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Master thesis

Moose (*Alces alces*) flight response when
disturbed by off-track skiing



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Abstract

Wildlife face high potential to be disturbed by humans due to habitat loss and increasing popularity of recreational activities. Animals respond to the human disturbance as the risk of getting predated was real. The responses vary among individuals and are dependent on different factors.

In this study, I investigated moose (*Alces alces*) behavioural responses for human activity. 12 free-ranging female moose were disturbed by off-track skiing in Sweden. I examined whether environmental factors, presence of calves and time of day affect to moose flush response and whether moose showed signs of habituation.

Moose flight initiation distance varied among individuals, but none of the predictors explained the variation in the response. Moose flush response was more intense during midday, when the snow was old and moose sank through it. Moose was more responsive when accompanied by a calf. Moose made more turns when the disturbance last longer. I could not find signs of habituation.

Moose might be more responsive to the human disturbance when they are accompanied by a calf. Moose flight response was more intensive in the midday and when the approacher sank through the snow. Human disturbance may have negative consequences during winter when there is less food available. Antipredator behaviour is always costly, but it can have more severe impact for the mothers, since they have to ensure the survival of their offspring.

Keywords: *moose, disturbance, flight response, winter recreation activity, habituation*

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1. Introduction

Habitat loss and fragmentation are amongst the most severe threats for the wildlife (Huxel & Hastings, 1999). At the same time human population and the popularity of outdoor recreation activities are increasing (Knight et al., 1995). Thus, animals have an increasing risk of being disturbed by the humans (Hammit, Cole, & Monz, 2015; Knight et al., 1995). To be able to control increasing encounters of wildlife and people, it is essential to study how human disturbance effects animals' behaviour.

Animals have developed different antipredator responses to avoid being captured. These are for example increased vigilance, grouping and flight reaction (Liley & Creel, 2008; Lima & Dill, 1990). Animals can experience non-lethal human disturbance as a real predation risk and apply antipredator strategies when encounter with people (Frid & Dill, 2002). Individuals in the hunted populations are more responsive for the human disturbance than individuals in other populations (Sand, Wikenros, Liberg, & Wabakken, 2006; Stankowich, 2008).

Antipredator behaviour is costly since it requires energy and reduces time available for other essential activities such as foraging and resting (Colescott, 1998; Lima & Dill, 1990; Naylor, Wisdom, & Anthony, 2009). Consequences are often short-term, but continuous disturbance might cause long-term effects. The animals can have chronic stress, which may lead to lower reproduction and even mortality (Knight et al., 1995; M. Beale, 2007; E. Reimers, Røed, Flaget, & Lurås, 2010). Long-term exposure to human disturbance may cause habituation (Eigil Reimers, Lund, & Ergon, 2011; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). This can have negative consequences since habituated individuals might be easier targets for predation or poaching. However, habituation may also mitigate some effects of human disturbance (Wheat & Wilmers, 2016).

Animals' responses to disturbance vary among individuals (M. Beale, 2007). For example, females with offspring have shown to be more vigilant (Childress & Lung, 2003; Stankowich, 2008). Several other factors, as type, predictability, time and place of human disturbance affect how animal experience the disturbance. Animals responses are dependent also on different environmental aspects, like habitat type, visibility and snow depth (Knight et al., 1995; L. Lima & M. Dill, 1990; Stankowich & Blumstein, 2005; Wikenros, Sand, Wabakken, Liberg, & Pedersen, 2009) .

The moose (*Alces alces*) is a common species in northern Europe where it has a long history of coexistence with humans (Lavsund, Nygrén, & Solberg, 2003). It has high cultural and economic value (Milner, Nilsen, Wabakken, & Storaas, 2005; Storaas, Gundersen, Henriksen, & Andreassen, 2001). The moose is the most important game species; in Sweden approximately 100 000 moose are harvested yearly (Lavsund et al., 2003). However, it is also a source of human-wildlife conflicts due to traffic accidents and damages in forestry (Ericsson, Edenius, Bergman, & Danell, 2002; Lavsund et al., 2003).

Cross country skiing is a popular winter recreation activity in Fennoscandia (Neumann, Ericsson, & Dettki, 2010), where The Right of Public Access (Swedish Environmental Protection Agency) enables people to move freely with few limitations in natural areas without landowners' permit. When cross-country skiing takes place off-track, disturbance is less predictable and thus animals' responses can be stronger (Stankowich, 2008; Taylor & Knight, 2003). Winter recreation activities might have more serious impact on animals than activities in other seasons (Andersen, Linnell, & Langvatn, 1996; Larson, Reed, Merenlender, & Crooks, 2016), as cold temperatures require more energy and snow increases the energy requirements for foraging and moving (Marchand, 2013).

In this study, I examined 12 free-ranging female moose and their behavioural responses to human disturbance. The moose were equipped with GPS-collars, allowing me to approach and track them by skiing. I wanted to see how presence of calves, time of day, snow depth and type, and type of disturbance affected moose flight decisions. I predict that moose is more responsive; moose will flee earlier and the fleeing movement will be more intense (faster and longer), when accompanied by a calf. I predict moose to move less when it sink more through the snow. I predict that moose response will vary in different times of day. I predict that when human disturbance lasts longer and is intentional, animals run faster and their track is more sinuous compared to unconscious, short duration disturbance. Each moose was approached several times, allowing me to study whether moose behaviour changed after repeated disturbance. I predict that moose do not show signs of habituation for the disturbance. Additionally, I studied if the flight initiation distance can explain moose fleeing movement.

2. Materials and methods

2.1 Study area

The study was conducted in Nordmaling (63°40' N 19°41' E), Västerbotten county in North-Eastern Sweden. The elevation is 42 ± 5.5 m (Singh, Börger, Dettki, Bunnefeld, & Ericsson, 2012). The study area is characterised by boreal forest, bogs and agricultural land (Pfeffer et al., 2017). Forest are dominated by Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*) and birches (*Betula pendula* and *B. pubescens*). The mean snow depth during study period was 0.40 m and the mean air temperature was -0.8 ° C. Human density in the area is 4.9 people per km² (Statistics Sweden 2017). Road density is 0.5 (roads/km²). There are 0.2 ± 0.01 moose per 1000 ha and 0.032 moose are shot in 1000 ha. Bear density is low (0.002 bears/1000 ha) and wolves are absent (Singh et al., 2012).

