Non-naivety in a long-lived ungulate

– learning effects of shooting moose calves?

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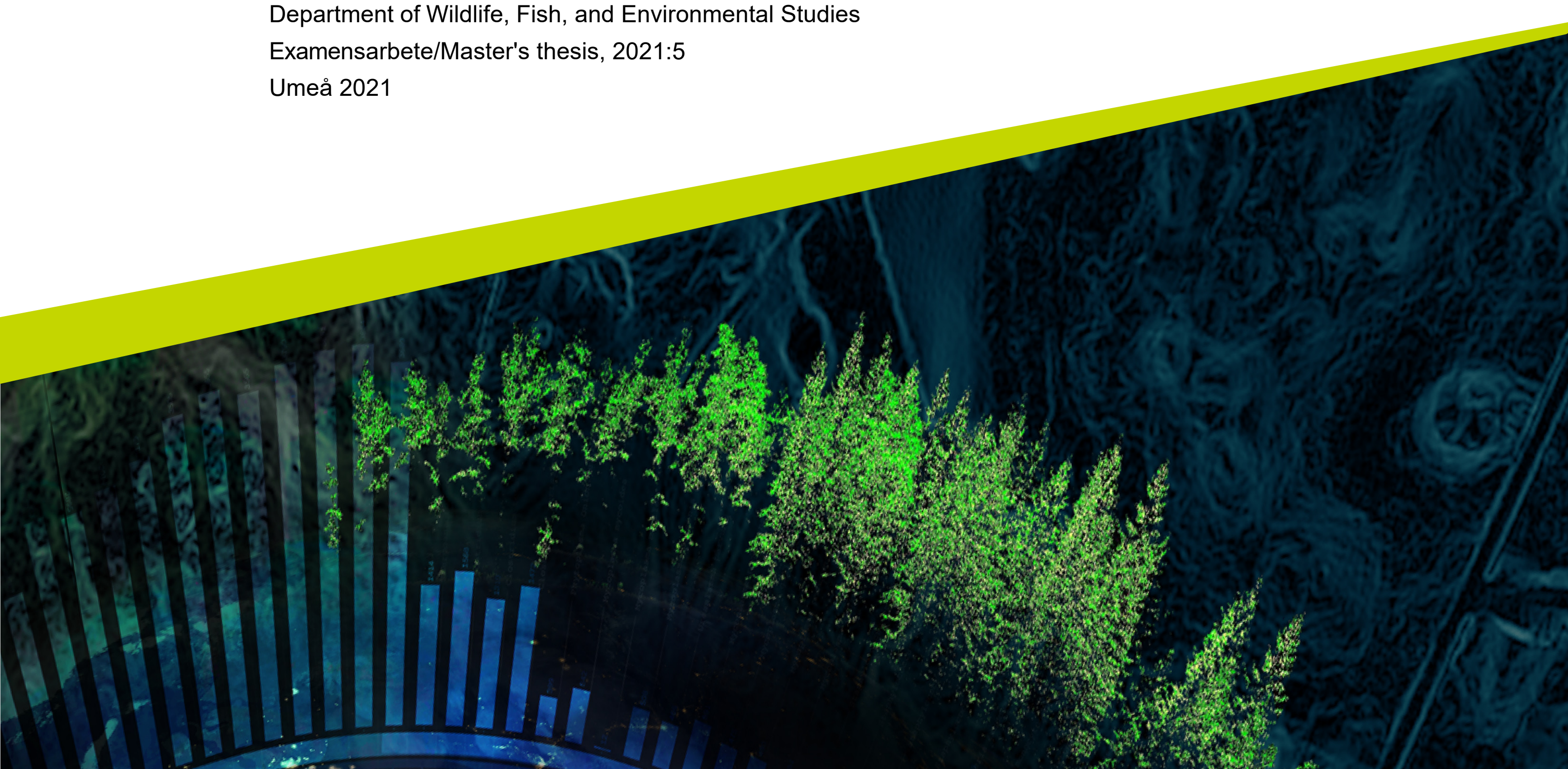
Master’s thesis • 30 credits
Swedish University of Agricultural Sciences, SLU
Department of Wildlife, Fish, and Environmental Studies
Examensarbete/Master's thesis, 2021:5
Umeå 2021



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Credits:	30 credits
Level:	Second cycle, A2E
Course title:	Master’s thesis in Biology, A2E - Wildlife, Fish, and Environmental Studies
Course code:	EX0971
Course coordinating dept:	Department of Wildlife, Fish, and Environmental Studies

Place of publication:	Umeå
Year of publication:	2021
Title of series:	Examensarbete/Master's thesis
Part number:	2021:5

Keywords:	Moose, *Alces alces*, integrated step selection function, habitat selection, anti-predator behavior

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Preface:

For my mother, whom I dearly miss and my father, who made all of this possible for me.

Abstract:

Habitat selection and movement are considered important factors for survival of game species when they are hunted by humans. To reduce their risk of predation, animals can adapt their behavior to their most abundant predator over time through experience. To test for learning capabilities in a long-lived ungulate, I used GPS-data of 19 male and 84 female moose (*Alces alces*) in two study areas in southern Sweden from 2008-2018. I matched the GPS-data with reproduction and survival data and analyzed movement rates and habitat selection in a heavily managed moose population. While not being a gregarious species, moose are expected to learn from non-lethal mortality when a female loses her calf to harvest. Hunters were more likely to harvest male moose that moved faster before the moose hunting season began. Female moose where more likely to get harvested when they selected more for open habitats. The results of my study suggest that female moose in my study areas increased their shyness in the next hunting season after losing a calf to harvest. Female moose increased nocturnal activity and increased their avoidance of open habitats. As they aged, female moose decreased their movement rates and avoided open habitats. Using these proxies for shyness indicates that being shyer is beneficial for moose to survive the hunting season. My study suggests that learning effects accumulate as moose age. Furthermore, my results help to understand the influence human hunters impose on behavior of moose in a heavily managed population.

*Keywords:*Moose, *Alces alces*, integrated step selection function, habitat selection, anti-predator behavior

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AIC	*Akaike Information Criterium*
GAMM	*generalized additive mixed models*
GLMM	*generalized linear mixed-effects model*
GPS	*Global Positioning System*
iSSF	*integrated Step Selection Function*
log-m/hr	log-transformed movement rate
VIF	*Variance Inflation Factor*

1 Introduction

Behavioral traits of animals are both inherited through genetic composition and earned through personal experiences (Sih *et al.* 2004; Dingemanse *et al.* 2010). Recent studies suggest that anti-predator behavior (the behavioral traits an animal displays to avoid predation) is, to a great extent, shaped by the experiences of an individual during its lifetime and animals adjust their behavior accordingly (e.g., they become shyer) (Thurfjell *et al.* 2017). The preyed-upon species can adjust their behavior and movement to minimize risk of predation by the most abundant predator (Lima 1992). Predation may not only be one of the major selective forces in evolution of anti-predator behavior (Lima & Dill 1990), but human hunters may also heavily select on certain behavioral traits within the shy-boldness continuum (Michelena *et al.* 2010; Ciuti *et al.* 2012). Two commonly used proxies for bold or shy behavior are habitat selection and movement rates (Ciuti *et al.* 2012; Thurfjell *et al.* 2017; Richter *et al.* 2020). Human hunters tend to harvest animals that express bolder behavior as they expose themselves more than shyer individuals by moving more and selecting more for habitats with less cover (Ciuti *et al.* 2012). Thus, bold behavior is expected to be linked to decreased survival when humans account for most of the mortality. Humans hunters and natural predators select differently for behavioral types or body conditions (Réale & Festa-Bianchet 2003; Sand *et al.* 2012). Moreover, more vigilant individuals can detect a predator earlier and therefore increase their likelihood of survival (Kitchen *et al.* 2010). Thus, in consequence of selection of certain behavioral types, genetic variance might diminish over time (Darimont *et al.* 2009; Leclerc *et al.* 2017; Ofstad *et al.* 2020).

Witnessing the kill of a conspecific, group member or an offspring can influence behavior and thus change habitat selection and movement of an animal (Manassa & McCormick 2012; Thurfjell *et al.* 2017). In response, animals show adjustments in habitat selection and movement based on the hunting regime (Lone *et al.* 2015), hunting season (Thurfjell *et al.* 2017) and predator activity (Kohl *et al.* 2018) to avoid predation. Animals may therefore increase their distance to roads during hunting season (Devoe *et al.* 2019) or show lower movement rates in hunted areas than they show in protected areas (Picardi *et al.* 2019). Furthermore, animals may trade-off favorable habitats for foraging in exchange for habitats that provide shelter, depending on human disturbance or the time of day (Kohl *et al.* 2018; Richter *et al.* 2020). The learning processes an individual experiences might vary; however, they may show very clearly in terms of habitat selection and movement rates. Thurfjell *et al.* (2017) showed in their study that older female elk (*Cervus elaphus)* are more adapted to human hunters and older (therefore more experienced) animals might become almost becoming invulnerable to hunters at a certain age (Wright *et al.* 2006; Ciuti *et al.* 2012).

