

# Should I Stay or Should I go

– An experimental study on reactivity and habituation to acoustic stimuli in free-ranging ungulates

*Elina Bertne*



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## Abstract

Negative consequences of anthropogenic sound on wildlife is a well-established phenomenon and have received substantial attention in scientific literature. This evokes questions of what type of sounds perceived as disturbing or aversive to animals. Further knowledge on this matter may contribute to development of acoustic tools to mitigate human-wildlife conflicts by deter animals from conflict areas. However, the use of acoustic stimuli as a deterrent agent, often lack long-term effects due to rapid habituation. The aim of my experiment is to examine how animals respond to novel acoustic stimuli and what factors that affect habituation to acute sound. I subjected free-ranging roe deer (*Capreolus capreolus*) to a sudden novel sound with no ecological relevance and followed individual response over time. Individuals was either subjected to low (40 dB, n=19) or high sound volume (70 dB, n=26). My results conclude that novel sound of high volume did not evoke a stronger response than a sound of lower sound volume, and that sound volume had no effect on habituation. Age, and whether individuals were alone or in a group, were factors that have the largest effect on response to sound. Fawns had lower response to the sound at their first exposure and expressed more pronounced habituation compared to older individuals. Animals in groups responded less strong compared to single animals. However, fawns were to a greater extent accompanied by other animals, compared to adults, which might contribute to their lower response. I found no difference in response to sound between males and females. Variation in response to sound were higher between individuals than within individuals, which indicate a personality aspect in sound reactivity. To determine if response to sound was linked to other traits in the tested population, I used data on response to handling during a capture event. However, no correlation between docility and sound reactivity were found. This indicate that the observed inter-individual variation in these behaviours are dependent on context rather than being part of a general personality trait. The results from my study contribute to a greater understanding on how acute sounds affect wild animals and may be of use to estimate habituation rate to sound.

*Keywords:* sound reactivity, novel sound, habituation, inter-individual variation, personality, roe deer

## Sammanfattning

Ljud förknippade med mänsklig aktivitet kan i många fall innebära störningar för djurlivet, men ljudsignaler kan också användas för att lösa vissa av de konflikter som kan uppstå mellan människa och djur. Det har exempelvis gjorts försök att skrämman bort skadedjur från områden där de är oönskade eller för att varna vilda djur för annalkande trafik och på så sätt minska risken för olyckor. Ett återkommande problem i flera av de studier som gjorts är att ljudets skrämmande eller varnande effekt avtar i takt med att djuren vänjer sig vid ljuden. Det finns därför ett behov av mer kunskap om vilka ljud som upplevs som skrämmande och hur snabbt djur vänjer sig vid dessa. Syftet med min studie var att undersöka hur vilda rådjur upplever plötsliga och nya ljud. Jag har tittat på hur de reagerar första gången de överraskas av ljudet, hur snabbt de vänjer sig, samt vilka faktorer som påverkar reaktion och tillvänjning. Mitt försök genomfördes på märkta vilda rådjur, vilket gjorde det möjligt att följa individer över tid. En rörelseaktiverad högtalare placerades vid platser där djuren matas regelbundet under vintersäsongen. Vid hälften av platserna spelades det upp ett högt ljud (70 dB) och vid resterande hälften ett lägre ljud (40 dB). Mina resultat bygger på 45 märkta individer som observerats när de aktiverade ljudet. Vid första aktiveringen reagerade fjolårskid mindre än vuxna rådjur. Yngre djur vände sig också snabbare vid ljudet jämfört med äldre djur. Djur som hade sällskap av andra individer reagerade mindre på ljudet än de djur som var ensamma. Att kid var mindre påverkade än vuxna kan delvis förklaras med att de oftare observerades i grupp med andra individer. Överraskande nog fann jag ingen skillnad i reaktion eller tillvänjning mellan de djur som upplevde det högre ljudet och de djur som upplevde det lägre ljudet. Ljudnivån verkar alltså inte ha någon mätbar påverkan på hur skrämmande de upplever ett överraskande nytt ljud. Det var stor variation mellan individer i hur de reagerade, vilket indikerar att det finns en personlighetsaspekt i hur rådjur upplever plötsliga ljud. Tidigare studier har funnit en konsekvent variation mellan individer kring hur de reagerar på hantering vid fångst. Alla märkta individer som deltog i mitt experiment har blivit fångade vid minst ett tillfälle, men jag fann inget samband mellan reaktion på plötsliga ljud och beteende vid fångst. Något stöd för generella personlighetsdrag som är konsekventa i flera olika situationer hittades således inte. Min förhoppning är att resultaten från studien kan bidra till ökad kunskap om hur vilda djur reagerar på plötsliga ljud och i vilken utsträckning de kan förväntas vänja sig vid dessa. Ökad kunskap inom detta område är användbar vid utveckling av metoder som använder ljud för att förhindra viltolyckor på vägar och järnväg.

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# 1 Introduction

Human activities, such as traffic, industry and recreation, alter the natural soundscape (Pijanowski et al., 2011). The negative consequences that wildlife suffer from anthropogenic sound have received substantial attention (Barber et al., 2010; Kight & Swaddle, 2011). Anthropogenic sound can affect wildlife by interference with intra-species communication (Bee & Swanson, 2007; Halfwerk et al., 2011), predator detection (Chan et al., 2010) and hunting (Luo et al., 2015). But sound has also been employed as an acoustic tool to solve human-wildlife conflicts, by preventing crop damage (Koehler, 1990; VerCauteren et al., 2005), reduce cetacean bycatch (Carretta, Barlow & Enriquez, 2008), or prevent vehicle collisions (Babińska-Werka et al., 2015; Backs et al., 2017). However, the long-term efficiency of sound alone as a deterrent agent, is often limited due to rapid habituation.

