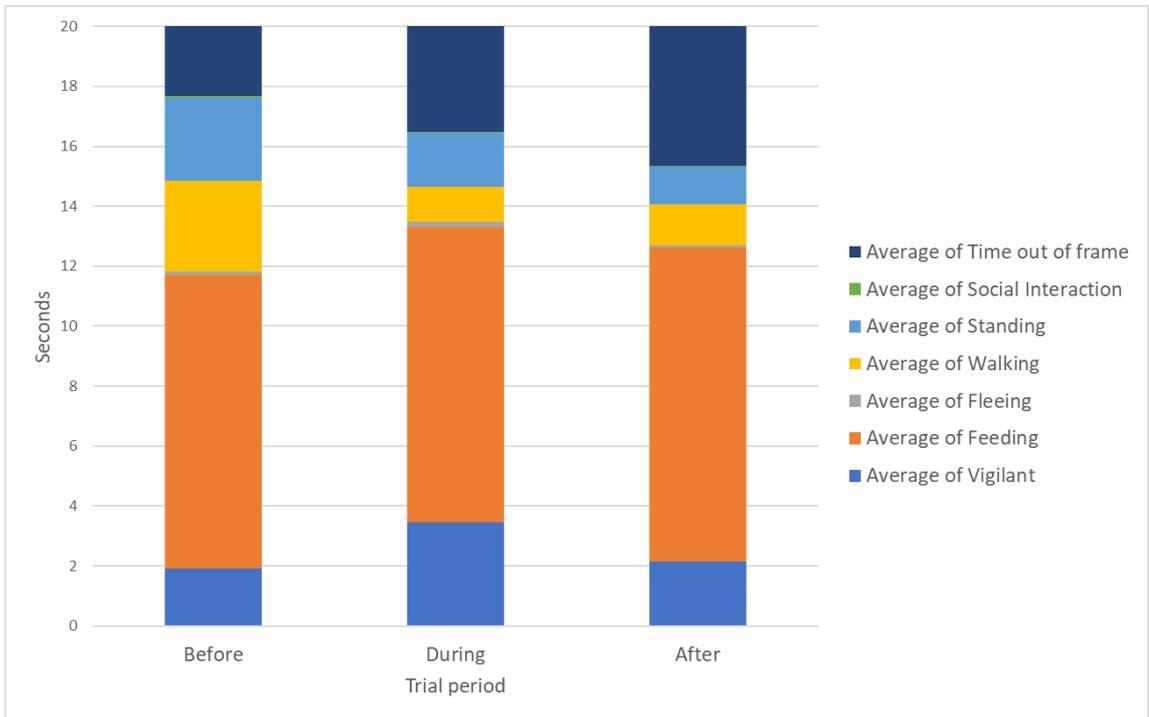


Figure 5. Average amount of time in seconds moose spent out of frame or displaying behaviours in ethogram when exposed to silent control. Divided into periods: before, during and after.

3.2. Leaving the site

Of the explanatory variables in the global model, all variables except wind were present in the top models ($\Delta AICc < 2$; table 6) and were therefore included in the logistic regression.

Table 6. AICc table for the candidate models for the leaving the site model. Showing top models ($\Delta AICc < 2$), the first model $\Delta AICc > 2$ and the null model.

Variables	AICc	$\Delta AICc$	AICc weight
Stimuli + Trial day	645.2	0.00	0.242
Stimuli + Trial day + Stimuli*Trial day	645.4	0.19	0.220
Stimuli + Trial day + Rain	646.8	1.63	0.107
Stimuli + Trial day + Stimuli*Trial day + Rain	647.2	1.95	0.091
Stimuli + Trial day + Wind	647.2	2.01	0.089
Null model	814.8	169.55	0.000

Moose left the site more after being exposed to any acoustic stimulus ($n = 187$) compared to the silent control ($n = 29$; $p < 0.005$; fig 6). Moose exposed to human stimuli left more often ($n = 103$; 75% of events) compared to dog stimuli ($n = 54$; 39% of events; $p = 0.03$) and compared to bird stimuli ($n = 30$; 11% of events; $p = 0.01$). There was no significant difference between dog stimuli and bird stimuli ($p = 0.13$). Rain did not have a significant effect on the probability for moose to leave ($p = 0.55$). With increased trial day, the likelihood for moose to leave a site decreased after being exposed to human stimuli ($p = 0.03$), and dog stimuli ($p = 0.04$). There was no significant decrease in the likelihood to leave after exposure to bird stimuli ($p = 0.11$) or to silent control ($p = 0.08$; fig 7; Appendix 2).