Recent technological advancements in satellite telemetry (i.e., higher fix-rates and more precise fixes), growing collections of datasets, alongside new or improved statistical methods allow for new ways to analyze animal movement data. These create possibilities to expand our understanding of the way an animal reacts to varying environmental conditions and life-history events. One method to link animal movement and habitat selections are integrated Step Selection Functions (iSSF) (Fortin *et al.* 2005; Thurfjell *et al.* 2014; Avgar *et al.* 2016). iSSFs allow to link animal movement parameters to habitat parameters and vice versa by generating random points that are generated from empirical distributions of movement parameters, thus allowing a simultaneous analysis of resource selection and movement parameters by comparing used and available habitat on a path level. Furthermore, iSSFs allow analyzing how individuals react to varying environmental factors, such as (perceived) predation risk (Thurfjell *et al.* 2017;

Richter *et al.* 2020) and may therefore be utilized to test for learning processes on individual and population level.

Throughout Sweden, moose (*Alces alces*) are the most dominant ungulate species (Jarnemo *et al.* 2018). Hunting accounts for 72-93% of all adult mortality in Sweden (Ericsson & Wallin 2001; Lavsund *et al.* 2003) and about ~31% percent of the summer population (~90.000 out of ~300.000 individuals) is shot (hereafter: harvested) per year (Ericsson & Wallin 2001; Svenska Jägareförbundet 2020). Additionally, the harvest rates for moose in Sweden rank amongst the highest in the world (Jensen *et al.* 2020). Moose hunting in Fennoscandia has a long tradition of using hunting dogs and is often done in large groups of hunters. Even though moose are not as gregarious as elk (Peek *et al.* 1974), they may be exposed to non-lethal mortality (and therefore possibly adjust their anti-predator behavior due to learning effects (Thurfjell *et al.* 2017)) for example when a female moose loses her calf to harvest and survives herself. Due to their relatively high lifespan of up to 20 years, a reproductive phase of up to 10 years (Ericsson & Wallin 2001; Ericsson *et al.* 2001) and the high annual harvest rates in Sweden there are plenty opportunities for female moose to experience the aforementioned non-lethal mortality when she loses her calf. To test for individual learning effects in anti-predator behavior, I will analyze GPS-data of collared moose in the regions around Växjö and Öster-Malma, as large carnivores (i.e., wolves (*Canis lupus*) and brown bears (*Ursus arctos*)) have been absent in my study sites (Swenson *et al.* 2007; Neumann & Ericsson 2018; Swedish Environmental Protection Agency 2020). Thus, hunting serves as the main source of mortality for adult moose in my study areas (Ericsson & Wallin 2001). The hunting season for moose in my study areas starts at the 2nd Monday of October (Svenska Jägareförbundet 2020).

To quantify learning effects and anti-predator behavior adjustments of moose, I will test the following hypotheses:

i. Shyer individuals have a higher likelihood of surviving the hunting season due to lower movement rates and higher use of habitats with denser vegetation.
ii. Females that have lost a calf to harvesting, increase their shyness (e.g., reduced movement rates and increased avoidance of open habitats).
iii. Females, that have lost their calf to harvesting will shift their activity peaks (i.e., have higher movement rates at night) and will show a higher proportional activity in habitat associated with foraging during the night than their conspecifics.
iv. As female moose age, they will become more experienced and learn to adjust their movement to avoid hunters, due to their higher probability of having lost calves during previous moose hunts. Therefore, they show lower movement rate and will prefer different habitat types than younger females. The result of this learning process will show as a function of age.

2 Materials and Methods

2.1 Collar Data

I analyzed Global Positioning System data (GPS) of 19 male and 84 female moose (Table 1) in two study areas (near Växjö and Öster Malma) in southern Sweden from 2008-2018 in this study. Moose have been tranquilized from a helicopter and equipped with GPS Plus Collars, as described in Ericsson and Wallin (2001) and Neumann *et al.* (2008). The GPS-collars have been set to a sampling rate of one hour per fix in the first year a moose was observed. After the first year, the sampling rate decreased to 3h per fix (Neumann 2020, personal communication). The age at capture has been estimated from tooth wear (Ericsson *et al.* 2001). I excluded moose from further analysis if the age could not be determined during capture. After visual examination of the data, I excluded relocations with a distance over 10.000m from the analysis, as those were most likely due to GPS-based errors. I furthermore removed the first 10 days after the capture event from the analysis (Morellet *et al.* 2009).

2.2 Data preparation

I used the *amt* package (Signer *et al.* 2019) to resample the relocations to a 3h-intervall between moose relocations by removing all relocations, where the difference between the subsequent relocations differed from 3h, with a 10 minute tolerance. The speed (hereafter: movement rates) between relocations of moose was calculated in meters per hour and then log-transformed the movement rates to fulfill assumptions of normal distribution. I used moose movement data from the 1st August of each year to the end of February of the next year, thus covering the entire hunting period for moose and the two months before it (Svenska Jägareförbundet 2020). I extracted the categorical time of the day (as day, night, dusk and dawn) of each relocation, using the *time_of_day* function from the *amt* package and pooled dusk and dawn as crepuscule.

Table 1 Overview on used data of moose individuals and relocations in each hypothesis.

Hypothesis	Sex	Individuals	moose years	GPS-Positions
I	M	19	42	25365
	F	44	153	100022
II & III	F	55	156	218177
IV	F	84	232	329662
SUM		**103**	**274**	**355027**

2.3 Individual information on moose

Data on the survival of moose was available from observations of the individuals throughout the year, as well as information the reproductive status of female moose in different years. I categorized the fate in the hunting season of each moose as harvested and survived. To analyze the potential learning effects after calf loss, I classified females that did not lose a calf (regardless of whether they had a calf in that year, as they did not experience non-lethal mortality, respectively) as having experienced no calf loss in the previous hunting season and females that did lose one or more calves were classified as having lost a calf, respectively. I updated data on the reproductive status of female moose for 12 individuals. I furthermore removed GPS-data of moose years from the analysis when the reproductive status of the female was never verified, or the observations were not sufficient to determine whether she lost a calf to harvest or not.

2.4 Statistical analysis

2.4.1 Movement analysis

To analyze movement of moose, I fitted multiple sets of generalized additive mixed models (GAMM) with the *mgcv* - package (Wood 2011) for each hypothesis (Table 2), using the log-transformed movement rates as the response variable and ranking them using Akaike Information Criterium (AIC) - model selection (Burnham & Anderson 2002). To assess multicollinearity I fitted linear mixed effects models for each model and analyzed variance inflation factors (VIF) with the *rms* package (Harrell Jr 2020), removing variables with VIF > 4 from analysis (Leclerc *et al.* 2019). I fitted smoothing factor splines over the Julian date (calculated from 1st of August as day 1) until the end of the hunting season or the end of the October, to allow for flexibility of movement rates throughout the season (Ciuti *et al.* 2012; Thurfjell *et al.* 2017; Leclerc *et al.* 2019). I used fate in season (e.g., harvested or survived) and calf loss in the previous year as covariates for the smoothing splines to test for difference in movement rates. Furthermore, I accounted for effects of presence of a calf on movement rates (Cederlund & Sand 1994). All models contained the ID of a moose as a random effect to account for repeated measurements of individual moose and had age as a linear predictor (Ciuti *et al.* 2012; Thurfjell *et al.* 2017) to account for adjustment of movement.

2.4.2 Habitat selection analysis

I analyzed habitat selection of moose by fitting an iSSF (Avgar *et al.* 2016). Every moose step was paired with five random steps (Thurfjell *et al.* 2014), using the *random_steps* function in the *amt* – package (Signer *et al.* 2019). Distributions for step lengths (meters between each relocation) of the random points were generated from a gamma distribution, whereas the turning angles of the random points were generated from a Von Mises distribution. I used a landcover raster map with 25x25m spatial resolution that has been updated with clear-cut data (Swedish Land Survey 2002) and extracted the landcover classes. As I was mainly interested the difference in habitat selection between open and closed habitats, I reclassified the habitat classes accordingly (see Appendix 2). Clear-cuts have been reclassified as closed, when the time-stamp of relocation was taken before the year of the clear-cut, classified as open when the difference between the year of the time-stamp and the year of the clear-cut was between zero and two years and again as closed when the difference was greater than 2 years (Courtois *et al.* 2002; Francis *et al.* 2020). To access selection for open habitats and movement parameters, I applied generalized linear mixed-effect models (GLMM) using a Poisson regression. I fitted the matched sets of used and available points as the response variable, using the *glmmTMB* –

package (Brooks *et al.* 2017) and following the approach introduced by Muff *et al.* (2020) to account for individual specific variation in habitat selection.