Animal reaction to sound is important to study to gain further insight of how wild populations perceive acoustic stimuli. In my study I subjected free-ranging roe deer (*Capreolus capreolus*) to an acute sound and followed individual responses over time to answer questions on how novel sound is perceived and what factors affect habituation to sound. To my knowledge, no previous study has investigated how wild animals respond to acute sound at individual level.

## 1.1 Habituation, sensitization & conditioning

Habituation may be defined as a “behavioural response decrement that results from repeated stimulation and that does not involve sensory adaptation/sensory fatigue or motor fatigue” (Rankin et al., 2009). Habituation is a form of non-associative learning i.e. response to an unconditioned stimuli, decreasing gradually as the stimuli is regarded as uninformative (Koch, 1999). Natural sounds associated with a threat, such as predation or intra-species aggression is suggested to be more persistent to habituation compared to artificial sounds. There is support for this in birds (Spanier, 1980) but less so in terrestrial mammals. A study on kangaroos reaction to various sounds found that the animals had a stronger flight response when subjected to artificial sound without biological relevance, namely a whip crack compared to sound of foot stomping, a kangaroo warning signal, but neither of the sounds caused habituation (Biedenweg et al., 2011).

Sensitization, where the response to the stimuli increased over trials (Groves et al., 1969), is sometimes described as the counterpart of habituation (Blumstein, 2016). However, the processes of habituation and sensitization are independent of one another and are governed by different neural mechanisms that shape the response (Davis et al., 1982).

In order to use sound as a warning signal to deter animals, sensitization to the stimuli would be the preferred response over time. Sensitization may occur if the intensity of stimuli is above certain threshold (Groves et al., 1969; Prescott, 1998). An alternative solution is to use fear or aversive conditioning; an associative process of learning, aimed to increase reaction to stimuli. In this process, a stimuli is conditioned with an aversive or fear inducing stimuli to result in an conditioned response (Maren, 2001; Blumstein, 2016). Aversive conditioning has been put to use in management practice. One example is to condition captive breed animals to be fearful of predators in order to increase probability of survival in the wild (McLean et al., 1999). Another example is how aversive conditioning by vibrations and noise from passing trains act to increase the intrinsic effect of warning sound aimed to deter wildlife from tracks (Babińska-Werka et al., 2015). Studies of the neural systems behind habituation and sensitization often employs loud sound to trigger a motor reflex, i.e. an acoustic startle response (ASR) (Pilz & Schnitzler, 1996; Koch, 1999). ASR has been used as a diagnostic tool for post-traumatic stress disorder, since inter-individual variation of ASR can be used to predict retention of memories associated with fear (Russo & Parsons, 2017). Evidence for a genetic base underlying sensitivity to sound have been found in rats, where different strains exhibited differences in habituation assessed by decreasing ASR (Glowa & Hansen, 1994).

## 1.2 Inter-individual variation

In the majority of studies on wild animals, their reaction to sound is studied at group or population level. However, inter-individual variation have relevance on ecology (Dall et al., 2012) as well as management issues (Merrick & Koprowski, 2017; Honda et al., 2018). Individual differences have been found to affect reaction to sound (in cattle: Lanier et al., 2000, and in dogs: Arvelius et al., 2014) and influence habituation of ASR in rats (Russo & Parsons, 2017) and humans (LaRowe et al., 2006). Inter-individual differences in behaviour that is consistent across time and context is often referred to as personality (Réale et al., 2007). Animal personality has gained increasing attention in wildlife management for the last decade and have proven to be an important factor to consider. (Sih et al., 2011; Lowry et al., 2013; Hertel et al., 2019). Personality is commonly assessed by the response to novelty; novel object (Andersson et al., 2014), novel area (Perals et al., 2017), novel food items (Bergvall et al., 2011). The outcome can be interpreted in terms of shyness-boldness or exploration-avoidance depending on the experimental setup i.e. if the stimuli are presented in a familiar environment, and if stimuli is perceived as threatening (Roche et al., 2016). According to Réale et al. (2007), the major distinction between shyness-boldness and exploration-avoidance



is that the first one describes response to a known stimuli, and the latter describes response to a novel stimuli.

Personality in roe deer has previously been assessed by inter individual variation in response to handling during a capture event (Debeffe et al., 2015, Bonnot et al., 2015; Bonnot et al., 2018). Bold individuals struggle more during handling and fled from capture site faster and shy individuals are more docile and calm during handling (Bonnot et al., 2018) Boldness assessed by handling can predict spatial and temporal use of habitat in roe deer, and willingness to use high risk habitat (Bonnot et al., 2015).

Response to novel sound has not received much attention in personality research on wild animals. An exception is a study by Found & St. Clair, (2016) that concluded that shy elks of species *Cervus canadensis*, were more responsive to novel sound and more likely to migrate than bold elks.

### 1.3 My experiment

In my experiment, I use acute sound of two levels of volume to study the initial reaction and habituation rate to a novel sound at individual level in a population of free-ranging roe deer.