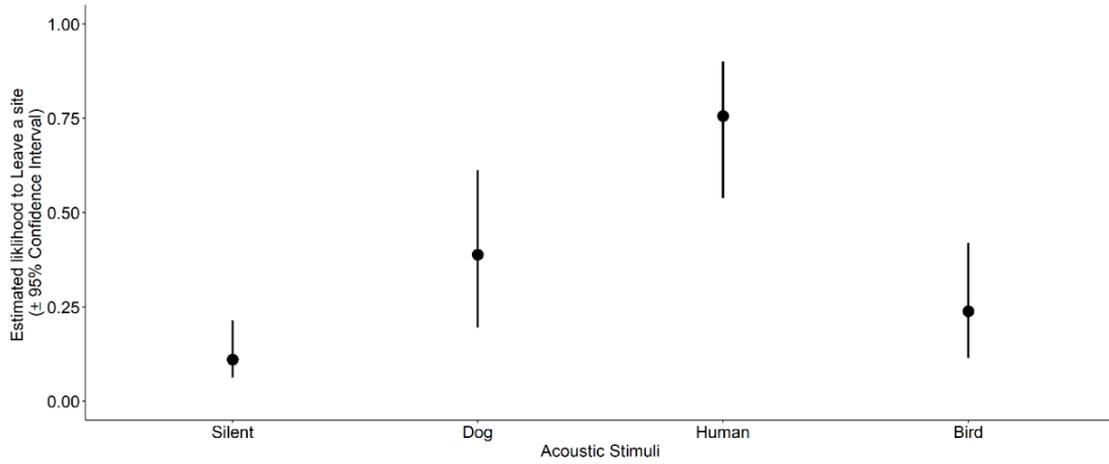


Figure 6. The estimated likelihood for moose leaving the site when being exposed to a silent control or acoustic stimuli: dog, human or bird.

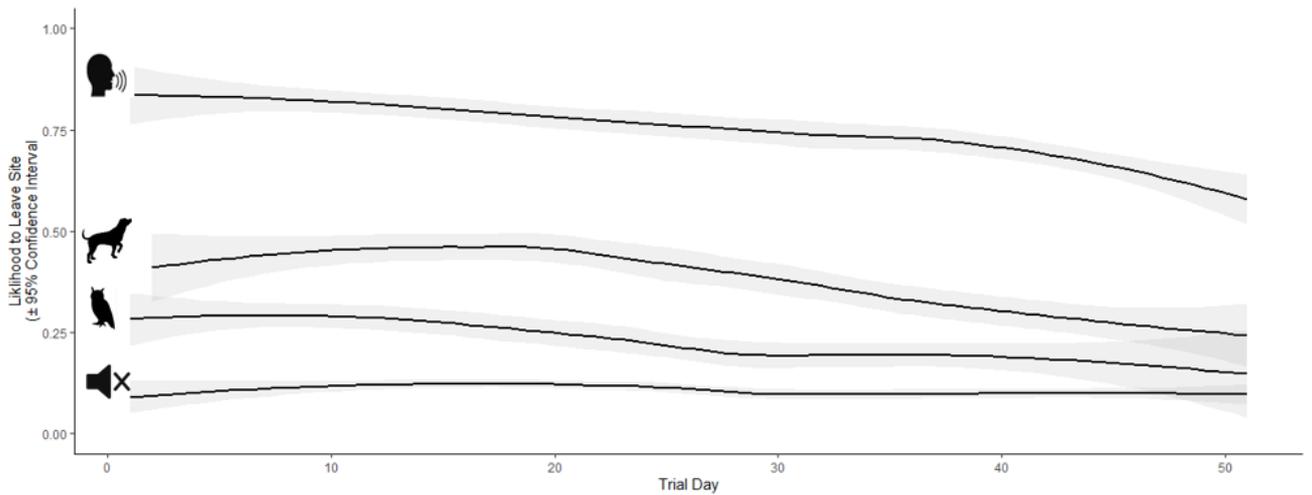


Figure 7. The estimated likelihood for moose leaving the site after being exposed to acoustic stimuli: dog, human or bird and the silent control over the trial period. The black lines reflect model estimates and grey area display 95% confidence interval.

3.3. Vigilance

In the vigilant model, all explanatory variables from the global model were present in top models ($\Delta AICc < 2$; table 7), and therefore included in the logistic regression.

Table 7. *AICc table for candidate models for the vigilant model. Showing top models ($\Delta AICc < 2$), the first model $\Delta AICc > 2$ and the null model.*

Variables	AICc	$\Delta AICc$	AICc weight
Period + Stimuli + Trial day + Period*Stimuli	1591.7	0.00	0.424
Period + Stimuli + Trial day + Wind + Period*Stimuli	1592.9	1.22	0.231
Period + Stimuli + Trial day + Rain + Period*Stimuli	1593.3	1.60	0.190
Period + Rain + Stimuli + Trial day + Wind + Period*Stimuli	1594.5	2.74	0.108
Null model	1908.0	316.31	0.000