All statistical analysis was conducted in R – version 4.0.2 (R Core Team 2020).

Table 2 Overview on fitted models, timespans of each model, model specifications and considered covariates in each model.

Hypothesis	***Model***	***Time span***	***Model Specification***	***fixed effects***
I	movement	August – End of October	Fit separately for Sex	Julian date[a], fate in season[b], age[c]
	habitat selection		Fit separately for Sex and fate	open[d], log-transformed movement rate[e], turning angle[f], age
II	movement	August – End of hunting season	only females	Julian date, previous loss[g], age, with calf[h]
	habitat selection		Fit separately by status of calf loss, only females	open, log-transformed movement rate, turning angle, age, with calf
III	movement	September – End of October	Only females	Julian date, previous loss, age, with calf, time of day[i]
	habitat selection	November – End of hunting season	Fit separately by status of calf loss and the categorical time of day, only females	open, log-transformed movement rate, turning angle, age, with calf
IV	movement	August – End of hunting season	only females	Julian date, age
	habitat selection		only females	open, log-transformed movement rate, turning angle, age
Variables			**[a]Julian date: continuous,** **[b]fate in hunting season: categorical,** **[c]age: continuous,** **[d]open: categorical,** **[e]log-transformed movement rate: numerical,** **[f]turning angle: numerical,** **[g]previous loss: categorical,** **[h]with calf: categorical,** **[i]time of day: categorical** **two-way interactions**	

3 Results

3.1 H I – Survival

Before the start of the moose hunting season, male moose that got harvested during the hunting season moved faster than male moose that survived the hunting season (*harvested*: edf = 5.467, Ref. df = 5.467, *F*-value = 21.76, $p < 0.001$, *survived*: edf = 8.599, Ref.df = 8.599, *F*-value = 76.45, $p < 0.001$, adjusted $R^2 = 0.032$, Figure 1). Moreover, I found a negative effect of age on movement rates of male moose ($t_{1,25211} = -0.014$, $p = 0.168$), meaning that male moose reduced their overall movement with age. Before hunting season starts, female moose that survived had higher movement rates than harvested females but started to show lower movement rates in September. After the start of the moose hunting season, females that survived showed lower movement rates than those who harvested (*harvested*: edf = 1.000, Ref.df = 1.000, *F*-value = 2.073, $p = 0.15$, *survived*: edf = 6.285, Ref.df = 6.285, *F*-Value = 95.694, $p < 0.001$, adjusted $R^2 = 0.01$). Like for male moose, age had a negative effect on movement of female moose ($t_{1,99959} = -0.037$, $p < 0.001$).

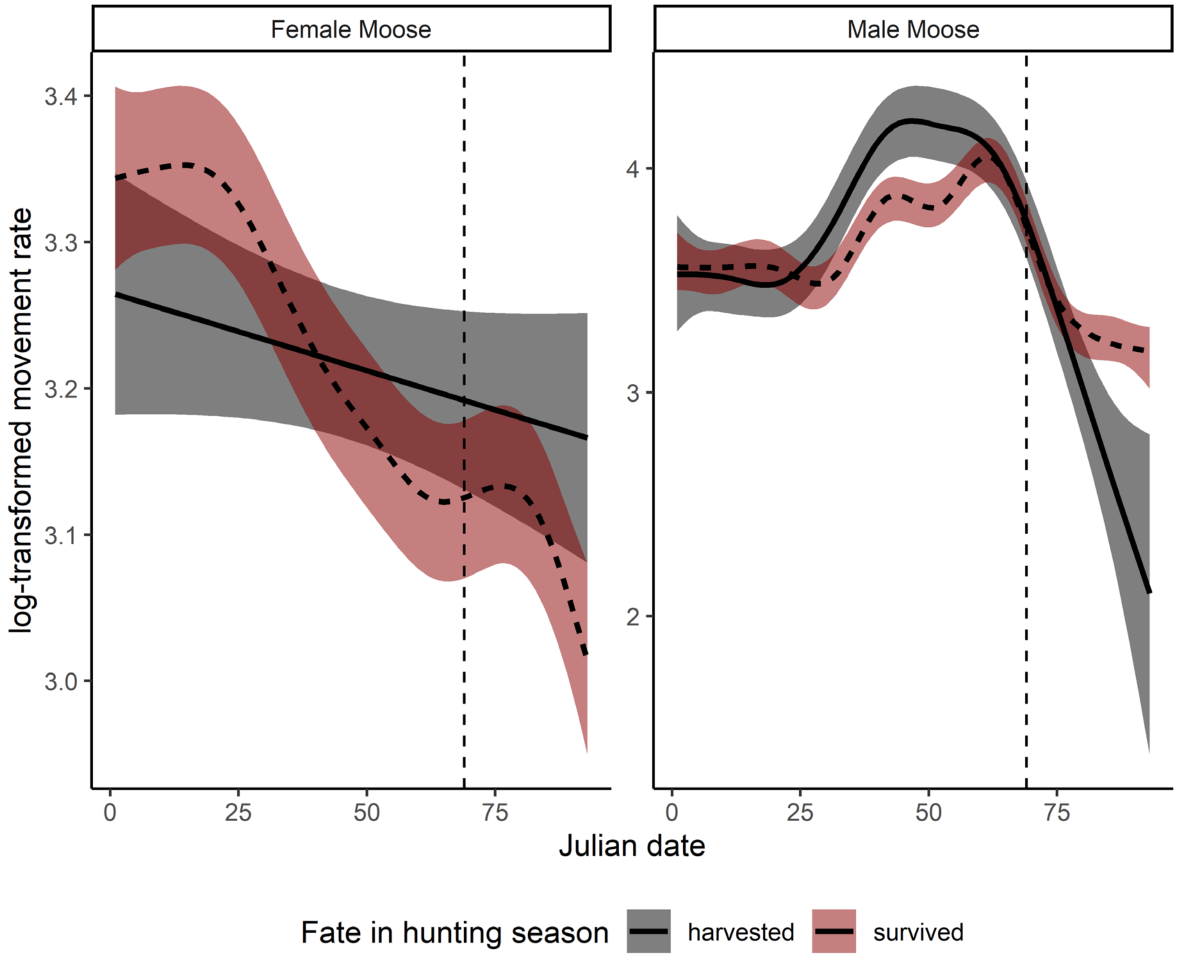

Figure 1 Predicted movement rates (log-transformed meter/h in 3-h intervals) of male and female moose. The dashed lines show movement rates of moose that survived the hunting season, solid lines indicate harvested moose. The red and grey bands indicate the 95% confidence intervalls of moose that survivided and got harvested, respectivly. The vertical dashed line indicates the approximate start of the moose hunting season in October.

Female moose that survived the hunting season selected less for open habitats and selected for shorter steps in open habitat (see Figure 2). Harvested females selected more for open habitats and selected for shorter steps in open habitats. Controlling habitat selection for age showed that older female moose increased their avoidance for open habitats. Both harvested male moose and male moose that survived hunting season selected less for open habitat and moved shorter steps in open habitat. Male moose in both groups increased their selection for open habitats as they aged.

