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Behavioral responses of moose (*Alces alces*)
to close proximity of wolves (*Canis lupus*) in Scandinavia

par

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English abstract

Predation has been recognized as a crucial selection pressure on prey species. It often leads to the development of anti-predator behaviors which increase the probability of successfully escaping predation. The loss of large predators in landscapes all around the world has caused many prey species to stop investing in those costly behaviors. With the recent return of large predators, whether by reintroduction or re-establishment, it has become increasingly interesting to test if and to what extent prey species still exhibit some anti-predator behaviors. This study investigated whether Scandinavian moose (*Alces alces*), previously known as a "naïve" population despite the return of the wolves, exhibited any anti-predator behaviors after close proximity with gray wolves (*Canis lupus*). We studied the movement behavior of 17 moose and 7 wolves with GPS-collars over three years in Scandinavia and used linear mixed models to identify factors associated with a change in behavioral pattern before, during or after close proximity. We used rate of movement (speed) and home range sizes as our response variables. We hypothesized that (i) moose would move faster during and after close proximity than before and (ii) that they would have larger home ranges after close proximity. Results confirmed that moose traveled faster during a close proximity event, especially if the event occurred at a closer range and during daylight. Contrary to our second hypothesis, moose home ranges were larger before a close proximity event and when the event occurred at a greater distance. Our results suggest that Scandinavian moose have developed some anti-predator behaviors against wolves and further studies will provide us with more details on the potential factors contributing to the slow re-adaptation to this predator.

Key words: anti-predator behavior, behavioral pattern, prey-predator relationship

French abstract

La prédation est reconnue comme une pression de sélection cruciale sur les proies, et peut les conduire à développer des comportements anti-prédateurs afin d'augmenter la probabilité de survie d'un individu. Le déclin des prédateurs dans le monde entier a incité de nombreuses espèces de proies à cesser d'investir dans ces comportements coûteux en énergie. Avec le récent retour des grands prédateurs, il sera intéressant d'étudier dans quelles mesures les espèces de proies présentent encore un comportement anti-prédateur. Cette étude explore si l'élan scandinave (*Alces alces*), auparavant connu comme une population "naïve" malgré le retour des loups, présente des comportements anti-prédateurs après des rencontres potentielles avec des loups gris (*Canis lupus*). Nous avons étudié le comportement de 17 élans et de 7 loups équipés de colliers GPS pendant trois ans en Scandinavie et avons utilisé des modèles mixtes linéaires pour identifier les facteurs associés à un changement de pattern de comportements avant ou après une rencontre potentielle. Nous avons étudié la vitesse de mouvement et la taille du domaine vital comme variables réponses. Nous avons émis l'hypothèse que (i) les élans se déplaceraient plus rapidement pendant et après une rencontre qu'avant et (ii) qu'ils auraient des domaines vitaux plus grands après une rencontre. Les résultats ont confirmé que les élans se déplacent plus rapidement lors d'une rencontre qu'avant ou après, surtout si la rencontre était à courte distance. Contrairement à notre deuxième hypothèse, les élans avaient un domaine vital plus grand avant une rencontre qu'après et lorsque la rencontre s'était produite à plus grande distance. Contrairement aux études passées, nos résultats suggèrent que l'élan scandinave a développé certains comportements anti-prédateurs.

Mots clés : comportement anti-prédateur, pattern de comportement, relation proie-prédateur.

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1. INTRODUCTION

Predation has been recognized as a crucial selection pressure on prey species and, as a consequence, leads them to develop counteractive anti-predator strategies in order to enhance the probability of successfully escaping predation (Harvey & Greenwood, 1978). Anti-predator strategies encompass all adaptations and strategies developed through evolution in which individuals invest energy to increase survival and lower predation pressure (Caro & Girling, 2005). Selection should, therefore, favor individuals that optimize the tradeoff between predation risk and the costs associated with anti-predator behavior (Lind & Cresswell, 2005).

Although large predators have been identified as being keystone species, crucial for the well-being, maintenance and sustainability of an ecosystem (Bond, 1994; Navarrete & Menge, 1996), different factors such as history, culture and legends have conditioned people worldwide to be aware, and often afraid, of them. Consequently, large predators have often been systematically culled and brought to the verge of extinction in many parts of the world. In the absence of natural predators, humans often become the main predator for a number of prey species (Ordiz et al. 2013). The absence of a natural predator can lead prey species to adapt their anti-predator behavior to humans, as preys tend to defend against their most commonly found predator (Åbjörnsson et al. 2004; Vermeij, 2012). Additionally, this can lead to a gradual decrease of the energy invested by prey species in anti-predator strategies, and the surplus energy can be invested in other activities, some of which may cause damage to habitats (Byers, 1997; Martin, 2014). However, recent years have witnessed the return of large predators to many parts of their historical ranges in Europe and North America (Chapron et al. 2014; Kujiper et al. 2016). The recent rise in predator populations worldwide has impacted herbivore population dynamics, either through direct (lethal) effects or indirect (non-lethal) effects, such the re-development of anti-predator strategies (Terborg & Estes, 2010). However, anti-predator strategies are often costly and can affect growth, survival and reproduction. As a result, a tradeoff exists between the costs and benefits of employing such strategies (Verdolin, 2006).