2.2 Moose

We captured 12 free-ranging adult female moose in February 2017 from a helicopter. Moose were immobilized using a dart gun and combination of an anesthetic and a tranquilizer; 50 mg xylazine (Rompun® Dry Substance, Bayer AG, Leverkusen, Germany) and 4.5 mg etorphine (Etorphine HCl® 9.8 mg/mL, Vericore Veterinary Products, Novartis Animal Health UK Ltd., Litlington, UK). We confirmed if the moose was accompanied by a calf during the captures.

The Ethical Committee on Animal Experiments (Uppsala, Sweden) approved the experiments.

2.3 GPS devices

The moose were equipped with radio collars which included a global positioning system (GPS) receiver, very high frequency (VHF) transmitters, and a Global System for Mobile communication (GSM) modem (Vectronic-aerospace, Berlin, Germany). The collars were scheduled to record a GPS position every 30 minutes as a default. Individuals selected for the approaches were scheduled to record the position every minute for three-hour period on approach days (from now on *approach period*). The GPS collars were not able to send the position as text message when the *approach period* was on. Thus, an hour before the *approach period* started the collars were scheduled to send the position every 5 min. My own ski tracks

were recorded by hand hold GPS (Garmin GPSMAP 64, Garmin Ltd, USA). GPS recorded the position every 10 meter, so approximately every 20 second.

2.4 Approaches and data collection

I approached the 12 female moose by cross country skiing from 23rd of February until 12th of March 2017. The approaches were conducted during different times of the day; in the morning (8:00–9:00), midday (11:00-12:00/12:00-13:00) and afternoon (13:00-14:00/14:00-15:00). Approaches included two parts; first an initial approaching and then I followed the moose tracks in the snow for approx. 30 min. The duration of the whole approach was approximately one hour. I recorded the time when I started approaching (*Start app*), when I arrived to the last known position (*At pos*), when I started tracking (*Start track*) and when I stopped (*Stop*). Each moose was approached 3 to 5 times.

Initial approaching

I received the moose last known GPS position and skied there as directly as possible. The aim was to be at the position when the *approach period's* second hour started (for example in the morning at 8:00, when the approach period was between 7.00-10:00). The collars were not able to send moose current position when the *approach period* was on, so the last known position I got was an hour old.

At the position, I stopped to record air temperature, wind strength, wind direction and whether it changed, precipitation type and intensity, visibility, habitat type, snow type, snow depth and moose sinking depth. I recorded temperature by thermometer and the wind strength by using categories weak, medium or hard. I estimated whether there was precipitation and the intensity of it (weak, medium or hard). Habitat type was classified as clear cut, young forest or old forest. I estimated whether snow was soft, mixed or hard. Soft snow was new powder snow. Mixed type snow was old and it sank. Hard snow had a supporting, hard top layer. I measured the depth of the snow, as well as moose sinking depth by using a measure stick. I took the measurements from five different moose sinking spots of the same track and the snow depth next to those. To measure visibility, I used cover cylinder which is 60 cm high, 30 cm in diameter and it has two sections; red upper part and white lower part (Ordiz et al., 2009). I placed the cover cylinder into moose last know position and by using compass and laser

measurement, I went to 10 m distance to each cardinal direction and recorded how many percent of the red and white part of the cylinder is visible.

Tracking

After initial approaching, I tracked the moose. I used handheld Very High Frequency (VHF) device and visual investigation of moose tracks. The duration of tracking was approximately 30 min.

2.5 Data analyses

For all the analysis I used the program R Studio 3.5.1 (R Development Team 2018). I explored the data using R packages *AdehabitatLT* (Calenge, 2006) and *ggplot2* (Wickham, 2016). I used residual plot from basic R and from the Dharma package to evaluate the normality and homogeneity of variance. Autocorrelation was checked by using the autoregressive function ACF (Hartig, 2019). The final models were selected according to the Akaike Information Criterion (AIC). Whether more than one model had $\Delta AIC < 2$, I selected the simplest one according to the principle of parsimony. I applied AICc (from *MuMin*), because the sample size was small (Symonds & Moussalli, 2011).

2.5.1 GPS data

From the moose GPS data, I extracted the positions that were in 1-min interval. I used *AdehabitatLT* to calculate the Euclidean distance between each consecutive position in 1-min interval. Thus, I got the cumulative distance moved by the moose. To receive regular data, I imputed the missing positions (2.51 %) by using *na.approx* function from R package *zoo* (Zeileis, 2005). I standardized the data by calculating the mean time between *Start app* and *At pos* (20 min) and set the data to start from that moment. If the interval was <20 min, I kept the initial start time. End of the data was the last position of 1-min interval data.

I converted my GPS positions to the same time interval as moose positions (1 min). The initial interval of my GPS positions was approximately 20 s; thus, I selected the ones that were closest to moose positions. I rounded the selected positions to the closest minute.

2.5.2 Habituation

To study if the moose showed signs of habituation, I calculated how many times each moose was disturbed. I call it as repetitions.

2.5.3 Changepoint analysis of moose flight response

I used changepoint analysis to detect automatically disturbance events based on movement alterations. The aim was also to identify the moment when the moose started to respond for the initial approaching and the moment when it settled down (Phase 1). Further, I wanted to find the moment when moose started to respond for the tracking and the moment when it settled down (Phase 2). Thus, I applied changepoint analysis to the moose' cumulative distance moved to investigate if statistical change would occur in data points (Killick, 2011). I used *changepoint* package from R (IA, 2016) with a pruned exact linear time (PELT) algorithm in mean and variance. I tried different data transformations to achieve normal distribution, but the data fitted best with gamma distribution. For the penalty function I chose AIC. Each approach was studied separately.

To identify the start of the Phase 1, I selected the first changepoint that occurred after *Start app*, if moose average speed exceeded 20 m/min. The end moment for the Phase 1 was identified as the next changepoint after *At pos*, if the mean distance between two further consecutive changepoints was < 20 meter and moose stayed there ≥ 2 min. Otherwise the subsequent changepoint was considered. To identify the start moment of the Phase 2, I used the first changepoint after *Start track*. The end moment of Phase 2 was identified as the next changepoint after *Stop*, if the distance between two further consecutive changepoints was < 20 meter and moose stayed there ≥ 2 min.