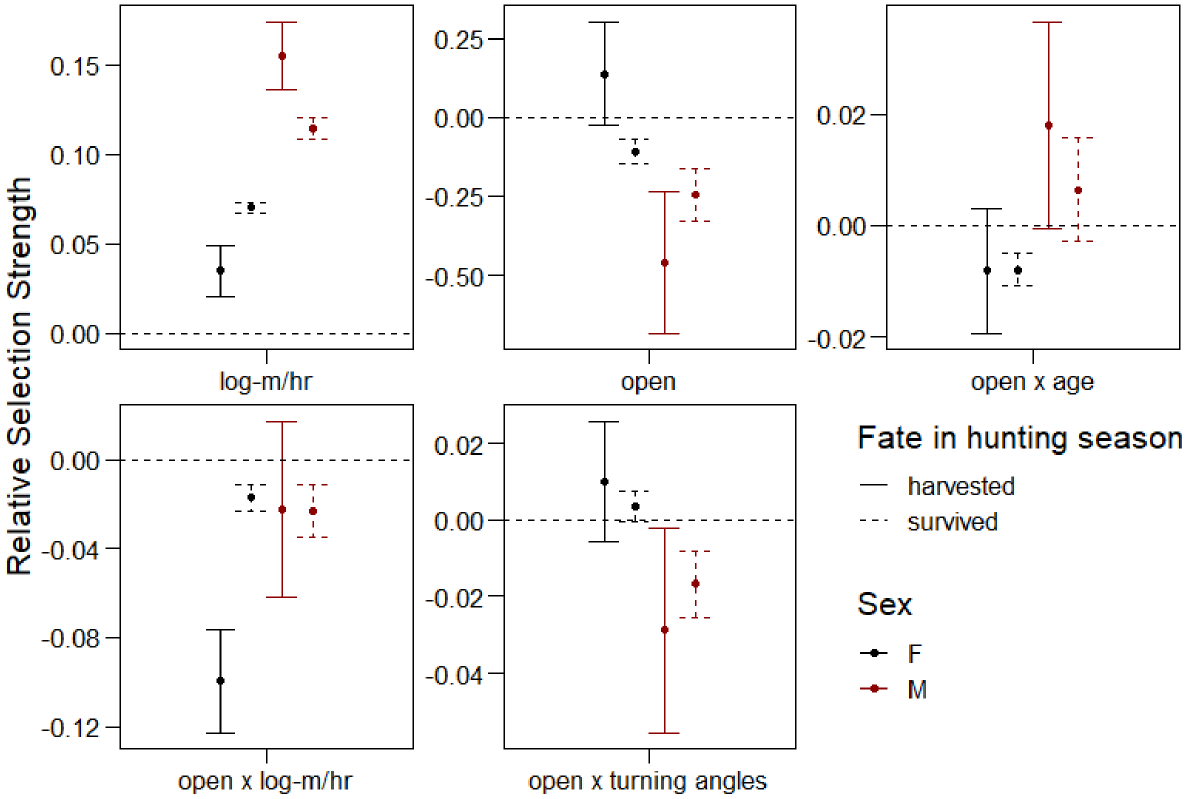

Figure 2 Habitat selection and movement (log-m/hr) parameters of harvested moose and moose that survived the hunting season. The y-axis shows the relative selection strength for each parameter, with the dashed horizontal line indicating no preference. Black error bars indicate parameters of female moose, red error bars indicate male, respectivly. Dashed error bars show parameters for moose that survived, whereas solid error bars indicate harvested moose. The dashed horizontal line indicates no preference.

3.2 H II – Learning effects after calf loss

Females that lost a calf the previous hunting season moved slower in August. This effect reversed in September, shortly before the hunting season begins. In the late hunting season, females that lost a calf in the previous hunting season moved faster again than those who did not (*previous loss*: edf = 7.682, Ref.df = 7.682, F-value = 165.9 $p < 0.001$; *no previous loss*: edf = 7.845, Ref.df = 7.845, F-Value = 223.5, $p < 0.001$, adjusted $R^2 = 0.014$, see Figure 3). Age affected moose movement rates negatively ($t_{1,218118} = -0.022$, $p < 0.001$), as well as the presence of a calf ($t_{1,218118} = -0.064$, $p < 0.001$).

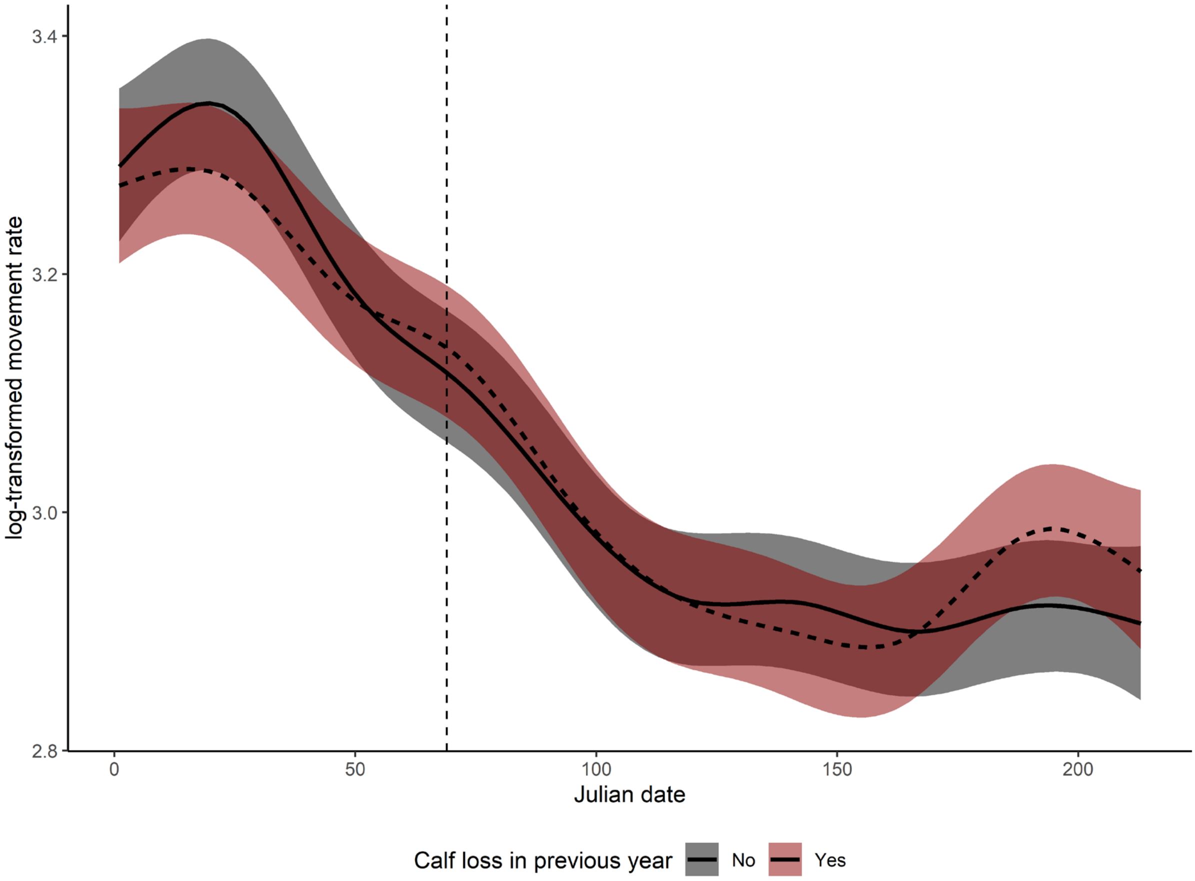

Figure 3 Predicted movement rates (log-transformed meter/hour in 3-h intervals) of female moose throughout hunting season. Dashed lines show movement rates of moose lost a calf in the previous season; solid lines indicate movement of females that did not loose a calf in the last season. The red and grey bands indicate the 95% confidence intervalls of female moose that lost a calf and those who did not, respectivly. The vertical dashed line indicates the approximate start of the moose hunting season in October.

Both females that lost a calf in the previous hunting season and those that did not selected less for open habitats in the following hunting season, however females moved less after calf loss and selected less for open habitats. Both groups selected for shorter steps in open habitat, with females after losing a calf in the previous hunting season being more active there. Controlling habitat selection with presence of a calf showed that females who lost a calf selected less for open habitats, than females who did not lose a calf. Controlling habitat selection for age showed that females that did not lose a calf selected less for open habitats (see Figure 4).