The aim of this study is to investigate the response of roe deer to acute novel sound. More specifically, I aimed to answer the following questions:

- 1) Are free ranging roe deer sensitive to a sudden novel sound with no ecological relevance in a feeding situation?
- 2) Do volume affect response and habituation to novel sound?
- 3) Is the response to novel sound related to a) sex, b) age classes, c) company from other individuals, or d) individual behaviour during capture events?
- 4) Is variation in response to novel sound higher between individuals than within the same individual?

## 2 Method

The fieldwork was carried out at Grimsö Wildlife Research Station located in central Sweden (59° 40 N, 15° 25 E). The research area is 130 km<sup>2</sup> and mainly consists of boreal forest with patches of farmland and bogs. The area is inhabited by natural predators to adult roe deer (*Aquila chrysaetos*, *Lynx lynx* and *Canis lupus*). The roe deer population at Grimsö has been monitored since 1973 in research purpose (Davis et al., 2016). Neonate fawns are captured and marked in spring, and recaptures of older fawns and adults occurs during winter. Capture during winter is done using box-traps (see Bergvall et al., 2017 for additional info on capture procedure) at evenly distributed sites across the research area where deer are fed throughout winter to maintain the motivation to visit trap sites regularly for capture purpose. Some trap sites are frequently visited by wild boar (*Sus scrofa*), European hare (*Lepus europaeus*) and various birds (e.g., *Garrulus glandarius*, *Turdus merula*, *Corvus monedula*), but no interaction between the species or simultaneous feeding was observed.

The experiment was conducted in March 2018, the ground was covered in snow for the whole duration of the experiment and natural food availability was scarce, thus roe deer had high motivation to forage at the traps. Each trap site had one open and video-monitored trap. Video surveillance was done with motion triggered cameras (Scout Guard SG-550M 14SHD and Digital Scouting Camera SG562-12mHD) placed at 5 - 7 meters distance from the traps.

A motion triggered loudspeaker (“Uppfartslarm”, article number 44499 from Biltema) was used to emit the sound, a signal comparable to a door bell with the duration of 3 seconds. The device could be set at either a low volume (40 decibel) or a high volume (70 decibel). Four traps received high volume treatment and the remaining half received low volume treatment. The loudspeaker was placed on top of the trap and the motion detector was placed in the back of the trap angled detect movement within 0,2 – 0,6 meter from the entrance of the trap (Fig. 1).

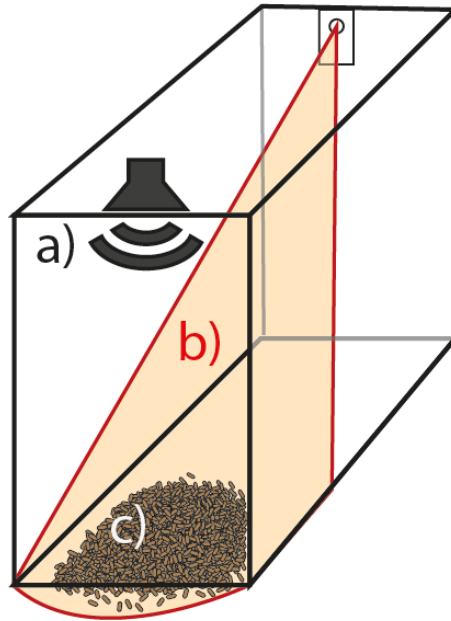


Fig. 1. A box trap with placement of a) loudspeaker, b), range of motion detector, and c) trap entrance with pellets.

## 2.1 Animals

During capture, blood samples, weight and measurements were collected, the behaviour during this procedure was rated on a score from 0 to 4 that reflects the stress response to handling (Table 1). Captured animals were provided with collars of either VHF or GPS type and ear clips. A unique combination of ear markings and color combination on collars enabled individual identification on video. In my study, I selected 8 trap sites in the area, with each site being visited by a unique subpopulation of roe deer. Movement between sites occur but are rare. During my experiment, no individual was observed at more than one site.

Table 1: *Score of behavior during handling at capture (after Bergvall et al. 2017).*

Score	Behaviour
0	Calm. No resistance. No screaming or kicking with legs.
1	Calm. No more than two screams. Very little kicking.
2	Stressed. Are screaming and some kicking but calm between these occasions.
3	Stressed. Are kicking and screaming but can still be handled.
4	Extremely stressed. Almost impossible to handle, no measurements can be taken.

## 2.2 Data collection

Each trap site yielded between 3-25 minutes of video per day. Data extracted from these videos included ID, sex, age, treatment, group size, reaction score and activation number. Each data point consists of a single activation of the sound for each present animal and the following response to the sound was scored (Table 2) only if the focal individual did trigger the sound by itself or was standing in direct proximity to the entrance of the trap while another individual triggered the sound. Present individuals that were farther away from the trap were included in the data set, but due to difficulties to determine reactions of animals at a distance, especially during night, no reaction to the sound was scored. Instead, each activation these individual experienced was included only as an activation number with no reaction score. Group size was defined as number of animals present in the recording while the sound is triggered, including the focal individual. Age of individuals was for most analyses divided in two age classes; adults (>1 year) and fawns (<1 year). The data was split into two sets, the first consists of only the first scored activation for each individual and was used to analyse the initial reaction to sound. Habituation was analysed by a larger data which included all scored reactions for all individuals.