2.5.4 Flight initiation distance

The flight initiation distance (from now on FID) is the distance between me and the moose at the moment when the moose started to flush (Ydenberg & Dill, 1986). I use it to measure how responsive the moose was for the disturbance.

I calculated the distance between me and the moose in each minute using Euclidean formula. Since my GPS data had missing fixes (15.7 %), the distance between us had to be imputed

using R package *imputeTS* (Moritz, 2017). I used only approaches when the moose was determined to be disturbed during initial approaching.

I applied generalized linear mixed model with gamma distribution, because the response variable was in continuous scale and the distribution was positively skewed. Moose ID was used as random factor to avoid pseudoreplication. However, the model did not converge due to small sample size. Linear mixed model had the same problem. Finally, I applied Generalized linear model with gamma distribution using log-link function. I used the time of day, repetitions, presence of calves, snow type, moose sinking depth (scaled) and wind direction as predictors to see if they influence to the FID.

2.5.5 Movement index

I extracted positions from the moose GPS data by the start and end time of both phases. I applied *Adehabitat LT* to calculate the Euclidean distance between two consecutive positions during phase 1 and phase 2. Thus, I got the total cumulative distance moved during both phases. This was done separately for each approach. I used only approaches where the moose was identified as disturbed during both phases.

Movement index was used to compare the intensity of flight response between two phases and as well to investigate which factors affected to moose flight response. This index was calculated as area under the curve (AUC) from distance moved during phase 1 and phase 2. The bigger the curve, the stronger the moose response. Since the length of the phases varied, I divided the AUC value by the duration of the phase.

I applied a linear mixed model (Bates, 2015) with AUC value as response variable. Moose ID was used as random effect to take account the variance among individuals. I used snow type, repetitions, flight initiation distance (scaled), phase and the presence of calves as predictors.

2.5.6 Sinuosity ratio

I used sinuosity ratio to study the linearity of the moose flush response. I calculated the ratio by dividing the displacement of the moose by the cumulative distance moved. Displacement is the distance between the first and the last positions while distance moved is the sum of distances between each consequent position. *AdehabitatLT* was applied to get the cumulative distance moved and the displacement of the moose data during phase 1 and 2. I analysed

separately each approach. I used only approaches where moose was determined as disturbed during both phases. Ratio close to 0 indicates sinuous movement whereas ratio close to 1 indicates more linear movement (Ericsson, Neumann, & Dettki, 2015).

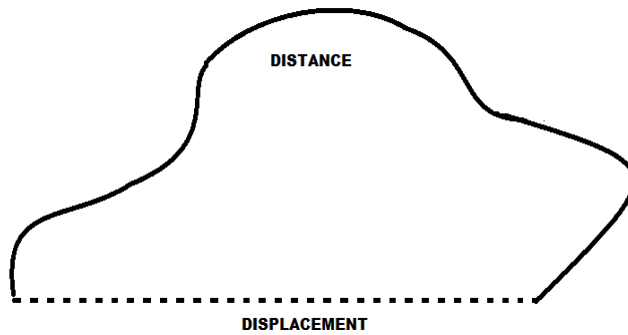


Figure 1. The illustration of the displacement and distance moved.

I built a linear mixed model and used moose ID as a random effect. Presence of calves, snow type, phase, time of day and FID (scaled) were used as predictors.

3. Results

I conducted in total 45 approaches where I disturbed the moose by off-track skiing. I omitted 11 approaches when the GPS collars failed to record the position in 1 min interval. One GPS collar never sent the position every 1 min, so I had 11 moose left for further analysis.

3.1 Changepoint analysis

I used changepoint analysis to investigate if moose responded for the disturbance in 34 approaches. The goal was also to determine start and stop moments for the two phases. I could determine the moments 28 times during the Phase 1 and 17 times during the Phase 2 (Fig. 2A). I did not consider moose as disturbed during Phase 1, if moose has been before and was not close to the last known position anymore ($n = 4$) or if the moose average speed did not exceed 20 m/min ($n = 1$, Fig. 2B). I did not consider approaches where it was not possible to distinguish the end of Phase 1 and start of Phase 2 ($n = 1$). The distance between me and the moose with speed < 20 m/min was at shortest approx. 150 m and stayed around 200 m until I started tracking. Thus, the moose did not flee. At once, moose continued active while the *approach period* ended (Fig. 2C). Thus, I used the last minute of *approach period* as end of the Phase 2.

I did not consider moose as disturbed during Phase 2, if moose average speed did not exceed 20 m/min ($n = 3$), if it did but the distance between us was > 400 m during whole tracking period ($n = 2$) or the tracking did not work ($n = 2$). Sometimes it was not possible to determine the start for the second phase, because the moose continued moving after the stop moment of Phase 1. ($n = 4$). To avoid the influence of tracking during the Phase 1, I decided to use the earliest possible decreasing changepoint if the distance between me and the moose was decreasing (Fig. 2D). If the distance between us was increasing, I used the changepoint when moose average speed was < 20 m/min.

The mean duration of the Phase 1 was 10 minutes ($n = 28$, range 2 – 57, SD = 12.15) and the mean duration of Phase 2 was 31 minutes ($n = 17$, range = 9 – 70, SD = 17.06).