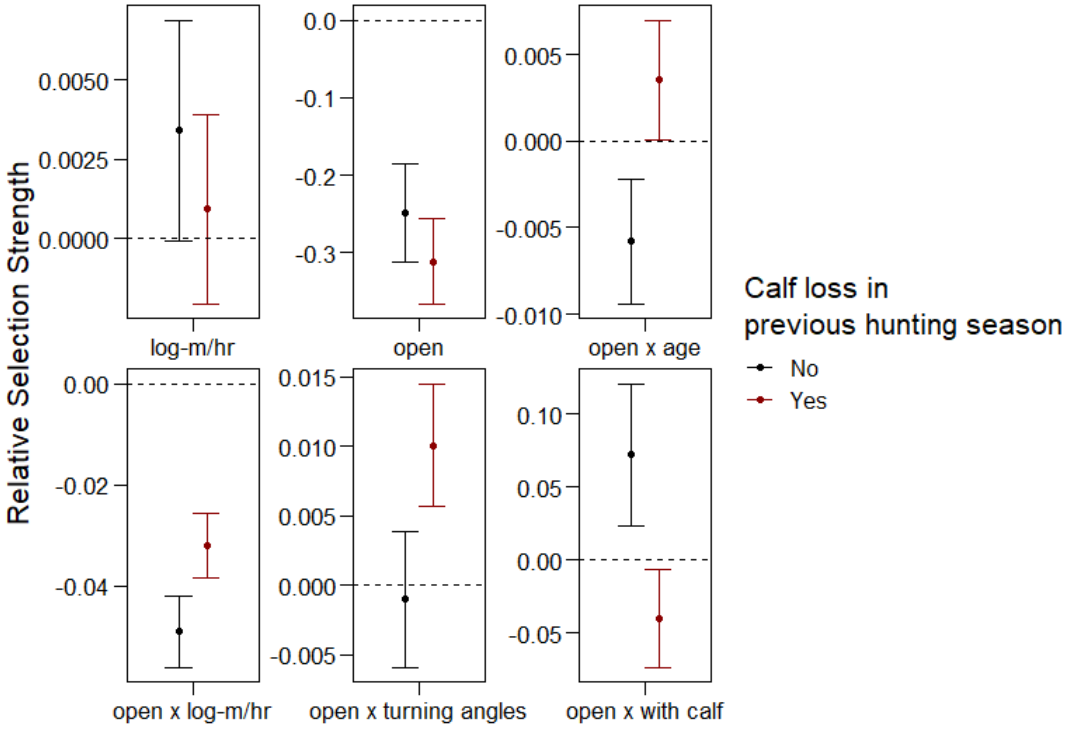

Figure 4 Habitat selection and movement (log-m/hr) parameters of female moose from the 1st August until the end of hunting season in February. The y-axis shows the relative selection strength for each parameter, with the dashed horizontal line indicating no preference. Black error bars indicate parameters of females that did not loose a calf, red error bars indicate parameters of females that experienced calf loss.

3.3 H III – Learning effects after calf loss by the time of day

In September and October, female moose were less active during the day and more active during dusk and dawn. Furthermore, females reduced their movement after losing a calf in the previous year but were more active in general when they had a calf again. Moreover, females that had lost a calf were less active during day and were less active during dusk and dawn (Table 3). From November on, females were more active after calf loss in the previous season and decreased their activity during the night. After calf loss, female moose were less active when they had a calf from November until February. Females that lost a calf before moved even less than females who did not lose a calf when they had a calf in the ongoing hunting season. Female moose reduced their movement towards the end of February (*Sept-Oct*: Julian date: edf = 6.617, Ref.df = 6.717, *F*-Value = 28.89, p < 0.001; *Nov-Feb*: edf = 7.073 , Ref.df = 7.073, *F*-Value = 7.766, p < 0.001).

Table 3 Parametric terms of the most parsimonious models to explain effects of calf loss of movement on female moose by the time of day in from September to October and from November to the end of the hunting season for moose in February. The confidence intervals are given within parentheses, significant parameters are indicated by a bold marked p-value.

	Female Moose (n = 55)			
	September - October		**November - February**	
predictors	*Estimates*	*p*	*Estimates*	*p*
Intercept	3.59 (3.48 – 3.7)	**<0.001**	3.01 (2.91 – 3.10)	**<0.001**
age	-0.02 (-0.03 – -0.01)	**<0.001**	-0.02 (-0.03 – -0.02)	**<0.001**
previous loss (yes)	-0.21 (-0.05 – 0.11)	**<0.001**	0.12 (0.05 – 0.18)	**0.001**
time of day (day)	-0.38 (-0.40 – -0.35)	**<0.001**	0.11 (0.09 – 0.13)	**<0.001**
time of day (dusk/dawn)	0.26 (0.20 – 0.33)	**<0.001**	0.52 (0.49 – 0.56)	**<0.001**
with calf (yes)	-0.12 (-0.19 – -0.04)	**0.004**	-0.01 (-0.07 – 0.05)	0.715
previous loss (yes) × time of day (day)	-0.04 (-0.08 – -0.00)	**0.034**	0.01 (-0.02 – 0.04)	0.63
previous loss (yes) × time of day (dusk/dawn)	-0.07 (-0.16 – 0.03)	0.174	0.02 (-0.03 – 0.07)	0.347
previous loss (yes) × with calf (yes)	0.21 (0.11 – 0.3)	**<0.001**	-0.11 (-0.18 – 0.04)	**0.003**
R^2	**0.030**		**0.018**	

Female moose selected more for open habitats during the day after calf loss in the previous year and selected for shorter steps in open habitats, in comparison to females that did not lose a calf. Controlling habitat selection with presence of a calf showed that females that lost a calf selected less for open habitats (Table 4). From November until February, female moose showed no preference for open habitats after calf loss, whereas females that did not lose a calf selected more for open habitats. Both groups moved less and were less active in open habitats. Presence of a calf did not influence habitat selection significantly in both groups from September to November (Table 5).

From September until the end of October, during the night, females avoided open habitats after the loss of the calf and showed higher activity in open habitats in comparison to females that did not lose a calf. In both groups, the presence of a calf had no significant influence on selection for open habitats. However, female moose were more likely to select for open habitats (Table 4). From November until February, both groups avoided open habitats during the night and were less active. Females that did not lose a calf previously showed higher selection rates for open habitats during the night (Table 5).

During dusk and dawn, females did not significantly select for either habitat type from September to October. However, females that previously lost a calf moved avoider open habitats stronger and moved less in open habitat than females who did not lose a calf. Females with a calf both selected more for open habitats during dusk and dawn in both groups. However, females that previously lost a calf were less likely to select for open habitats (Table 4). From November until February females selected less for open habitats and showed higher activity during dusk and dawn. Both groups selected more for open habitats when a calf was present. Females showed less activity in open habitats when they lost a calf in the previous hunting season. Again, when controlling habitat selection with presence of a calf, females that previously lost a calf were less likely to select for open habitats (Table 5).

Table 4 β - coefficients the habitat selection analysis for female moose from September until the end of October, during the day, the night and the crepuscular period (dusk/dawn). Significant differences in habitat selection are marked in bold, standard errors are given within parentheses.

	Female Moose (n = 55)					
Predictors	**previous loss**			**no previous loss**		
	β Day	β Night	β Crepuscular	β Day	β Night	β Crepuscular
open	**0.462** **(± 0.131)**	**-0.526** **(± 0.125)**	-0.613 (± 0.436)	0.027 (± 0.123)	-0.04 (± 0.117)	-0.297 (± 0.419)
log-m/hr	**-0.031** **(± 0.007)**	**0.133** **(± 0.008)**	**0.2** **(± 0.028)**	**-0.026** **(± 0.006)**	**0.118** **(± 0.008)**	**0.275** **(± 0.028)**
open × log-m/hr	**-0.154** **(± 0.015)**	0.004 (± 0.015)	**0.165** **(± 0.061)**	**-0.145** **(± 0.013)**	**-0.038** **(± 0.014)**	-0021 (± 0.054)
open × turning angles	-0.003 (± 0.011)	0.009 (± 0.009)	-0.02 (± 0.034)	> 0.001 (± 0.01)	-0.01 (± 0.009)	0.029 (± 0.031)
open × age	-0.006 (± 0.008)	-0.001 (± 0.007)	-0.031 (± 0.025)	-0.001 (± 0.007)	-0.009 (± 0.006)	0.002 (± 0.022)
open × with calf	**-0.303** **(± 0.084)**	0.11 (±0.076)	0.263 (± 0.248)	**0.242** **(± 0.095)**	-0.01 (± 0.088)	0.344 (± 0.316)

Table 5 β – coefficients of the habitat selection analysis for female moose from November until the end of the hunting season in February during the day, the night, and the crepuscular period (dusk/dawn). Significant differences in habitat selection are marked in bold, standard errors are given within parentheses.

	Female Moose (n = 55)					
Predictors	**previous loss**			**no previous loss**		
	β Day	β Night	β Crepuscular	β Day	β Night	β Crepuscular
open	-0.014 (± 0.134)	**-0.459** **(± 0.090)**	-0.139 (± 0.234)	**0.402** **(± 0.124)**	**-0.499** **(± 0.091)**	**-0.740** **(± 0.235)**
log-m/hr	**-0.023** **(± 0.006)**	**-0.098** **(± 0.004)**	**0.197** **(± 0.013)**	**-0.025** **(± 0.006)**	**-0.109** **(± 0.004)**	**0.157** **(± 0.012)**
open × log-m/hr	**-0.136** **(± 0.015)**	**-0.030** **(± 0.009)**	**-0.102** **(± 0.03)**	**-0.156** **(± 0.014)**	-0.004 (± 0.009)	-0.034 (± 0.027)
open × turning angles	0.006 (± 0.01)	0.005 (± 0.007)	0.027 (± 0.019)	0.007 (± 0.01)	0.003 (± 0.007)	0.0001 (± 0.017)
open × age	0.002 (± 0.008)	0.004 (± 0.005)	0.004 (± 0.014)	**-0.016** **(± 0.007)**	-0.004 (± 0.005)	0.001 (± 0.012)
open × with calf	0.059 (± 0.08)	0.037 (± 0.055)	0.093 (± 0.139)	-0.062 (± 0.097)	**0.178** **(± 0.073)**	**0.609** **(± 0.187)**

3.4 H IV – Learning effects of aging moose

While female moose aged, they reduced their movement rates during the hunting season ($t_{10.59} = -0.03$, $p < 0.001$). After being most active before the hunting season, female moose strongly reduced their activity throughout hunting season. Towards the end of the hunting season in February, female moose slightly increased their movement again (edf = 8.587, Ref.df = 8.587, *F*-Value = 623.1, $p < 0.001$, adjusted $R^2 = 0.016$, see Figure 5).