Before being exposed to acoustic stimuli, the amount of time moose spent vigilant did not differ among the three acoustic stimuli and the silent control ($p > 0.25$; fig 8). When exposed to acoustic stimuli, moose were significantly more vigilant compared to silent control ($p = 0.0001$). Moose spent the most time vigilant when exposed to dog stimuli ($p = 0.04$). The time spent vigilant when exposed to human stimuli or bird stimuli were equal ($p = 0.2$). After exposure to dog stimuli and human stimuli, moose were significantly more vigilant compared to silent control ($p = 0.01$). After exposure to bird stimuli, moose were not significantly more vigilant than silent control ($p = 0.17$). After exposure to dog stimuli or human stimuli, moose spent equal time vigilant ($p = 0.73$). After exposure to bird stimuli, moose spent less time vigilant compared to dog stimuli ($p = 0.02$) and compared to human stimuli ($p = 0.01$).

The weather variables rain and wind did not have a significant effect on the time spent vigilant ($p = 0.51$; $p = 0.37$). Trial day had a significant effect overall ($p = 0.005$; Appendix 3).

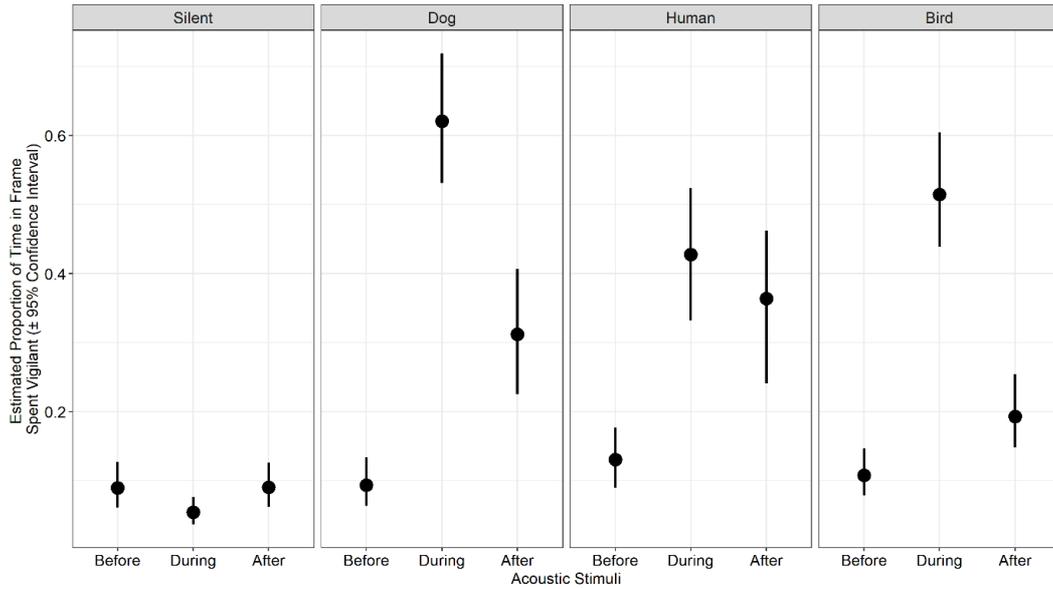


Figure 8. The estimated proportion of time moose spent vigilant before, during and after they were exposed to either a silent control or acoustic stimuli: dog, human or bird.

3.4. Feeding

In the feeding model, all explanatory variables from the global model were included in the top models ($\Delta AICc < 2$; table 8), and therefore included in the logistic regression.

Table 8. AICc table for candidate models for the feeding model. Showing top models ($\Delta AICc < 2$), the first model $\Delta AICc > 2$ and the null model.

Variables	AICc	$\Delta AICc$	AICc weight
Period + Stimuli + Trial day + Rain + Wind + Period*Stimuli	2256.3	0.00	0.497
Period + Stimuli + Trial day + Rain + Period*Stimuli	2257.2	0.91	0.315
Period + Stimuli + Trial day + Wind + Period*Stimuli	2259.5	3.24	0.098
Null model	2639.0	382.74	0.000

Moose spent less time feeding before being exposed to human stimuli compared to silent control ($p = 0.01$). However, they fed equally long before dog stimuli, bird stimuli and silent control ($p > 0.051$; fig 9). When exposed to any acoustic stimuli, moose spent less time feeding compared to when exposed to silent control ($p = 0.0001$). When exposed to dog stimuli or human stimuli, moose spent equal amount of time feeding ($p = 0.2$), but less time than when exposed to bird stimuli ($p = 0.01$). After exposure to acoustic stimuli, moose were feeding less compared to silent control ($p < 0.02$). They spent equal amount of time feeding after exposure to dog

stimuli and human stimuli ($p = 0.4$), and still less than after exposure to bird stimuli ($p = 0.01$).

The weather variable wind did not have significant effect on the time spent feeding ($p = 0.09$), however rain had a significant effect on the time spent feeding ($p = 0.04$), where moose spent less time feeding with increased rain. Trial day had a significant effect overall ($p = 0.0002$; Appendix 4).