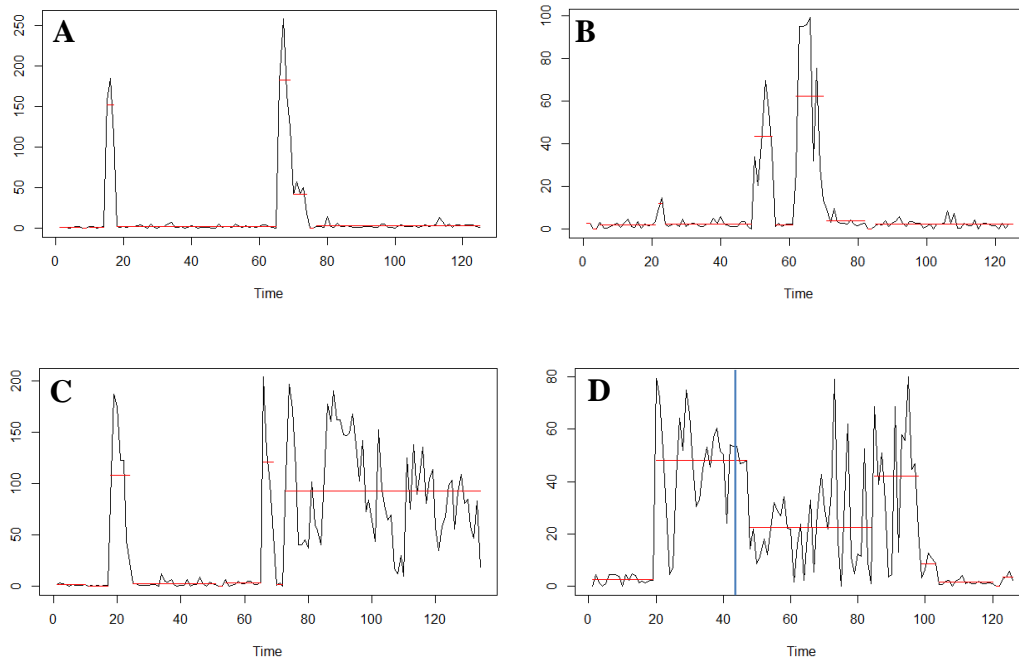


Figure 2. Examples of the result of the changepoint analysis. x-axis: time, y-axis: moose movement between two consecutive positions (m/min). A) Clear example of start and stop moments for both phases. B) Moose average speed did not exceed 20 m/min, so the approaches was omitted from further analysis. C) Moose stayed active after while the approach period ended. D) In this situation it was not possible to determine start moment for the phase 2. Vertical blue line presents the time when I started tracking.

3.2 Flight initiation distance

I analysed 28 FIDs of 11 different individual moose. Mean FID was 125.89 m (range = 55.28 – 240.56, SD = 53.64). FID varied among individuals, which can be seen in Fig. 3, but due to small sample size I could not use moose ID as random effect.

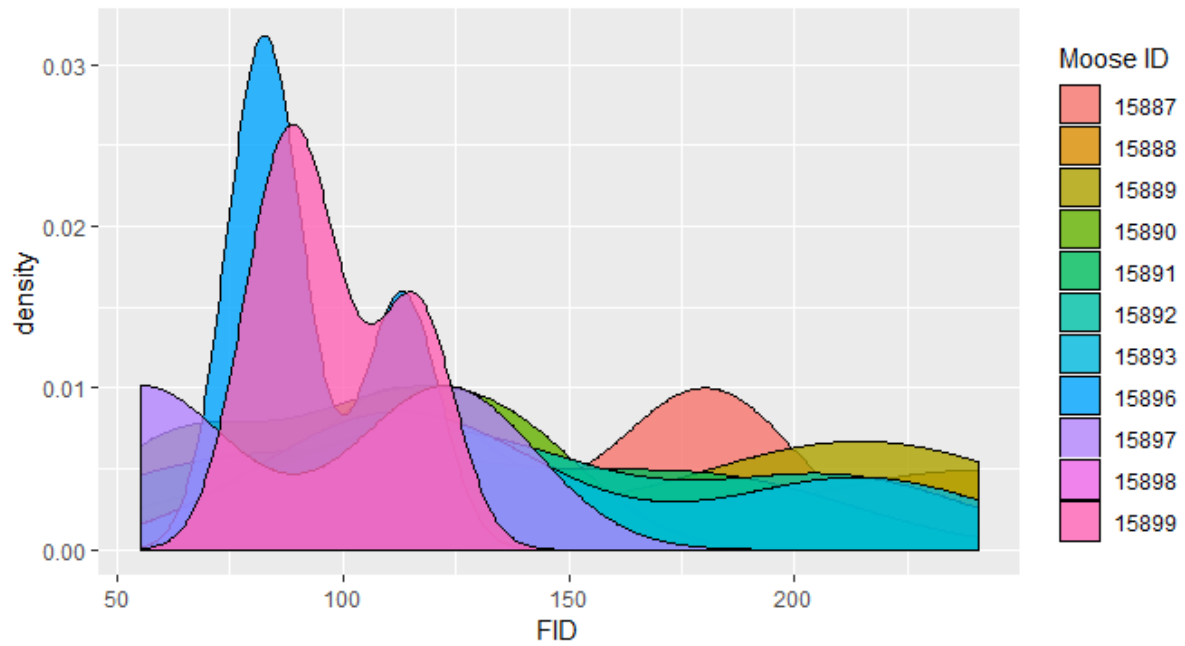


Figure 3. Density plot shows that FID varied among individuals.

I used GLM to examine if the presence of calves, time of day, snow depth and type, repetitions and wind direction can explain the length of FID. Due to the small sample size, I could not include all the predictors in the same model. Snow type and snow depth were not together in the same model because of the collinearity. The model with Calves as a predictor had the lowest AICc value (Table 1.). However, the most parsimonious model was the model with only an intercept, since it also had $\Delta AIC < 2$. Therefore, none of the predictors could explain the variation in FID.

Table 1. AICc table of the FID model.

Model	LogLik	AICc	delta AIC	df	weight
Calves	-146.46	299.92	0	3	0.33
Intercept	-148.09	300.65	0.73	2	0.23
Calves + Sinking depth	-146.30	302.35	2.43	4	0.10
Sinking depth	-148.01	303.02	3.10	3	0.07
Calves + Time of day	-145.52	303.78	3.86	5	0.05
Time of day	-147.23	304.19	4.27	4	0.04

3.3 Movement index

Movement index of 10 individual moose was used to evaluate factors that affected moose flight responses and to compare the response between the two phases. The mean movement index during the first phase was 56.71 (range = 13.82 – 107.31, SD = 32.90) and during the second phase 56.24 (range = 23.39 – 93.64, SD = 19.57). The model with the lowest AICc includes the presence of the calves, time of day and snow type (Table 3). I used repetitions as categorical variable and it had five levels, so due to small sample size I had to leave it from the complex models.