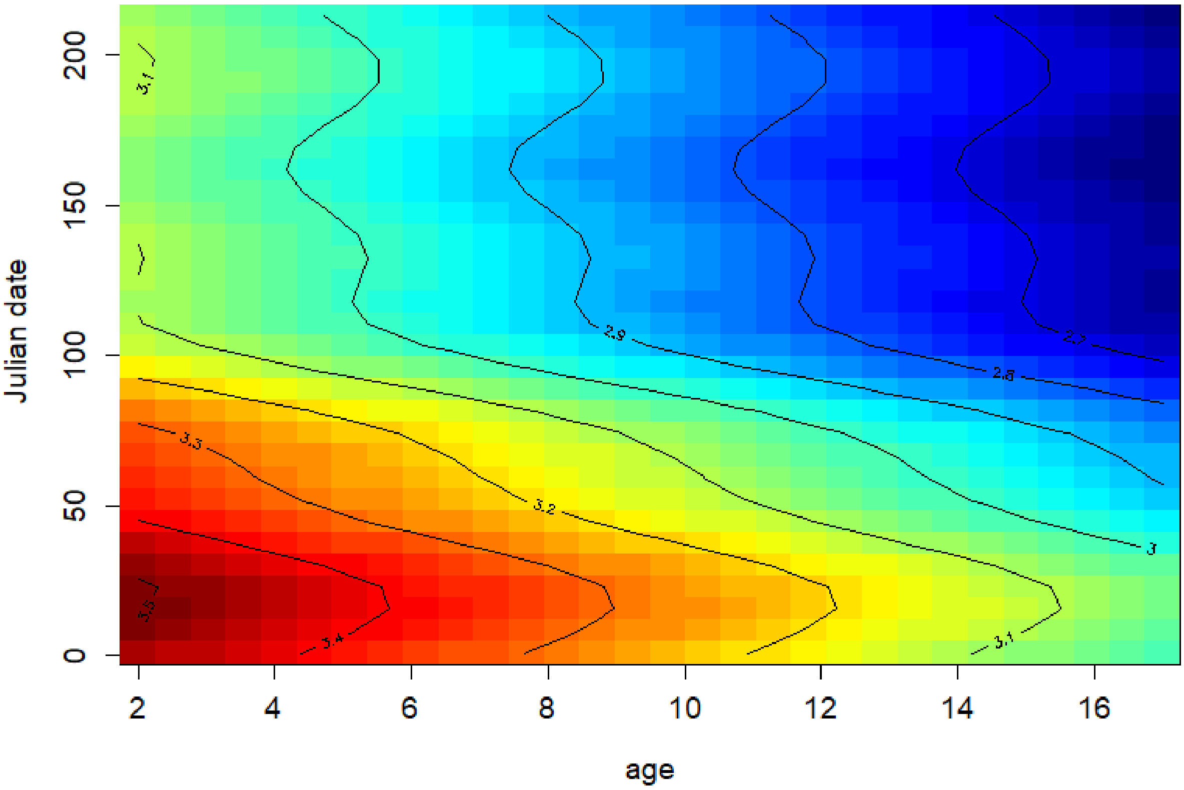

Figure 5 Predicted log-transformed movement rates of female moose throughout the hunting season. The y-axis shows the Julian date, from 1st *of August (as day 1) to the end of hunting season in February, the x-axis shows the age of the moose. Red colors indicate higher movement rates, yellow, green and blue colors represent lower movement rates, respectively. Black lines represent fitted smoothing splines.*

While female moose generally selected less for open habitats (Table 6), I did not find any indication that age influenced selection for open habitats of female moose throughout the hunting season.

Table 6 β - coefficients of the habitat selection analysis for female moose to test whether female moose adjust their selection for open habitats as they age. Significant differences in habitat selection are marked in bold, standard errors are given within parentheses.

	Female Moose (n = 84)	
Predictors	*β*	*p*
open	***-0.199*** ***(± 0.19)***	***> 0.001***
log-m/hr	*> -0.001* *(± 0.001)*	*0.98*
open × log-m/hr	***-0.031*** ***(± 0.030)***	***> 0.001***
open × turning angles	*-0.004* *(± 0.002)*	*0.0561*
open × age	*-0.002* *(± 0.002)*	*0.126*

4 Discussion

By using telemetry data from 2008-2018 I was able to show that moose, a non-gregarious cervid species, learnt from experiencing non-lethal mortality and increase their shyness after experiencing calf loss by increasing avoidance of open habitats, reducing their movement rates and shifting activity to the night. This suggests adaptation of anti-predator behavior in moose to their most common predator. My results furthermore emphasize that movement and habitat selection affect moose survival during the moose hunting season.

4.1 Selection for different behavioral traits by hunters

The expression of different behavioral traits increased survival chances for moose in my study. For male moose, exhibiting shyer behavior (in terms of habitat selection) lead to increased mortality. In contrast to increased mortality through shyer behavior, male moose showing bolder behavior (in terms of higher movement rates) were more likely to get harvested. For female moose, being shyer (by avoiding open habitats) increased their survival in the hunting season, confirming importance of shelter for female moose. In addition to impaired visibility for human hunters and less opportunities for hunters to apply safe shots, hiding in dense vegetation could make it harder to determine whether a female is accompanied by a calf. Since hunters are also compelled to shoot the calf before the mother, this uncertainty could make hunters reluctant to harvest female moose, despite having seen them.

In conclusion, my first hypothesis that being shyer can be advantageous for survival of male and female moose is partially supported. This suggest that selection for behavioral traits of human hunters in moose is highly complex. Similar results were reported by Ciuti *et al.* (2012), however my results are not as distinct as in their study. However, the harvest of moose that express bolder behavior subsequently favors the survival of shyer moose. Especially as behavioral traits are not only learned through experience but can also be inherited (Sih *et al.* 2004; Dingemanse *et al.* 2010), this selective pressure might lead to surviving moose becoming shyer. Thus, moose might become increasingly harder to harvest, assuming no adaption to moose behavior by their human hunters. Whilst this is an unfavorable trait of moose for human hunters, it is a beneficial trait for moose.

4.2 Effects of calf loss on movement and habitat selection

Female moose in my study increased their shyness in the hunting season following calf loss confirming my second hypothesis. They selected less for open habitats and reduced their movement rates, possibly adopting these behavioral traits to avoid for human hunters (Thurfjell *et al.* 2017) and adapting to the most common predator in Sweden (Lima 1992; Ericsson & Wallin 2001; Svenska Jägareförbundet 2020). The increased shyness of female moose after losing a calf in the previous hunting season also indicates a direct learning effect from non-lethal mortality (as calf loss) in female moose. Increased shyness after witnessing non-lethal mortality was also reported in other cervid species, for example in elk (Thurfjell *et al.* 2017). Here, increasing shyness of female elk (a gregarious cervid species) was linked to witnessing the death of other elk. Avoiding open habitats might especially be beneficial when hunted by a visual predator (Kohl *et al.* 2018), since human hunters are compelled only to shoot when they have a clear shot on the animal. As mentioned before, when hiding in dense vegetation, visibility for human hunters is impaired. Consequently, it is beneficial for moose to hide there. Furthermore, due to the possibility of bullets being deflected by branches, hunters may hesitate even more to shoot moose in dense vegetation.