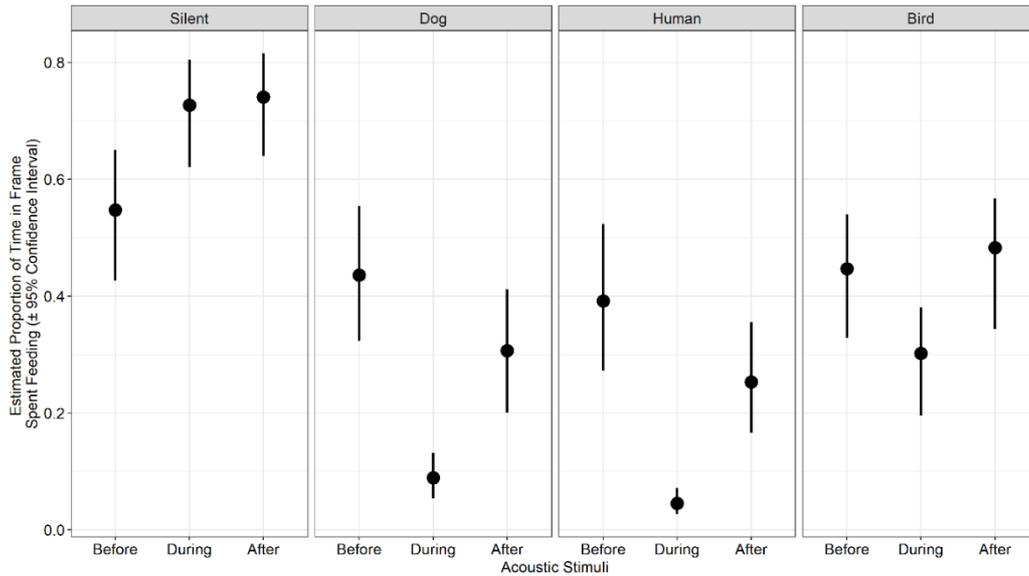


Figure 9. The estimated proportion of time moose spent feeding before, during and after they were exposed to either a silent control or acoustic stimuli: dog, human or bird.

3.5. Time out of frame

In the time out of frame model, all explanatory variables from the global model were included in the top models ($\Delta AICc < 2$; table 9), and therefore included in the logistic regression.

Table 9. AICc table for candidate models for the time out of frame model. Showing top models ($\Delta AICc < 2$), the first model $\Delta AICc > 2$ and the null model.

Variables	AICc	$\Delta AICc$	AICc weight
Period + Stimuli + Trial day + Rain + Wind + Period*Stimuli	2141.3	0.00	0.573
Period + Stimuli + Trial day + Wind + Period*Stimuli	2142.3	0.97	0.354
Period + Stimuli + Trial day + Period*Stimuli	2146.6	5.29	0.041
Null model	2429.7	288.38	0.000

Before being exposed to acoustic stimuli or silent control, moose spent equal amount of time out of frame ($p > 0.3$; fig 10). When moose were exposed to human stimuli, they spent more time out of frame compared to silent control ($p = 0.001$). They spent equal amount of time out of frame when they were exposed to silent control, dog stimuli and bird stimuli ($p > 0.2$). After exposure to human stimuli, moose spent more time out of frame compared to silent control ($p = 0.0001$). After exposure to dog stimuli, moose spent more time out of frame compared to silent control ($p = 0.002$). After exposure to the bird stimuli, moose spent equal amount of time out of frame compared to silent control ($p = 0.10$).

The weather variable rain did not have a significant effect on the time spent out of frame ($p = 0.19$). However, wind had a significant effect on the time spent out of frame ($p = 0.01$), where moose spent less time out of frame with increased wind. Trial day had a significant effect overall ($p = 0.0004$; Appendix 5).