Table 2. AICc table of the movement index analysis.

Model	LogLik	AICc	Delta AIC	Df	weight
Moose ID + Calves + Time of day + Snow type	-127.71	277.18	0	8	0.70
Moose ID + Time of day + Snow type + Phase	-129.62	281.00	3.82	8	0.10
Moose I2D + Time of day + Snowtype + FID	-129.70	281.15	4.00	8	0.10
Moose ID + Time of day + Snowtype	-132.14	282.59	5.41	7	0.05
Moose ID + Calves + Time of day + Phase	-132.91	284.12	6.94	7	0.02
Moose ID + Calves + Time of day + FID	-133.03	284.36	7.18	7	0.020

Moose movement index was higher in the midday and when snow type was mixed. Soft snow had negative effect to the movement index. Whereas, presence of the calf had a positive effect (Figure 4). FID and phases did not explain the variation in FID. The estimates had relatively long confidence intervals indicating of uncertainty.

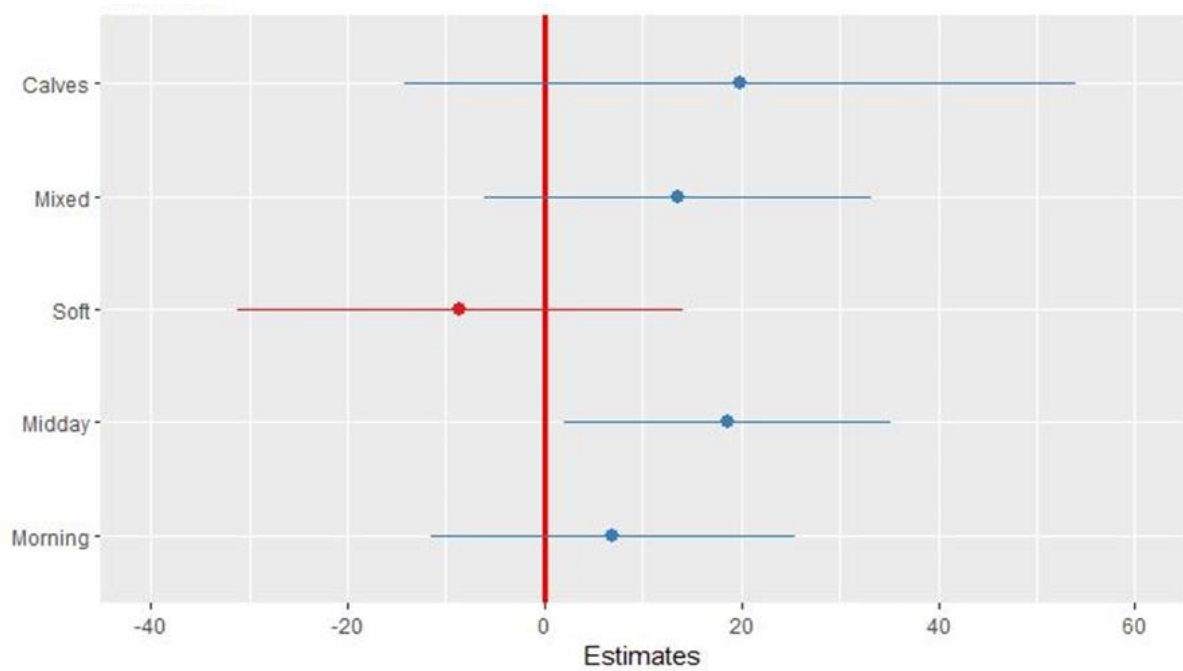


Figure 4. The parameter estimates of the Movement index analysis. Moose movement was more intense when the moose was accompanied by a calf. Mixed snow type and midday also caused higher movement index value.

3.4 Sinuosity ratio

I used Linear mixed model to study the sinuosity of the moose flush response. The sinuosity ratio varied among moose individuals. Mean sinuosity ratio in overall was 0.73. The model with the lowest AICc included phase variable. Moose movement was more sinuous during the second phase (Table 3). Time of day was not in the final models because it caused overfitting.

Table 3. AICc table of the movement index analysis.

Model	LogLik	AICc	delta AIC	df	weight
Moose ID + Phase	11.69	-14.01	0	4	0.62
Moose ID + Phase + FID	11.95	-11.75	2.26	5	0.20
Moose ID + Intercept	8.83	-10.85	3.15	3	0.13
Moose ID + FID	8.47	-7.56	6.45	4	0.02
Moose ID + Calves	7.84	-6.29	7.71	4	0.01
Moose ID + Calves + Phase + FID	10.18	-5.25	8.76	6	0.01

The mean sinuosity ratio was 0.82 during the first phase and 0.61 during the second phase (Table 4).

Table 4. The parameter estimates of the top model in sinuosity ratio analysis

Predictor	Estimate	Lower CI	Upper CI
Intercept	0.82	0.75	0.89
Phase 2	-0.18	-0.28	-0.07

3.5 Habituation

FID did not decrease in the group level (Fig. 5), but the two individuals had lower FIDs over time. The frequency of individual represented in the analysis varied; 7 individuals three times, 3 individuals twice and 1 individual once. The repetition level 1 was represent 7 times, level 2 eight times, level 3 eight times, level 4 four times and level 5 once (Fig. 6).

(Fig. 6). Movement index did not decrease in the group level (Fig. 7). In the individual level there was some decline in the movement index. The frequency of individual represented in the analysis varied; three individuals had 4 movement index values and 7 had four movement index values. The repetition level 1 was represent four times, level 2 once, level 3 seven times, level 4 four times and level 5 once (Fig. 8).