Table 2: *Definitions of behavioural score for reaction to the sound.*

Reaction score	Observed behaviour
0	Individual are not displaying any visible signs of distress or discomfort.
1	Individual making a shorter pause in current activity (i.e. eating) but resume within 10 seconds OR the animal do not pause but exhibits signs of distress (i.e. twitches, flickering ears or tense posture).
2	Individual cancel current activity (i.e. feeding or exploring) and do not resume within 10 sec or until film has ended).
3	Individual departs in a quick pace, either out of frame or a substantial distance from trap (>7meters), does not return to feeding during video.
4	Individual flees as rapidly as possible when the sound is triggered, always out of frame, does not return to feeding during video.

## 2.3 Statistical analysis

All statistical analyses were carried out in R (Version 1.1.463 – © 2009 - 2018 RStudio, Inc.), models were created with Lme4 package in R (Bates et al., 2015). I defined habituation as the decrease in response over the first 75 activations, this is illustrated by a trend line, fitted by a local polynomial regression on the reaction score over activation number (Fig. 3). I restricted my analysis to include only the mean and initial handling score for each individual due to a very large variation in number of handlings (M=2.46, SD=2.08) and time between handlings. For this

reason, statistical means to include effect of habituation in the analysis, were limited.

A Generalized linear mixed model fitted by maximum likelihood with reaction as response variable (Table 4) was used to estimate which factors affect habituation to novel sound. Activation number (square root transformed to achieve normality), sex, age class, sound level and group size was included as fixed effects with animal ID as random factor.

Intra-individual variation in reaction score was calculated by intraclass correlation (ICC), a method commonly used for this purpose (Bell et al., 2009). ICC estimates and 95% confident intervals was calculated using the r-package *irr* based on a mean-rating (k=3), absolute-agreement, 2-way mixed-effects model (test selection derived from Koo & Li, 2016). In order to meet the requirements of ICC only individuals with 5 or more activations were included in the analysis (n= 27).

## 3 Results

### 3.1 Demographics

The mean number of individuals per site was 5.62 (SD=2.33). For sex, age and treatment (high/low sound volume) distribution, see table 2. All but 5 individuals activated the sound more than once. Mean activations per individual was 26.67 (SD=33.68). Mean number of captures was 2.46 (SD=2.08). Mean age was 2.91 (SD=2.07) years.

Table 3. *Individuals sorted by sex, age class (adult/fawn) and treatment (high/low sound).*

	Female			Male			Grand Total
	Adult	Fawn	Total female	Adult	Fawn	Total male	
High	10	3	13	8	5	13	26
Low	7	3	10	5	4	9	19
Total	17	6	23	13	9	22	45

### 3.2 Response to novel sound

32 of 45 individuals (71%) demonstrated a strong reaction and fled the first time they encountered the sound (reaction score 3 and 4) while 13 individuals (29%) did not flee (reaction score 0-2). 36 of 45 individuals (80%) triggered the sound themselves at their first scored reaction i.e. were naïve to the sound. The remaining 9 individuals (20%) had been observed at the trap site while the sound was triggered by another individual prior to the first time they triggered the sound themselves i.e. had previous experience. Individuals with previous experience of the sound had heard the sound a mean number of 2.33 times (SD=1.87) before their first scored reaction. 75% of the naïve individuals fled the first time they activated the sound compared to 56% of the experienced individuals (Fig. 2). Response decreased rapidly over the first 15 activations, thereafter, the line flattened out (Fig. 3). Number of individuals decreased for each activation number (see upper margin histogram in Fig. 3).

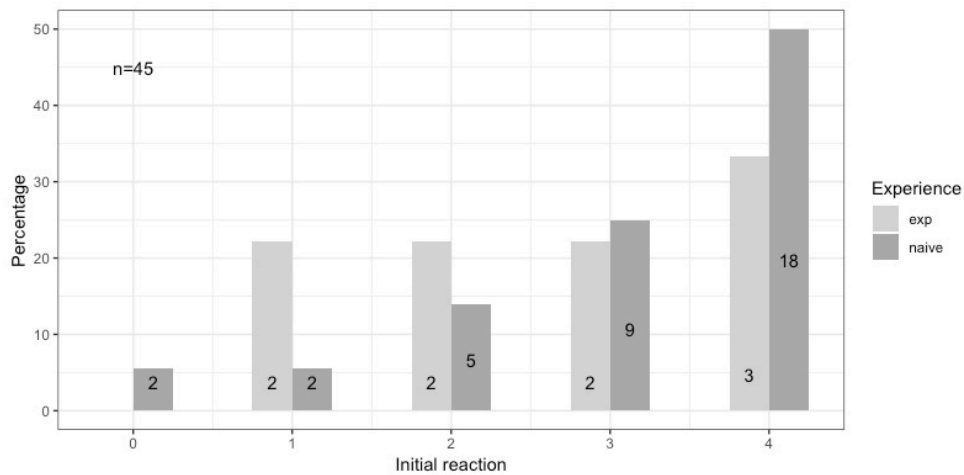


Fig. 2. Percentage for each reaction score of all individuals initial reaction, sorted by individuals with experience of the sound prior to the initial activation (light grey) and naïve individuals (dark grey). Count of individuals in each bar, total  $n = 45$ . Data based on marked roe deer observed in South-central Sweden in March 2018.