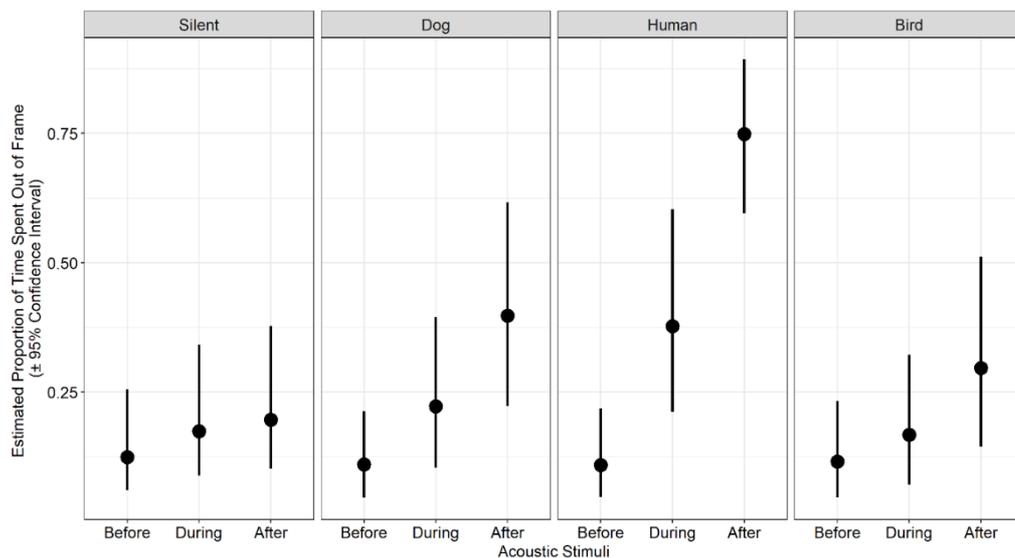


Figure 10. The estimated proportion of time moose spent out of frame before, during and after they were exposed to either a silent control or acoustic stimuli: dog, human or bird.

3.6. Time to return

In the time to return model, all explanatory variables from the global model were included in the top models ($\Delta AICc < 2$; table 10), and therefore included in the logistic regression.

Table 10. AICc table for candidate models for the time to return model. Showing top models ($\Delta AICc < 2$), the first model $\Delta AICc > 2$ and the null model.

Variables	AICc	$\Delta AICc$	AICc weight
Stimuli Before + Trial day	10528.3	0.00	0.164
Stimuli Before + Trial day + Rain + Wind	10528.3	0.03	0.162
Stimuli Before + Rain + Wind	10528.4	0.11	0.156
Stimuli Before + Trial day + Wind	10528.5	0.19	0.150
Stimuli Before + Trial day + Rain	10528.5	0.26	0.145
Stimuli Before + Wind	10528.7	0.46	0.131
Stimuli Before	10539.8	2.48	0.048
Null model	10582.2	53.92	0.000

After exposure to acoustic stimuli, moose took longer time to return compared to silent control ($p < 0.0001$; fig 11). They took longer to return after being exposed to human stimuli compared to dog stimuli ($p = 0.01$) and compared to bird stimuli ($p = 0.01$). The time to return after exposure to dog stimuli or bird stimuli did not differ ($p = 0.97$). Weather variables rain and wind did not have a significant effect on the time to return ($p = 0.19$; $p = 0.09$). Trial day did not have a significant effect on the time to return to a site ($p = 0.08$; Appendix 6).

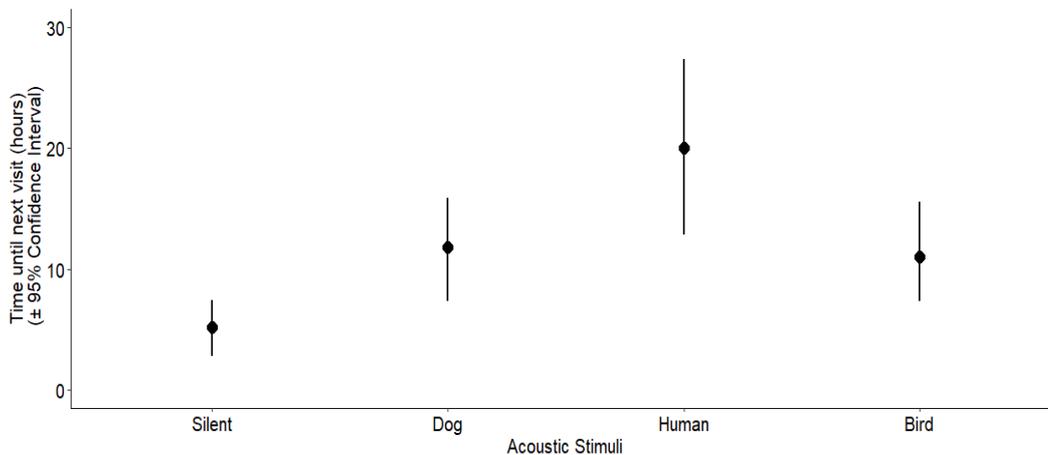


Figure 11. The time back transformed to hours showing the time it took for moose to return to a site after being exposed to either a silent control or acoustic stimuli: dog, human or bird.

4. Discussion

Disturbances such as sound have been shown to elicit antipredator behaviour in ungulates (Babińska-Werka *et al.*, 2015). Therefore, I predicted moose to exhibit higher proportion anti-predator behaviours: leaving the site, vigilant and spending more time out of frame when moose were exposed to human stimuli or dog stimuli, and in the same time a lowered proportion of the natural behaviour feeding. I also predicted that moose would take longer time to return after exposure to dog stimuli or human stimuli. For all my predictions (1-4), I expected that the response to bird stimuli would be equivalent to the silent control.