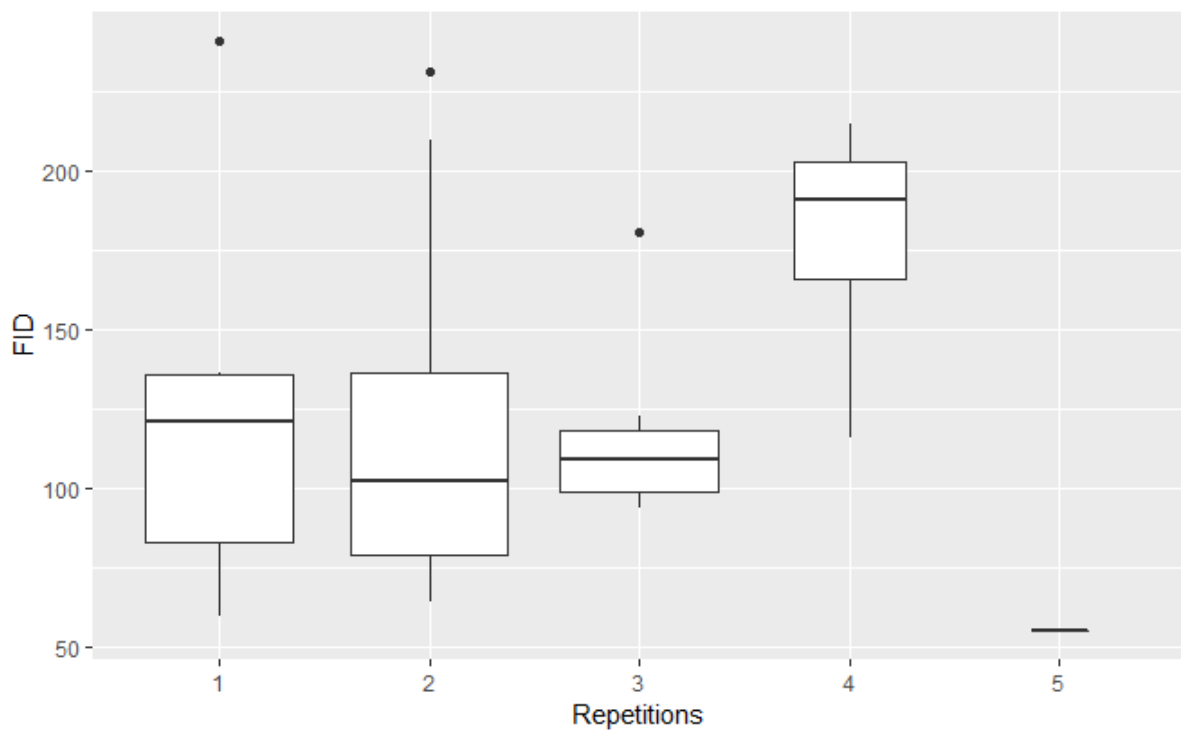


Figure 5. The mean FID over time in the group level.

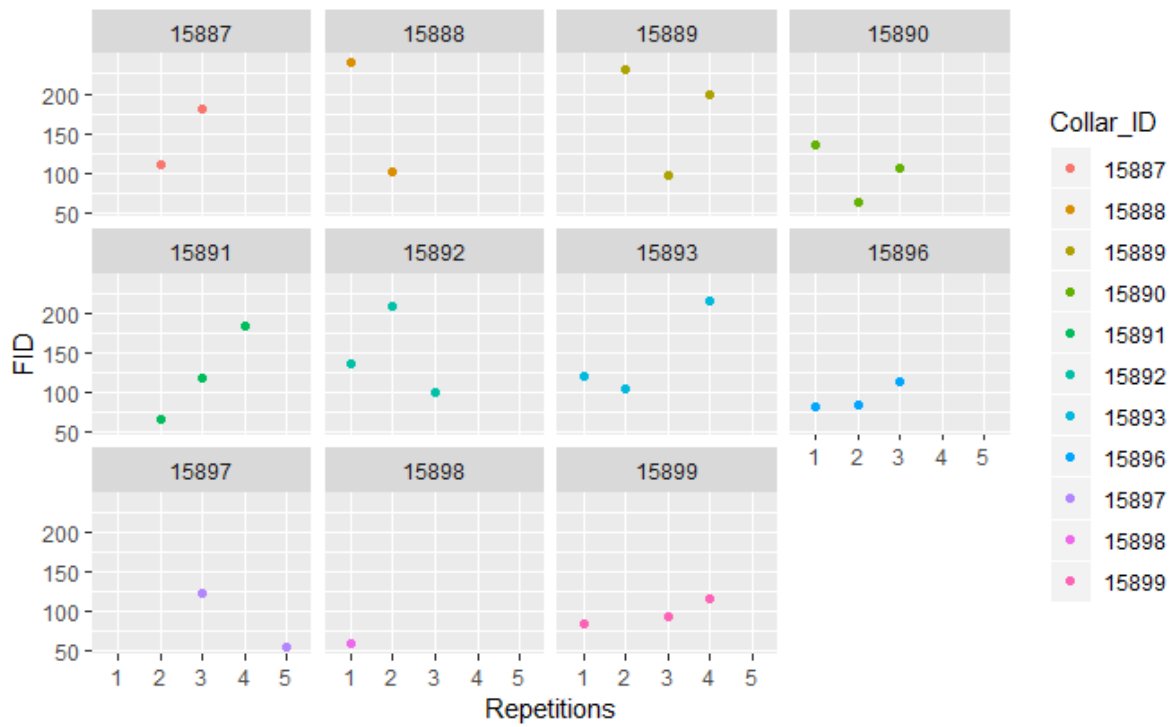


Figure 6. The flight initiation distance of each individual moose during different disturbance events (repetitions).