4.3 Adjusting behavior to avoid hunters

Female moose became more nocturnal after calf loss during the first part of the hunting season, confirming my third hypothesis that moose adjust their behavior to avoid hunters after losing a calf. The increase of nocturnal activity (Fattebert *et al.* 2019; Richter *et al.* 2020), reduction of movement rates (Thurfjell *et al.* 2017) and avoidance of open habitats (Bonnot *et al.* 2013) as behaviors to avoid predation are found in multiple cervid species. Becoming more nocturnal after calf loss in the early hunting season and avoidance of open habitats during the day after losing a calf in the previous season is a strong behavioral response and possibly an adaption in anti-predator behavior towards human hunters. Female moose were also less active during dusk and dawn after calf loss. Females that were accompanied by one or more calves furthermore avoided open habitats more after calf loss, possibly to further protect their offspring. These behavioral adaptions probably derive from the learning effect of calf loss in the last hunting season. As a direct consequence of this behavior, female moose might be less likely to be noticed by hunters and therefore be less vulnerable to harvest or losing their calf. Though I did not test for this, this might also increase fitness of females.

4.4 Increasing shyness with age

Female moose decreased movement rates during the hunting season as they age, possibly adopting this behavioral strategy to avoid hunters and indicating learning as they age. This supports my fourth hypothesis, that moose get more experienced in avoiding hunters as they age. In contrast to the avoidance of open habitats during the hunting season, avoidance of open habitats only marginally increased with age. However, I cannot rule out that there might be other learning mechanisms in habitat selection and movement I did not account for. For example, moose might avoid certain vegetational types more than others or might learn how to efficiently escape hunting dogs. Analyzing learning effects in habitat selection on the basis of open and closed habitats only provides for a rough estimate of shyness and ignores structural vegetational composition (Hebblewhite *et al.* 2008), ruggedness of terrain or distance to roads (Thurfjell *et al.* 2017). The high turnover rates of the moose population in Sweden (Lavsund *et al.* 2003; Jensen *et al.* 2020; Svenska Jägareförbundet 2020), alongside the selection of hunters for bolder moose, might have already modified behavior of female moose to the point where they cannot become shyer in terms of habitat selection as they age. Furthermore, similar study designs in countries with lower harvest rates might give clearer insights on habitat selection and movement of female moose under risk of predation and learning processes. Human hunters have contributed for the majority of mortality in adult moose in Sweden for multiple centuries now (Ericsson & Wallin 2001). When harvest rates are lower, moose might have less need and chances to adapt to human hunters. Assuming this, it could be expected that in countries with lower harvest rates, moose behavior might not be as adapted to human hunters as in Sweden. Consequently, the pressure for moose to adapt to human hunters might be lower and moose are not pressured as much into become shyer to survive the hunting season or to avoid calf loss. Furthermore, as moose are less likely to lose a calf to harvest when harvest rates are low, they have less opportunity to learn from their own mistakes. Therefore, moose there might be more naïve and express bolder behavior and learning effects might become more apparent.

However, hunting dogs (as an olfactory hunting support) may eradicate benefits of hiding in dense vegetations as they either could flush the moose out or guide hunters towards the moose. The hunting of different kind of game species with support of different breeds of hunting dogs (e.g., pointers or flushing dogs) has a long tradition in Fennoscandia more common than in many other European countries and is for example forbidden in the US (Sand *et al.* 2006). The purpose of those dogs is either to hold the moose at bay until a hunter shoots the moose or to force the moose to flee and eventually drive it towards a hunter. Ericsson *et al.* (2015) reported that potentially non-naïve (thus experienced) moose occasionally moved straight away from the attacking dog and that this behavior might be related to age. This tortuous escape behavior was reported to potentially influence survival in situations when dogs are involved in moose hunting (Ericsson *et al.* 2015). While this behavior seems counterintuitive, as females expose themselves more to hunters, they might escape from the hunting grounds of the hunting team. Thus, these brief expressions of this behavior in these situations could severely influence survival of a moose. Possibly they further differentiate between experienced and naïve moose (Baskin *et al.* 2004; Sand *et al.* 2006). In areas where ungulate densities are high, escaping in tortuous manner and running long distances might also hold more advantages for survival of moose. Chasing dogs might get distracted from the moose when they encounter other game species during the chase and start chasing those instead of the moose. Due to the relatively coarse sampling rate of 3h between relocations I could not analyze this. The utilization of hunting dogs could therefore marginalize benefits of the anti-predator behaviors I analyzed in this study.

The absence of relevant predators than humans for moose (Ericsson & Wallin 2001), such as wolves and bears, in my study areas provided for a unique opportunity to study anti-predator behavior and learning processes in a heavily managed moose population, where harvest accounts for the majority of the mortality of moose (Ericsson & Wallin 2001). Bears for example predate mainly on moose calves (Swenson *et al.* 2007). Previous studies showed that some cervid species can reduce their movement rates as they age (Thurfjell *et al.* 2017). There is a higher expected possibility of calf loss in life with increasing age and thus a possible autocorrelation between age und calf loss in life. Thus, I decided to analyze (known) calf loss in the previous hunting season rather than (known) calf loss in life. Otherwise, female moose would show lower movement rates when being classified as having lost a calf in their lifetime (thus, ultimately being shyer) by default. While analyzing (known) calf loss in the previous hunting season over (known) calf loss in life might have lessened differences in habitat selection and movement between my control groups, it allowed me separate learning affects from calf loss and age. A further limitation in my study is that hunters may hesitate to harvest collared moose (Neumann 2020, personal communication). This applied for all moose analyzed within this study, resulting in a similar harvest risk across all moose in my study. The reclassification of landcover classes in open and closed habitats (Swedish Land Survey 2002) with information on clear-cuts allowed me to account for effects of clear-cuts in habitat selection of moose (Courtois *et al.* 2002; Francis *et al.* 2020). However, I did not have data on the exact date any clear-cut was carried out. Consequently, I used the year the clear-cut was carried out as a coarse measurement for openness of the raster cells. Furthermore, I did not take into consideration whether clear-cuts were left to natural succession or if trees were planted after the clear-cut was carried out.

5 Conclusion

I conclude that female moose learn from losing calves to harvest and that those learning effects can accumulate over time. Furthermore, they adjust their behavior to avoid human hunters and reduce predation risk. Using two proxies for anti-predator behavior, I have shown that female moose learn from non-lethal mortality and adapt their behavior accordingly. Future studies might focus on learning behavior regarding hunting dogs in moose, as suggested in Ericsson *et al.* (2015) or analyze habitat selection in combination with light detection and ranging (LiDAR) technology to access the structural vegetational composition. This could further improve our understanding on learning processes and anti-predator behavior in female moose.

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7 Acknowledgments

Firstly, I want to thank my supervisors, Wiebke Neumann and Henrik Thurfjell, for offering me the opportunity to write my thesis at SLU in Umeå and for giving me directions on where to go to with my analysis when I was getting lost. I have thoroughly enjoyed working on this project with you and our weekly meetings have helped me develop as a scientist. Furthermore, I highly appreciated the freedom you gave me in this project. Surely, I have learned quite a lot during my time at SLU and hopefully I will be able to use this knowledge for my future projects. I also want to thank John Ball for providing the fantastic computer lab I have been working in for the past months and our long talks in the evenings. Thanks also to Fabian Knufinke for always listening and commenting on the ideas I had for this project during our long Zoom-sessions. Likewise, I want to thank Kerren Volkmar (and Fabian again) for occasionally commenting this manuscript. Both of you helped me to increase the quality of this manuscript significantly. Lastly, I want to thank my father for looking after my dog while I was working on my thesis in Umeå.

Tack så mycket.

8 Appendix

Appendix 1 Overview on used variables and their (predicted) links to movement and habitat selection of male and female moose.