4.1. Behavioural response to acoustic stimuli

4.1.1. Leaving the site

The results show that moose left the site significantly more when exposed to human stimuli (Prediction 1). For ungulates, the appearance of a human is often associated with threat (Stankowich, 2008). The response to leave the site were stronger to human stimuli than to dog stimuli. The degree of anti-predatory behaviour towards threatening sounds may differ, for example uncommon predators (e.g. humans) tend to elicit stronger responses than common predators (e.g. wolves) (Proffitt *et al.*, 2009; Zbyryt *et al.*, 2018). The sound of a dog could probably be closer to a natural predator, where the human might be a more unreliable source of threat.

4.1.2. Behaviours: Vigilant, Feeding and Time out of frame

The behavioural response of moose who did not leave the site showed that the dog stimuli resulted in the highest increase in vigilance. These results suggest that the dog induce a clear behavioural change, but not so strong that moose use energy for leaving the site, only being more alert. When hunting moose with the use of a dog, the behaviour shown by moose is often to being bayed and be observant towards the dog, which is a method widely used (Svenska Jägareförbundet, 2012). This could explain moose behaviour towards the dog stimuli. Moose might recognise the sound of a dog and increase their vigilance, trying to locate the dog. Again, a

possible explanation to this response is that moose might perceive the dog as a more common “natural” predator (Proffitt *et al.*, 2009).

Contrary to my predictions (1-4), moose displayed significant response to the bird stimuli as well. These results show that being exposed to a sound with non-threatening context can induce anti-predator behaviour as well. When comparing the bird stimuli to dog stimuli and human stimuli, moose were significantly less vigilant in the after period, and were feeding significantly more in the after period. They also spent more time in frame compared to being exposed to human stimuli and dog stimuli. These results suggest that although the bird stimuli elicit a response, moose tend to go back quicker to displaying non-disturbed behaviour, suggesting that there is a shorter lag effect for the bird stimuli. Furthermore, in prey-species the behavioural responses to a threat is dependent on the animal’s recent history and experience, this will determine how they respond to predator cues (Brown *et al.*, 2015). The behavioural response to bird stimuli could therefore be a neophobic response, meaning the fear of something new (Brown *et al.*, 2013), which in this case were a sudden sound of a bird on the ground coming out of nowhere. In Sweden, the sound of the Boreal owl is usually heard between February until end of May. The drumming by a Black Woodpecker is also displayed during early spring. For moose, it is natural to hear these birds in early spring. During the trial period these two bird sounds do not occur naturally, this could be another explanation to why moose reacted to them. Another reason moose might have reacted strong to the bird stimuli is the decibel level. Since the decibel level was set to be the same for all acoustic stimuli, the bird might have appeared loud and unnatural to the moose, causing them to react.

Moose were overall feeding less with increased rain but were also overall spending more time in frame with increased wind. These results suggest that there might be an overall effect on moose behaviour with increased rain and wind.

4.1.3. Time to return

In contrast to prediction 4, any acoustic stimuli resulted in moose taking longer time to return to a site. Giving more evidence to that moose display a behavioural response to both threatful and non-threatful acoustic stimuli. Still, moose took significantly longer to come back after exposure to human stimuli, once again giving evidence to human stimuli resulted in a strong behavioural response, whereas there were no difference between dog stimuli and bird stimuli. Although it is important to point out that in this study, I only evaluated if a moose came back. Since Grimsö wildlife research area did not have marked individuals, I could not say with certainty that it was the same moose coming back. Therefore, for the future it would be of interest to conduct a similar study on marked individuals. In this way, we could detect changes over time for a given individual.

4.1.4. Habituation

A common problem with many frightening devices is the short duration of efficacy due to rapid habituation by the target species (Gilsdorf *et al.*, 2004). The extent to which an animal habituate is influenced by prolonged and frequent exposure to the acoustic stimuli (Bomford & O'Brien, 1990; Winslow *et al.*, 2002; Biedenweg *et al.*, 2011).

My study show a slight impact of trial day for the amount of time spent vigilant, feeding, time out of frame and also on the proportion of moose leaving the site. When using an attractant as saltlick stone, the risk of exposing the same moose more intensively over a short time period is higher, leading to the greater risk of habituation to the different stimuli (Babińska-Werka *et al.*, 2015). Additionally, even while moose are not at the saltlick stone and in the video frame, they could still be near the site when other animals activate the system, meaning that moose probably heard the acoustic stimuli more times than the 422 that was caught on camera. When exposing roe-deer to acoustic stimuli at a railway segment, they showed similar escape frequency over a trial period of 5 years, over which they had only 146 events (Babińska-Werka *et al.*, 2015). It is possible that in 'real-world' situations, the number of events over a short time period is much lower, leading to ungulates habituating slower. Therefore, it would be interesting to conduct a similar experiment, but in a 'real world' situation without any attractants drawing the animals to the sites. This would also be interesting since it may show how moose react when acoustic stimuli are displayed at a site where something might reinforce the stimuli. Such as for example at a railway where an upcoming train could reinforce as a threat. This might in fact lead to sensitivation instead of habituation.