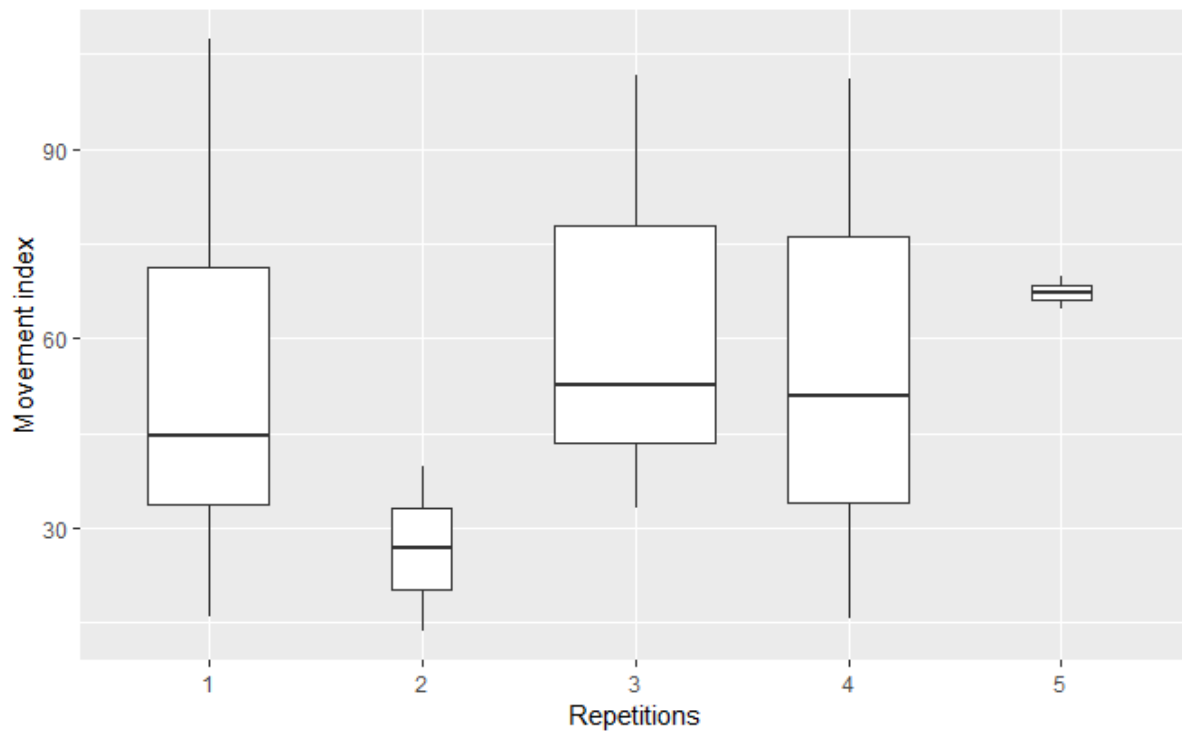


Figure 7. The mean movement index value over time in the group level.

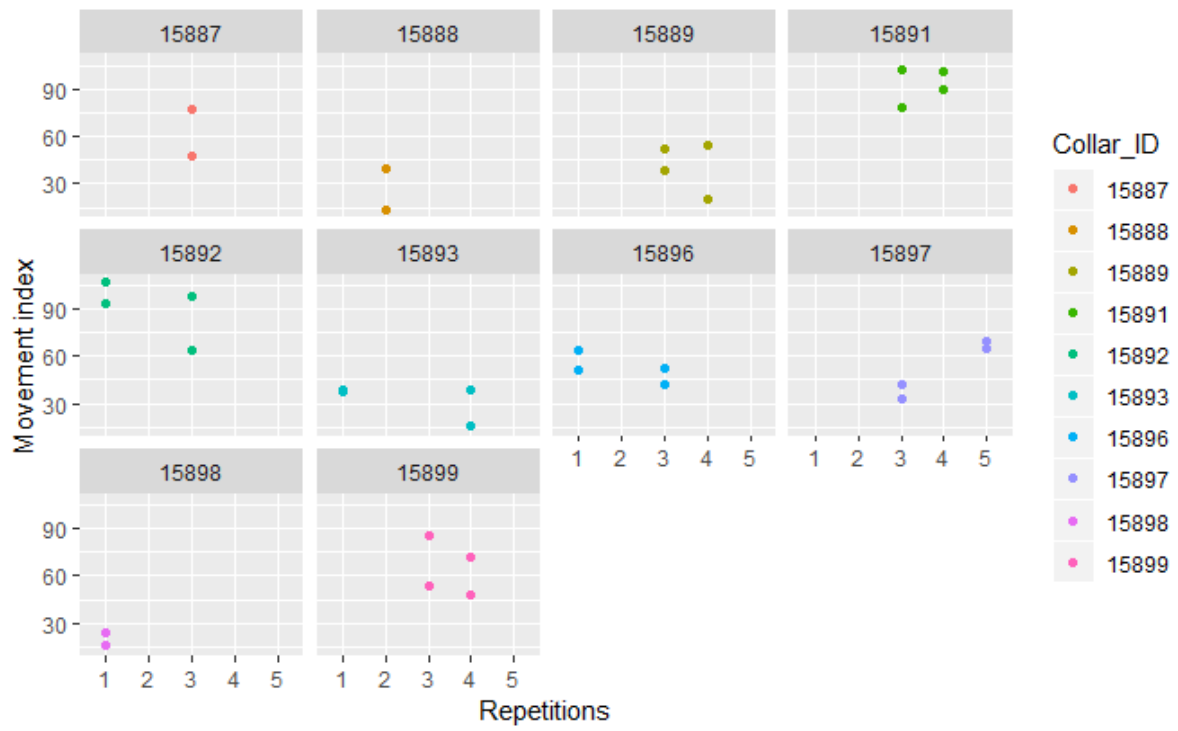


Figure 8. The movement index value of each individual moose during different disturbance events (repetitions).

4. Discussion

I studied the behavioural response of 11 female moose which were disturbed by off-track skiing in Sweden. Experimental study of moose movement data suggested that moose response for human disturbance in winter might be influenced by presence of calves, snow type, time of day and duration of the disturbance. Moose did not show signs of habituation for repeated disturbance trials.

4.1 Flight initiation distance

Due to small sample size, none of the predictors explained the variance in FID. Since I could not use moose ID as random effect, individual variance may have caused noise to the model. FID analysis might miss some important variables, like visibility. Animals are more vigilant when they have less protecting cover around them (Liley & Creel, 2008) and thus flight initiation distance can be longer (Moen, Støen, Sahlén, & Swenson, 2012). Instead, animals that are hidden well by the surrounding landscape may spend more time on considering whether to stay or flee (Ydenberg & Dill, 1986). My initial plan was to use visibility as explanatory variable, but the position where I measured it and the position where moose flushed were too far apart from each other. Due to variability of the landscape, the visibility would not have been comparable between those two positions.