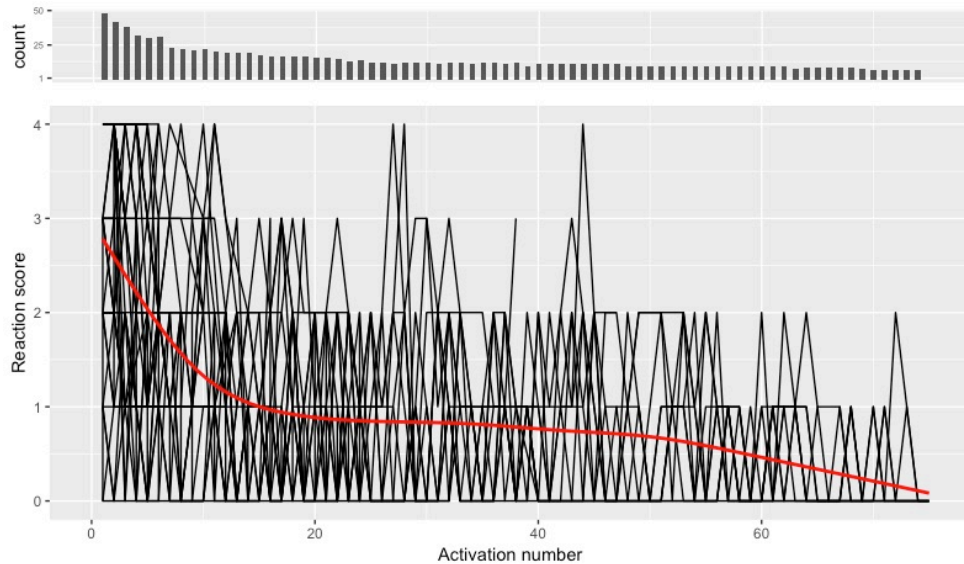


Fig. 3. Reaction score of activation number for all individuals ( $n = 45$ ), with local polynomial regression curve fitted (red line). Graph in upper margin is a histogram of sample size given as individuals per each activation. Data based on marked roe deer observed in South-central Sweden in March 2018.

### 3.3 Effect of sound volume

Individuals subjected to low sound volume reacted similar to those who were subjected to high sound volume (Fig. 4). There was no significant difference in initial reaction between individuals subjected to high and low volume (Wilcoxon test,  $p = 0.42$ ). The pattern was the same when comparing reactions for high and low

sound volume over all scored reactions, (Wilcoxon test,  $p = 0.43$ ). Amount of activations were the same for individuals experiencing high respectively low sound volume ( $t\text{-test}_{41; 208}$ ,  $p = 0.92$ ).

Local polynomial regression curves for low sound volume and high sound volume was very similar (Fig. 5), and a Two factor ANOVA revealed no effect of sound volume on reaction over time ( $F_{84; 952} = 0.68$ ,  $p = 0.99$ ).

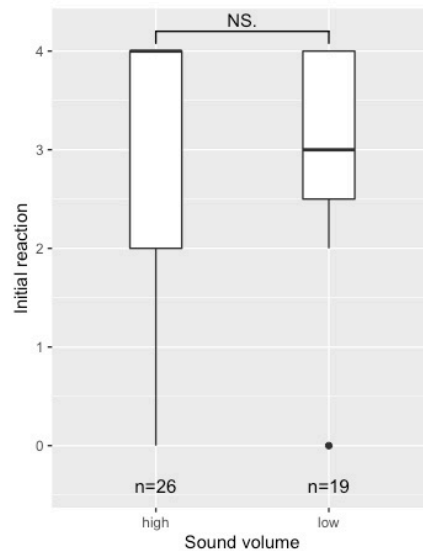


Fig. 4. Initial reaction to high (70 dB) and low sound volume (40 dB). Descriptive statistics are median (thick line), interquartile range (box) and 95% confidence interval (whiskers). Data based on marked roe deer observed in South-central Sweden in March 2018.

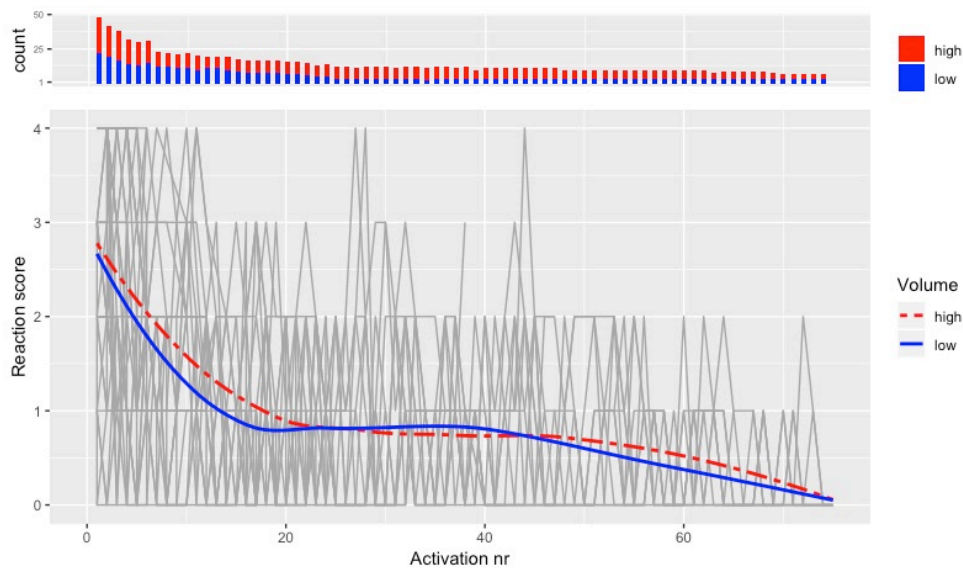


Fig. 5. Reaction score over activation number for all individuals ( $n = 45$ ), with local polynomial regression curves fitted for high (70 dB) and low sound volume (40 dB). Graph in upper margin is the sample size given as a stacked histogram of individuals per each activation. Data based on marked roe deer observed in South-central Sweden in March 2018.