Habituation may also vary in habitats with different levels of human access. For example, ungulates in areas with high human recreation tend do have reduced flight response (Stankowich, 2008). Behaviours are also plastic and can change throughout the year. For example, during hunting seasons (Stankowich & Blumstein, 2005). Thus, the risk of habituation to acoustic stimuli likely vary among habitats with different context and thorough the year. The response of moose in this study is likely to be applicable to moose living in areas with similar hunting pressure and recreational activities. Prolonged studies in landscapes with varying access to humans may help address how these factors influence moose response to acoustic stimuli.

Another aspect is considering how moose hear the stimuli. There are no studies reviewing how moose perceive sound (Mackenzie Gas Project, 2005), but studies have been executed for mammals, giving evidence to many domesticated ungulates and reindeer (*Rangifer tarandus*) have a mean low-frequency limit at 60dB from 70 Hz to 38 Hz (Flydal, *et al.*, 2001). Another study was executed on elk (*Cervus*

elaphus canadensis) calves, showing that at a range of 3 meter and exposed to recorded mine noise at a decibel level of 100, they consistently moved further away (Kuck *et al.*, 1985). Captive desert mule deer (*Odocoileus hemionus crooki*), reacted with increased heart rate when being exposed to simulated jet aircraft noise with a maximum level ranging from 92.5-112.2dB (Weisenberger *et al.*, 1996). Therefore, one could argue that moose should hear the stimuli presented at the decibel levels in this study.

4.2. Management implications

The results indicate that the use of acoustic stimuli is context specific and the acoustic stimuli with threatening context are more sufficient when the aim is to elicit anti-predator behaviour.

Moose is one of the ungulate species that have received attention in recent years since moose are involved in about one third of all ungulate-train collisions in Sweden, and cause high socio-economic costs (Seiler & Olsson, 2017). The annual number of collisions increase, which calls for new solutions. Standard mitigation like fences and passages are costly and therefore only defendable in areas with high collision rates, a more cost-effective solution is desirable (Seiler & Olsson, 2017).

These results indicate that the human voice stimuli would be most effective of the three acoustic stimuli in situations where the aim is to induce a quick response where moose leave. These results could be of further interest to management, aiming to make moose alert and leave an area. This could be applicable if moose is standing at a railway and a train is approaching. Studies show that when moose encounters train, they occasionally flee ahead of the train or alongside the railway (Seiler & Olsson, 2017). With the use of acoustic stimuli, moose might leave the railway before they encounter the train.

The results indicate that the dog stimuli would suitable to use in management where the aim is to induce an avoidance behaviour. This could be applicable when the aim is to prevent moose from accessing an area. For example, if moose are detected approaching a railway opening, dog barking might stop moose before accessing the railway when a train is approaching.

Acoustic stimuli might not be as effective when using them at attractive sites since moose did show signs of habituation. Therefore, it might be questionable if they can be effective for deterring ungulates from sites with highly attractive and vulnerable food plant i.e., plantations, gardens, graveyards or crop fields. If using acoustic stimuli at crop fields, one might need to add something to further induce a threat such as for example a moving object.

4.3. Further questions

Moose did show behavioural response to acoustic stimuli with a threatening context and a non-threatening context. These results raise further questions and suggestions for the future. It would be of interest to explore how moose behave if exposed to sounds that do not carry any information, such as an artificial electronic sound, a bell, siren or similar. This could help clarifying if the reaction is truly to the information in the acoustic stimuli or if it is a neophobic response. Combining the signals in different ways might also be a way to avoid habituation (Biedenweg *et al.*, 2011). It would also be of interest to evaluate how moose would react to different sound levels and explore if the reaction differs for the same stimuli at different decibel levels.

If conducting a similar study, it would be of interest to describe the movement directions after exposed to a stimulus, if the moose leave. The movement direction is important if the aim is to further use deterrent signals at a railway, making sure that moose leave the tracks.

4.4. Conclusion

In this study, I have shown that acoustic stimuli do elicit behavioural changes in moose. Acoustic stimuli could serve as a novel management tool in situations where the aim is to evoke quick behavioural response. They may hence serve as a potential measure to prevent ungulate-vehicle collisions.

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Appendix

Appendix 1. Distance given in meter between the sites with saltlick stones where the experiment where executed

Site	1	2	3	4	5	6	7	8
1		8112	9342	10317	6853	4174	2645	8883
2	8112		1377	2234	2038	5327	6557	2774
3	9342	1377		1024	2743	6200	7583	2265
4	10317	2234	1024		3767	7223	8604	2999
5	6853	2038	2743	3767		3457	4877	2174
6	4174	5327	6200	7223	3457		1637	5073
7	2645	6557	7583	8604	4877	1637		6662
8	8883	2774	2265	2999	2174	5073	6662	

Appendix 2. Model estimate output for the leaving the site model.