4.2 Movement index

4.2.1 Presence of calves

Female ungulates accompanied by calves are more vigilant comparing to females without calves (Childress & Lung, 2003; Pernille & Eric, 1997). The results support this since higher movement index of moose was explained by the presence of calves. This was in line with my prediction and with previous findings (Hansen & Aanes, 2015). Though, Fritz (2008) found that female moose with calves moved faster only during hunting season. The moose hunt in the study area ended only a month before I conducted the disturbance trials, so I assume that the moose may have been sensitized to disturbance from hunters.

Female moose accompanied by a calf prefer habitat which offers protection against predators (Dussault et al., 2005; White & Berger, 2001). Thus, they might be more selective when

choosing rest sites. Another moose mothers' antipredator strategy is to spend less time foraging and more time scanning the environment (Childress & Lung, 2003; White & Berger, 2001).

4.2.2 Time of day

Time of predation can be unpredictable (Lima & Dill, 1990), but human activities occur mainly at daytime. Hence, all approaches in this study were conducted during daytime hours, but 'morning' and 'afternoon' were close to crepuscular hours, when moose in general are more active (Cederlund, 1989). The moose fled faster during midday which corresponds to my prediction that moose is more vigilant during middle of the day. In contrast, previous studies have found ungulates to be more responsive during morning (Naylor et al., 2009; Taylor & Knight, 2003). I found that moose was more responsive during the morning than the afternoon.

4.2.3 Snow

Moose movement ratio was higher when the snow was categorized as mixed. In such situations the snow was dense but not supporting. For me it was hard to ski in that snow type, but it may not have influence to moose. The model estimates were uncertain due to small sample size, so the direction of each snow types' effect can be different or snow might not have any effect on moose speed. This might be the case since moose is morphologically well adapted to move in snow (Telfer & Kelsall, 1984) and the snowfall was minor during the study period.

The moose sinking depth may have provided more accurate information on how the moose fled in different snow conditions. I measured snow depth and moose sinking depth only from the moose last known position. Therefore, I could not use those measurements to evaluate how they affected the moose movement when it was fleeing later. Sometimes habitat type changed during tracking, so snow depth could have changed as well. Snow depth is often deeper in the open areas (Winkler, Spittlehouse, & Golding, 2005). Thus, the measurement of snow depth in the dense forest would not correspond with snow depth in a bog. Since snow quality and air temperature have found to be highly correlated (C. Lundmark & J. P. Ball, 2008), I assumed snow type to be more dependent on ambient temperature and therefore vary less among different habitat types. Anyhow, snow measurements are complex. Same snow type can in other situations save moose energy whereas in other situations it reduces it (C. Lundmark & J. Ball, 2008)

4.3 Type of disturbance

The movement index did not differ between initial approaching and tracking. This was in contrary to my prediction that moose would be more responsive during tracking. I assumed moose to experience tracking more threatening and thus flight faster and further (Coss & Stankowich, 2006). Disturbance during initial approaching was unpredictable which might explain moose strong responsiveness (Harris, Nielson, Rinaldi, & Lohuis, 2014; Stankowich, 2008). Duration of the moose response for tracking was longer than the duration of the moose response for initial disturbance, which can explain that moose were not able to keep high speed during tracking.

As I predict, moose movement was more sinuous during tracking. Sinuous flee response is a strategy to escape from a predator (Coss & Stankowich, 2006). Tracking phase lasted longer, so moose had more time to change the direction. Also, habitat type might have an effect on turning movement. In the dense forest the moose likely turn more often than in open habitat. When the flight is sinuous, moose use more energy (Coss & Stankowich, 2006). The distance between me and the moose and my speed may have influenced to both intensity of flight and sinuosity. Animals often adjust their speed to predators' speed (Stankowich, 2008; Ydenberg & Dill, 1986).

4.4 Habituation

The moose did not in general show signs of behavioural habituation for the repeated disturbance; neither FID or speed decreased over time. That is in line with the findings from the previous study of the moose in northern Sweden (Neumann et al., 2010). Since moose in Sweden are killed mainly by humans and hunting is intensive (Ball, Ericsson, & Wallin, 1999; Sand et al., 2006), I assume that the moose vigilant behaviour towards humans will not change after repeated approaches. Even if an animal would show decreased responses, it might not be a sign of habituation. Sometimes they do not have alternative habitat where to go (Gill, Norris, & Sutherland, 2001) or they estimate the costs of fleeing higher than the costs of staying (Ydenberg & Dill, 1986).

I did not find signs of habituation when I observed the data at the group level. Though, some individuals had decreased FIDs and movement ratios over time. Habituation can vary among individuals, since animals' response to human disturbance is affected by their previous

experiences and age (Ciuti et al., 2012). Regardless, the period of this study was relatively short for investigating changes in moose behaviour. Also, the frequency of disturbance events was small. Repetition levels did not have equal amount of data; some individuals were represented for example only once in the analysis. To better understand habituation, it would be good to repeat the disturbance trials more frequently and over longer period, like has done for reindeer in Svalbard (Hansen & Aanes, 2015).

4.5 Study methods

Detecting the right changepoints from the moose movement data was challenging. There was sometimes for example several possible changepoints I could have chosen. AIC tend to overestimates the number of parameters (Killick, 2011), but I used it since it fitted visually the best to data. I applied also MBIC penalty function, but it seems to in contrast underestimate the data.

I made a mistake with the settings in GPS that recorded my positions. It would have been better to have the positions in same time interval as moose positions.

Increasing the size of the data set would have avoided problems in data analysis. Versatile habitat data would allow us to take into account aspects that can affect the moose antipredator behaviour. To get habitat data from the tracking period, it could be possible to use a video camera to film surrounding habitat. After disturbing the animal, I would recommend to use data to find the position where the animal flushed and go afterwards to measure visibility. It could be interesting also to estimate if moose are accompanied by other adults, since grouping is one of moose antipredator strategies (Baskin, Ball, & Danell, 2004).

4.6 Conclusion

Moose might be more responsive for the human disturbance when they are accompanied by a calf. Moose flight response was more intensive in the midday and when the approacher sank through the snow. Human disturbance may have negative consequences during winter when there is less food available. Antipredator behaviour is always costly, but it can have more severe impact for mothers, since they have to ensure the survival of their offspring.

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