### 3.4 Effect of sex and age

No differences in reaction between males and females were found neither in the first activation (Wilcoxon rank sum test,  $p = 0.74$ ), nor in all activations thereafter (Wilcoxon rank sum test,  $p = 0.99$ ).

The initial reaction was significantly different for fawns and adults (Wilcoxon rank sum test,  $p = 0.01$ ). Fawns had a lower initial reaction compared to adults (Fig. 6). No significant difference in initial reaction was found between adult roe deer between age 2 to 8 years (Kruskal-Wallis,  $df = 7$ ,  $p = 0.32$ , Fig. 6).

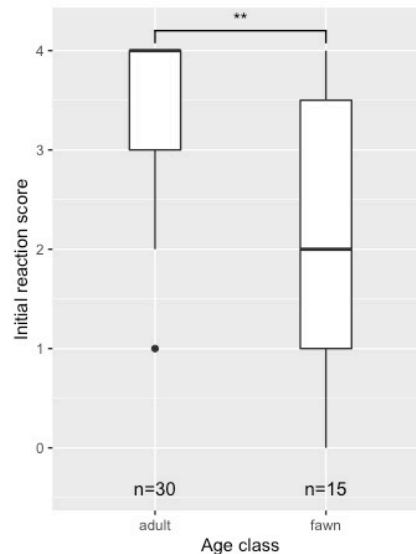


Fig. 6. Initial reaction to novel sounds by age class. Data based on marked roe deer observed in South-central Sweden in March 2018.

### 3.5 Effect of group size

Being alone or accompanied by other individuals had no significant impact on the initial reaction to the sound (Kruskal-Wallis rank sum test<sub>df=3</sub>,  $p = 0.99$ ). On the first encounter with the sound, fawns and adult are accompanied by other individuals to the same extent (t-test<sub>df=21; 489</sub>,  $p = 0.48$ ). However, when taking all activations in to account, fawns and adults differ significantly in how often they are observed together with other animals, fawns are more often in a group together with at least one other animal (t-test<sub>df=951; 22</sub>,  $p < 0.001$ , Fig. 7).

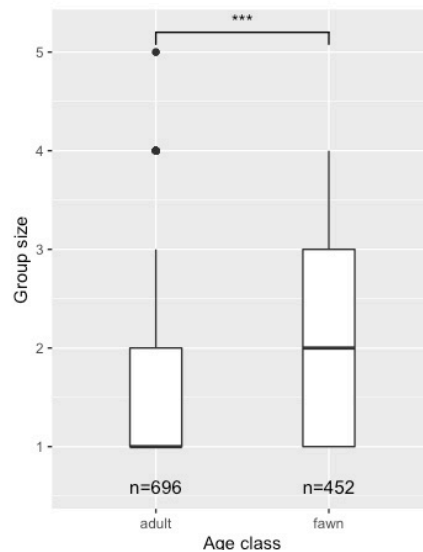


Fig. 7. The number of individuals present during each activation including the triggering individual, for adults and fawns respectively. Data based on marked roe deer observed in South-central Sweden in March 2018.

### 3.6 Factors affecting habituation

In the generalized linear mixed model used to analyse what factors that impacts the reaction to sound over repeated activations, activation number had the strongest effect (Table 4). Neither sex, nor sound volume had any significant effect on reaction while both age class and company had significant effects. Fawns exhibit lower reaction scores than adults and with increasing number of individuals present, reaction score decreases (Table 4).

Table 4: Summary of generalized linear mixed model fitted by maximum likelihood of the reaction to sound over a number of repeated activations with activation number (Activation nr), gender (Sex), age class, sound level (Sound volume) and present individuals (Company) as fixed effects and with animal ID as a random factor. Estimate is the coefficient output per variable, SD the standard deviation of that estimate.

	Estimate	SE	Error z	value Pr(> z )
Intercept	1.57	0.13	11.93	< 0.001 ***
Activation nr	-0.21	0.01	-16.61	< 0.001 ***
Sex	0.16	0.12	1.33	0.18
Age class	-0.47	0.13	-3.64	<0.001 ***
Sound volume	0.01	0.12	0.082	0.93
Company	-0.14	0.04	-3.42	<0.01 ***

### 3.7 Handling score

The initial reaction to sound and the mean handling score at capture showed a low and non-significant relationship (Spearman's rank correlation  $R_S = 0.17$ ,  $p = 0.2$ ,

Fig. 8). The relationship between initial reaction to sound and initial handling at capture was even weaker (Spearman's rank correlation  $R_S = 0.13$ ,  $p = 0.40$ ).