Grouping variable	variable	Variables association with moose behavior (movement rate and habitat selection)	Predicted link with habitat selection and movement rates
Individual behavior	fate in hunting season	Survived or harvested	higher step lengths are expected for harvested moose
	Julian date	-	allow for flexibility in moose step lengths throughout the year
	Reproductive status	Presence of one or more calves at the onset of hunting season	The presence of a calf is expected to lower the step lengths and shift habitat selection
Individual experience	age	age	Older moose will move less and will change their habitat use due to experience
	(known) calf loss	Calf loss in previous hunting season	Calf loss will increase shyness (lower step lengths; increased avoidance of open areas)
Environment	Open areas	Openness of an area	Open areas are expected to be selected more by individuals that did not experience calf loss.
	Day period	day, night, crepuscule	Higher movement rates and differing habitat selections between factors

*Appendix 2 Reclassification table of the landcover classes. The landcover classes were updated with data on clear-cuts and updated accordingly. 1 indicated open raster cells, 0 closed raster cells, respectively. Clear cuts (marked with an *) are reclassified accordingly to the year they were carried out.*

Landcover class	*Openness of the raster cell*
1.1.1 Continuous urban fabric	1
1.1.2.1.1 Discontinuous urban fabric with more than 200 inhabitants with minor areas of gardens and greenery	1
1.1.2.1.2 Discontinuous urban fabric with more than 200 inhabitants with major areas of gardens and greenery	1
1.1.2.2 Discontinuous urban fabric with less than 200 inhabitants	1
1.1.2.3 Solitary houses with property	1
1.2.1 Industrial or commercial units, public services and military installations	1
1.2.2 Road and rail networks and associated land	1
1.2.3 Port areas	1
1.2.4 Airports	1
1.3.1.1 Sand and gravel pits	1
1.3.1.2 Other mineral extraction sites	1
1.3.2 Dump sites	1
1.3.3 Construction sites	1
1.4.1 Green urban areas	1
1.4.2.1 Sport grounds, shooting ranges, motor, horse and dog racing tracks	1
1.4.2.2 Airfields (grass)	1
1.4.2.3 Ski slopes	1
1.4.2.4 Golf courses	1
1.4.2.5 Non-urban parks	1
1.4.2.6 Camping sites and holiday cottage sites	1
2.1.1 Arable land	1
2.2.2 Fruit trees and berry plantations	1
2.3.1 Pastures	1
3.1.1.1 Broad-leaved forest not on mires	0
3.1.1.2 Broad-leaved forest on mires	0
3.1.1.3 Broad-leaved forest on open bedrock	0
3.1.2.1.1 Coniferous forest on lichen-dominated areas	0

3.1.2.1.2.1 Coniferous forest 5-15 m	0
3.1.2.1.2.2 Coniferous forest >15 m	0
3.1.2.2 Coniferous forest on mires	0
3.1.2.3 Coniferous forest on open bedrock	0
3.1.3.1 Mixed forest not on mires	0
3.1.3.2 Mixed forest on mires	0
3.1.3.3 Mixed forest on open bedrock	0
3.2.1 Natural grassland	1
3.2.2 Moors and heathland	1
3.2.4.1 Thickets	1
3.2.4.2 Clear-felled areas	*
3.2.4.3 Younger forest	0
3.1.2.1.2 Coniferous forest not on lichen-dominated areas	0
3.3.1 Beaches, dunes, and sand plains	1
3.3.2 Bare rock	1
3.3.3 Sparsely vegetated areas	1
3.3.4 Burnt areas	1
3.3.5 Glaciers and perpetual snow	1
3.2.1.1 Grass tundra	1
3.2.1.2 Meadow grasses	1
4.1.1 Inland marshes	1
4.1.2.1 Wet mires	1
4.1.2.2 Other mires	1
4.1.2.3 Peat extraction sites	1
4.2.1 Salt marshes	1
5.1.1 Water courses	1
5.1.2.1 Lakes and ponds, open surface	1
5.1.2.2 Lakes and ponds, surface being grown over	1
5.2.1 Coastal lagoons	1
5.2.2 Estuaries	1
5.2.3.1 Sea and ocean, open surface	1
5.2.3.2. Sea and ocean, surface being grown over	1

Appendix 3 Candidate models to test the variance in movement between harvested female moose and female moose that survived hunting season. Bold terms were fitted with smoothing splines to allow for flexibility of movement. Candidate models are sorted so that the most parsimonious model is at the top of the table. All models contained the moose-ID as a random intercept. Models are listed with the degrees of freedom, AICc-value, the difference to the most parsimonious model and the weight of each model.

Candidate model	*df*	*AICc*	*ΔAICc*	*weight*
Julian Date by hunting season Fate + Age	8	332270.12	0.00	1.00
Julian Date + Age	6	332284.01	13.89	0.00
Julian Date + Age	5	332298.41	28.29	0.00
Julian Date	4	332518.70	248.58	0.00
Age	4	332843.61	573.49	0.00
None	3	333057.18	787.06	0.00

Appendix 4 Candidate models to test the variance in movement between harvested male moose and female moose that survived hunting season. Bold terms were fitted with smoothing splines to allow for flexibility of movement rates. Candidate models are sorted so that the most parsimonious model is at the top of the table. All models contained the moose-ID as a random intercept. Models are listed with the degrees of freedom, AICc-value, the difference to the most parsimonious model and the weight of each model.

Candidate model	*df*	*AICc*	*ΔAICc*	*weight*
Julian Date by hunting season Fate + Age	8	90557.15	0.00	0.97
Julian Date + Age	6	90564.32	7.17	0.03
Julian Date	4	91370.86	813.71	0.00
Julian Date + Age	5	91372.39	815.24	0.00
None	3	91378.72	821.57	0.00
age	4	91380.38	823.22	0.00

Appendix 5 Candidate models to test the variance in movement between the two different categories of calf loss. Bold terms were fitted with smoothing splines to allow for flexibility of movement rates over time. Candidate models are sorted so that the most parsimonious model is at the top of the table. All models contained the moose-ID as a random intercept. Models are listed with the degrees of freedom, AICc-value, the difference to the most parsimonious model and the weight of each model.

Candidate model	*df*	*AICc*	*ΔAICc*	*weight*
Julian Date by loss in previous hunting season + Age + with calf	9	722462.85	0.00	1.00
Julian Date by loss in previous hunting season + Age	8	722487.90	25.05	0.00
Julian Date + Age	6	722490.12	27.27	0.00
Age + Julian Date + with calf	6	723003.49	540.64	0.00
Age + Julian Date	5	723034.03	571.18	0.00
Julian Date	4	723227.10	764.25	0.00
Age	4	725416.35	2953.50	0.00
with calf	4	725423.55	2960.70	0.00
None	3	725445.94	2983.08	0.00

Appendix 6 Candidate models to test the variance in movement in female moose after calf loss by the time of day from September until the end of October. Bold terms were fitted with smoothing splines to allow for flexibility of movement rates. Candidate models are sorted so that the most parsimonious model is at the top of the table. All models contained the moose-ID as a random intercept. Models are listed with the degrees of freedom, AICc-value, the difference to the most parsimonious model and the weight of each model.

Candidate model	*df*	*AICc*	*ΔAICc*	*weight*
Julian Date + loss in previous hunting season + Age + with calf + loss in previous hunting season × with calf + loss in previous hunting season × time_of_day	13	214496.88	0.00	1.00
Julian Date + loss in previous hunting season × time_of_day + Age	11	214512.75	15.87	0.00
Julian Date + loss in previous hunting season + Age + with calf + loss in previous hunting season × time_of_day	12	214513.33	16.44	0.00
Julian Date + time_of_day + Age	8	214523.41	26.52	0.00
Julian Date + loss in previous hunting season + Age	7	216418.82	1921.94	0.00
Julian Date + Age	5	216426.31	1929.43	0.00
Julian Date + Age	6	216428.31	1931.43	0.00
Julian Date	4	216456.90	1960.01	0.00
None	3	216596.28	2099.40	0.00

Appendix 7 Candidate models to test the variance in movement in female moose after calf loss by the time of day from November until the end of the moose hunting season in February. Bold terms were fitted with smoothing splines to allow for flexibility of movement rates. Interaction terms are marked with an x. Candidate models are sorted so that the most parsimonious model is at the top of the table. All models contained the moose-ID as a random intercept. Models are listed with the degrees of freedom, AICc-value, the difference to the most parsimonious model and the weight of each model.

Candidate model	*df*	*AICc*	*ΔAICc*	*weight*
Julian Date + loss in previous hunting season + Age + with calf + loss in previous hunting season × with calf + loss in previous hunting season × time_of_day	13	214496.88	0.00	1.00
Julian Date + loss in previous hunting season + Age + with calf + loss in previous hunting season × time_of_day	12	214513.33	16.44	0.00
Julian Date + loss in previous hunting season × time_of_day + Age	11	395923.64	181426.76	0.00
Julian Date + time_of_day + Age	8	395930.22	181433.33	0.00
Julian Date + loss in previous hunting season + Age	7	397672.81	183175.92	0.00
Julian Date + Age	6	397682.82	183185.94	0.00
Julian Date + Age	5	397712.94	183216.06	0.00
None	3	397798.56	183301.67	0.00
Julian Date	4	397800.52	183303.63	0.00

Appendix 8 Candidate models to test if female moose adjust their movement rates as they age. Bold terms were fitted with smoothing splines to allow for flexibility of movement. Candidate models are sorted so that the most parsimonious model is at the top of the table. All models contained the moose-ID as a random intercept. Models are listed with the degrees of freedom, AICc-value, the difference to the most parsimonious model and the weight of each model.

Candidate model	*df*	*AICc*	*ΔAICc*	*weight*
Julian Date + Age	6	1091378.49	0.00	1.00
Julian Date	5	1091703.05	324.56	0.00
None	3	1096374.66	4996.16	0.00

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