Conditional averages					
	Estimate	Std. Error	z value	p value	
Intercept	-1.589465	0.345530	4.592	4.4e-06	***
Dog Stimuli	1.609904	0.272687	5.893	< 2e-16	***
Human Stimuli	3.294562	0.295360	11.134	< 2e-16	***
Bird Stimuli	0.831337	0.297095	2.793	0.00522	**
Trial day	-0.018666	0.008171	0.008186	0.02259	*
Dog Stimuli*Trial day	-0.044600	0.022095	2.015	0.04392	*
Human Stimuli*Trial day	-0.050648	0.022625	2.234	0.02545	*
Bird Stimuli*Trial day	-0.038955	0.024276	1.602	0.10922	
Rain	-0.070059	0.117582	0.595	0.55203	

Appendix 3. Model estimate output for the vigilant model.

Conditional averages					
	Estimate	Std. Error	z value	p value	
Intercept	-2.015504	0.285069	7.066	< 2e-16	***
During	-0.521783	0.354367	1.472	0.14115	
After	0.033390	0.310819	0.107	0.91451	
Dog Stimuli	0.004702	0.351568	0.013	0.98934	
Human Stimuli	0.375151	0.324509	1.155	0.24796	
Bird Stimuli	0.135522	0.345947	0.391	0.69543	
Trial day	-0.014942	0.005367	2.782	0.00540	**
During*Dog	3.334496	0.485896	6.858	< 2e-16	***
After*Dog	1.463501	0.469162	3.117	0.00182	**
During*Human	2.154084	0.466057	4.619	3.9e-06	***
After*Human	1.267251	0.502956	2.518	0.01180	*
During*Bird	2.717355	0.483046	5.622	< 2e-16	***
After*Bird	0.657163	0.477412	1.376	0.16893	
Wind	-0.057892	0.064689	0.894	0.37113	
Rain	0.049037	0.073686	0.665	0.50601	

Appendix 4. Model estimate output for the feeding model.

Conditional averages					
	Estimate	Std. Error	z value	p value	
Intercept	-0.377614	0.243529	1.550	0.12118	
During	0.778893	0.183589	4.240	2.24e-05	***
After	0.852352	0.187280	4.548	5.41e-06	***
Dog Stimuli	-0.395917	0.202417	1.955	0.05062	.
Human Stimuli	-0.528079	0.206938	2.550	0.01076	*
Bird Stimuli	-0.315059	0.207723	1.516	0.12958	
Trial day	0.017623	0.004782	3.683	0.00023	***
During*Dog	-2.883049	0.390832	7.372	< 2e-16	***
After*Dog	-1.436803	0.326288	4.401	1.08e-05	***
During*Human	-3.444814	0.487356	7.064	< 2e-16	***
After*Human	-1.574602	0.423171	3.719	0.00020	***
During*Bird	-1.422985	0.318922	4.459	8.23e-06	***
After*Bird	-0.713130	0.313247	2.275	0.02290	*
Rain	-0.165966	0.079245	2.093	0.03635	*
Wind	0.083696	0.048927	1.710	0.08735	.

Appendix 5. Model estimate output for the time out of frame model.

Conditional averages					
	Estimate	Std. Error	z value	Pr(> z)	
Intercept	-1.210618	0.381090	3.175	0.001497	**
During	0.416287	0.240798	1.728	0.084007	.
After	0.571468	0.241729	2.363	0.018131	*
Dog Stimuli	-0.316922	0.312700	1.013	0.311078	
Human Stimuli	-0.343353	0.316786	1.083	0.278679	
Bird Stimuli	-0.284904	0.318322	0.895	0.371030	
Trial day	-0.017850	0.005048	3.534	0.000409	***
During*Dog	0.465198	0.401004	1.159	0.246265	
After*Dog	1.212936	0.385645	3.144	0.001669	**
During*Human	1.275978	0.391924	3.254	0.001138	**
After*Human	2.823222	0.403139	6.999	< 2e-16	***
During*Bird	0.034696	0.417663	0.083	0.933830	
After*Bird	0.668832	0.401797	1.664	0.096165	.
Rain	0.086075	0.065025	1.323	0.185827	
Wind	-0.147549	0.057357	2.571	0.010135	*

Appendix 6. Model estimate output for the time to return model.

Conditional averages					
	Estimate	Std. Error	z value	p value	
Intercept	5.823414	0.295813	19.668	< 2e-16	***
Previous stimuli_Dog	0.746832	0.178113	4.187	2.83e-05	***
Previous stimuli_Human	1.292789	0.178409	7.235	< 2e-16	***
Previous stimuli_Bird	0.741114	0.181879	4.069	4.73e-05	***
Trial day	0.008822	0.005083	1.733	0.0830	.
Rain	0.108699	0.083452	1.301	0.1934	
Wind	-0.092342	0.054533	1.691	0.0908	.