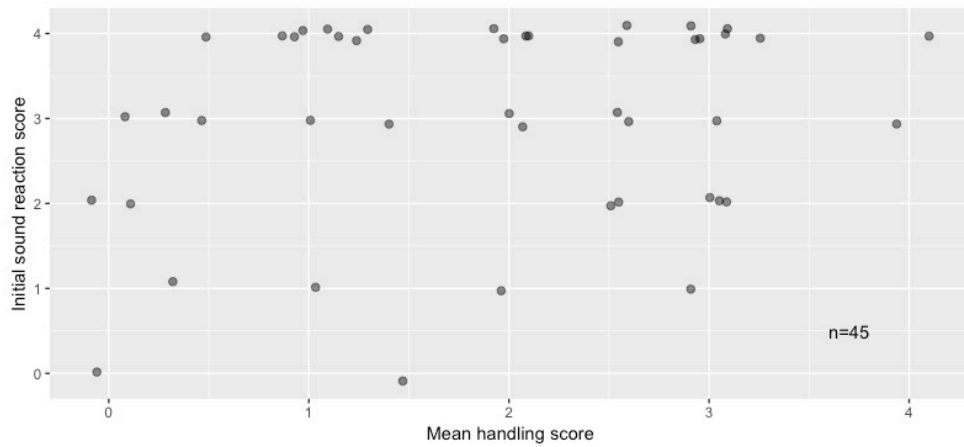


Fig. 8. Relationship between initial reaction to sound and mean handling score. Each dot represent one individual ( $n = 45$ ). Data based on marked roe deer observed in South-central Sweden in March 2018.

### 3.8 Intra-individual variation

The intra-individual variation in reaction score was calculated by the intra-class correlation estimate (ICC). The average ICC for reaction to sound was 0.62 with 95 % confidence interval from 0.27 to 0.92 ( $F_{(5,47,6)} = 6.11$ ,  $p < 0.001$ ) implying that reaction scores are more similar within than among individuals.

## 4 Discussion

Despite the lack of biological relevance of the sound used in my study, most roe deer were sensitive to the sudden novel sound. However, large variation in reaction was observed. Notably, volume had no impact on the initial response when the individuals were naïve to the sound and habituation rate was comparable between the two sound volumes. No differences between sexes were observed, instead age had a large effect on reaction, fawns had a significantly lower reaction compared to adult individuals. Company from other individuals did not affect reaction to the sound on the first encounter, but for all following reactions individuals had a significantly lower reaction to the sound when they visited the trap accompanied by other individuals. The response to novel sound and handling during a capture event was uncorrelated. Variation in response to sound over repeated exposures, was found to be higher between individuals than within individuals.

### 4.1 Reaction to novel sound

Intuitively, one would expect a prey species to flee when surprised by a sudden noise, and most individuals in my study did indeed do so. Surprisingly enough, near 1/3 of the individuals did not flee, some individuals even appeared to be totally unaffected by the stimuli (Fig. 2). Group size was based on the number of present individuals that were observed in the video, but due to the limited camera range, number of present individuals are likely to be underestimated. Only 9 out of 45 individuals were known to have experienced the sound prior to their first scored reaction. 5 of these 9 individuals still fled the first time they activated the sound themselves, why I conclude that experience does not explain the variation in reaction to the novel sound.

### 4.2 Effect of age and company

The lowered response to a loud sound in a feeding situation likely reflects a trade-off between maximizing feeding opportunity and anti-predator vigilance (Dammhahn & Almeling, 2012). According to the model (Table 4) group size did have a significant effect on reaction. Group size have previously been found to

have effect on foraging and vigilance for roe deer (Fattorini & Ferretti, 2019), likewise birds have been found to be less neophobic when in a flock (Coleman & Mellgren, 1994).

When comparing individuals of different age, the one group that stands out by having lower reaction scores are fawns. This may partly be explained by group size since fawns were overall more often observed together with other individuals. For the initial reaction, fawns and adults were accompanied by other individuals to the same extent, but fawns still had a lower reaction to the sound compared to adults. A possible explanation to why fawns appear to be more tolerant to the sound could be that fawns have more to gain by trading vigilance for foraging as they are more vulnerable to emaciation (Aguirre et al., 1999). A similar pattern, where younger individuals responded less compared to older individuals, was found in an experiment on captive elk (*Cervus canadensis*). Here, calves responded with more pronounced habituation to human presence in a feeding situation, compared to adult elk (Found, 2019).

### 4.3 Male and female responses

Sex had no effect on reaction to novel sound. No difference between males and females in reaction to the sound. This suggests that roe deer males and females are equally tolerant to acoustic stimuli, which is corroborated by Padié et al., (2015). However, gender differences has been observed in other ungulate species; male moose were found to be more sensitive to traffic noise (Laurian et al., 2012), in domestic sheep rams are less fearful than ewes in a surprise test involving a novel object, but also in other contexts (Vandenheede & Bouissou., 1993).

### 4.4 Effect of sound volume

Sound volume had no impact on the response, reactions to high and low sound was comparable for both first exposure to the sound and on the rate of habituation. Hearing range of ungulates is different from that of men (Flydal et al., 2001), however disturbing a particular sound may be to a human ear, it may not be perceived the same way for another specie (Heffner, 1998). Similar to the results in my study, Brown et al., (2012) found very low effect of noise level on the behaviour of wild ungulates experiencing anthropogenic disturbance. On the contrary, a study of domestic pigs showed an increased heart rate when exposed to loud sounds compared to a sound of lower volume (Talling et al., 1998). However, the sound in this study were at 85 and 97 dB respectively, which is distinctively louder than the volumes used in my experiment.

### 4.5 Habituation

The response to the sound decreased with increasing experience of the stimuli (Table 4). However, no individual remained stable on the lowest reaction score

despite extensive experience of the sound. Instead, individuals fluctuate between score 0 and 2 (see Fig. 3), which suggest that even the individuals who visited the trap most frequently remained responsive to the sound. This result may be an effect of ungulate foraging patterns; vigilance is costly in terms of reduced feeding efficiency, but ungulates can decrease this cost by matching handling of food (i.e. chewing) with scanning for predators (Illius & FitzGibbon, 1994). Studies of ungulate foraging patterns commonly distinguish between routine vigilance (i.e. vigilance while chewing) and induced vigilance (i.e. responding to a stimuli without chewing) where the former is considered to be cost-free (Fortin et al., 2004; Blanchard & Fritz, 2007; Bergvall et al., 2016). This almost cost-free vigilance might explain the observed pattern in my data, where the individuals interrupt feeding and remain seemingly vigilant. The scope of my experiment was not to study foraging patterns, why my data collection did not include the necessary parameters to analyse this further. Inclusion of routine vigilance versus induced vigilance would be recommended for further studies on the subject.

Peaks in reaction score after multiple reactions with lower score (Fig. 3 and 5) are most likely explained by spontaneous recovery from habituation. Long time intervals between activations give individuals opportunity to recover and thus will exhibit higher reaction after recovery (Thompson, 2009). Time elapsed between activations was not included in my analysis, therefore this effect was not further investigated. For future research this is clearly a matter for consideration.

The term “habituation” have been used to describe a decrease of reaction in a wide variety of contexts (Rankin et al., 2009). However, other mechanisms can yield similar observations in behaviour (Blumstein, 2016). Bejder et al., (2009) argues that the term habituation often is misused in wildlife management. The decision on how to react to disturbing stimuli may be affected by the current state of the animal, since fatigue and/or starvation may force the animal to tolerate disturbance. Thus, it is in most cases more appropriate to talk about increased tolerance than habituation (Bejder et al., 2009). Since foraging opportunities was motivating roe deer to visit the trap sites and tolerate the disturbance, I cannot exclude hunger to be the driving factor behind the decreased response observed in my study.

## 4.6 Inter-individual variation

Inter-individual variation in response to the sound were higher than the variation within individuals which indicates that tolerance to sound is linked to personality in roe deer. Since the individuals in my study were free to avoid the sound, there is a risk for bias, where shy individuals with low exploratory behaviour may be partly missing from my data. Studies of animal response to novel stimuli is often carried out on domestic or wild animals in captivity, with experimental designs that do not allow avoidance of the stimuli (Cavigelli & McClintock, 2003; Martin & Réale, 2008; Andersson et al., 2014). In an experimental setup where seals had the option of escaping into another pool when subjected to a high pressure sound, showed that most of the subject choose to do so and thereby neglecting feeding opportunities (Götz & Janik, 2011). In my experiment there were indeed some

individuals who appeared on the video but never activated the trap ( $n=3$ ) and was therefore excluded from the data. This indicates that the inter-individual variation in reaction to sound may be even larger than my estimation.

According to my results, there is no correlation between reaction to novel sound and response to handling. In roe deer, docility has previously been linked to response to novelty, Monestier et al. (2017) found docile animals to be more neophobic. Similar to my results, missing correlation between docility and other behavioural traits, have been observed in other species; marmots (Petelle et al., 2013), chipmunks (Martin & Réale, 2008) and bighorn sheep (Réale et al., 2000). In my experiment, animals were exposed to the stimuli in a feeding situation, and foraging decisions have previously been linked to personality in deer. Bergvall et al. (2011) found bold fallow deer (*Dama dama*) to be more prone to decrease vigilance in a feeding situation involving a novel object. Due to the missing link any between docility and reaction to novel sound in my study, I refrain from describing the observed inter-individual variation in terms of shyness, boldness or curiosity. Labels, like the aforementioned, is commonly used in studies where personality is assessed in multiple situations (Roche et al., 2016). The concept of personality often assumes generalization of traits across context, but lack of correlation between context suggests traits to be adapted for specific contexts (Wilson, 1998). This raises the question: is response to sound in this species independent from other traits that reflect response to novelty?

## 4.7 Practical implications

One area where my results may have impact is in development of acoustic warning systems to prevent wildlife collisions on roads and railroads. If loudness has no impact on the aversiveness of an acoustic stimulus, which my results indicate, deterrent devices that use sound may not need to be particularly loud. Instead, the effectiveness of sound as a deterrent agent might rely on other factors.

According to my results, not all individuals responded to the novel sound by fleeing, especially fawns were tolerant to the sound even at first exposure. This implies that a wildlife warning system that uses artificial sound may be ineffective on parts of the population. How wild animals perceive other properties of sound remains to be investigated, such as intermittent versus constant sound (Talling et al., 1998); uniform versus non-uniform sound (Johns et al., 2015); artificial versus natural sound (Biedenweg et al., 2011).

Another problem to solve is how to avoid animals from habituating to the sound. The individuals in my study habituated readily to the artificial sound, but natural warning calls and sounds from predators have been found to be efficient as a deterrent stimuli over a longer time scale (Babińska-Werka et al., 2015). However, there is a need for further research on wild animals respond to sound over repeated exposures, what properties of sounds to use and how to prevent habituation in order to successfully use sound to deter animals from areas of conflict.





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