In Scandinavia, the wolf population was hunted to extinction in the 1960s to avoid attacks and damage on free-ranging livestock herds, as well as to preserve the moose population, which is a very important economic and cultural resource. In the 1980s and 1990s, a small number of wolves dispersed from the Russian-Finnish border and their descendants now comprise the Scandinavian

wolf population (Wabakken et al. 2001; *Norwegian Environment Agency*, 2017). Management strategies for wolves, especially in Norway, still strive to keep the population low to avoid conflicts with livestock and other activities related to wild ungulates (Skonhøft, 2006). Prey species populations, on the other hand, started to rapidly increase after the disappearance of wolves (Lavsund et al., 2003). Several generations of prey populations have existed with very little predation pressure from natural predators, and have been referred to as "naïve" by scientists (Sand et al. 2006). Prey naivety has been described as the "lack of predator recognition" or "lack of effective anti-predator defenses" (Kovalenko et al. 2010).

Over the past 20 years, several studies have observed Scandinavian moose population low or no visible adaptations in the Scandinavian moose population to the return of wolves (Nicholson et al. 2014; Sand et al. 2006; Wikenros et al. 2016). Sand et al. (2006) found no evidence of anti-predator behaviors in moose to the returning wolf population, compared to moose in North America that had been continuously exposed to wolf predation. Nicholson et al. (2014) showed no behavioral effect of wolves on moose in relation to habitat use. Furthermore, Wikenros et al. (2016) found no significant differences in travel speed, seasonal home range and linearity of movement before and after the establishment of wolves in the territory. More recently, van Beeck Calkoen et al. (2018) found that wolf space use in young forest plantations was not the main factor influencing moose browsing patterns in Sweden.

Interestingly, a 2015 study exposed Scandinavian moose to baying dogs and found that they were more active, left the area and had a larger 24h activity range after the disturbance, thus showing some anti-predator behaviors (Ericsson et al. 2015). Nonetheless, those moose were shown to relocate fairly nearby which was concluded to be because of a lack of alternative habitats to go to (with no potential predators, including humans) (Ericsson et al., 2015).

Several hypotheses have been suggested to explain this apparent lack of adaptation of moose to the re-established predator. Firstly, with the disappearance of the wolf from the Scandinavian landscape, humans and more particularly hunters became the main predator and, thus, predation risk on moose and other prey species (Zimmermann et al. 2019). The Scandinavian moose population has indeed been continuously exposed to high human hunting pressure, to control the increase in population but also to improve population structure (Lykke, 2005). Therefore, it simply may be more advantageous for moose to develop anti-predator behaviors that are specific to the

risk posed by hunters. Secondly, as wolves are still reestablishing themselves on the territory, especially along the Norwegian-Swedish border, wolf densities are very low compared to moose densities in the same area (Eriksen et al. 2009). This could lead to a lower probability of encountering a wolf, and therefore a lower predation risk, for any individual moose. Thirdly, because anti-predator strategies used against one predator can be maladaptive against another, this may result in a dilemma depending on which predator and which strategy the prey has selected (Chitwood et al. 2017). For example, moose in North America were found to have a higher probability of surviving an encounter with a wolf if they stood their ground (Mech et al., 2015). However, the same strategy is counter-intuitive when moose are hunted by humans, as it increases the probability of getting shot.

This present study aims to investigate the potential behavioral response of moose to close proximity with a wolf in Scandinavia. The objective is to explore whether moose have developed anti-predator strategies, such as increased rate of movement or differential use of space after being in close proximity to a wolf. We defined a close proximity event as any simultaneous GPS positions where a moose and a wolf were within 1500 m from each other on the same date and at the same time. Our hypotheses were that: (i) moose would increase their rate of movement after close proximity with a wolf, as observed in previous studies (Latombe et al. 2013); and (ii) moose would have larger daily home ranges after a close proximity event compared to before.

The purpose of this study is to increase our understanding of both prey-predator interactions and prey behavioral responses to the return of a large predator. Results can serve to better anticipate potential conflicts and improve management of those species across the Norwegian-Swedish border.

2. METHODS

2.1. Study area

We monitored moose and wolves from March 2018 to February 2020 in the south-central part of the Scandinavian peninsula (59° - 61° N, 11° - 16° E approximately 85 000 km², see Fig.1). The study area was mostly characterized by coniferous forest composed of Norway spruce (*Picea abies*), Scots pine (*Pinus silvestris*) and some deciduous species such as aspen (*Populus tremula*) and birch (*Betula pendula*, *B. pubescens*). Although dominated by forest management and comprising a very large network of roads present throughout the area, the human density in the study zone remains very low overall and concentrated in settlements. Average human density in

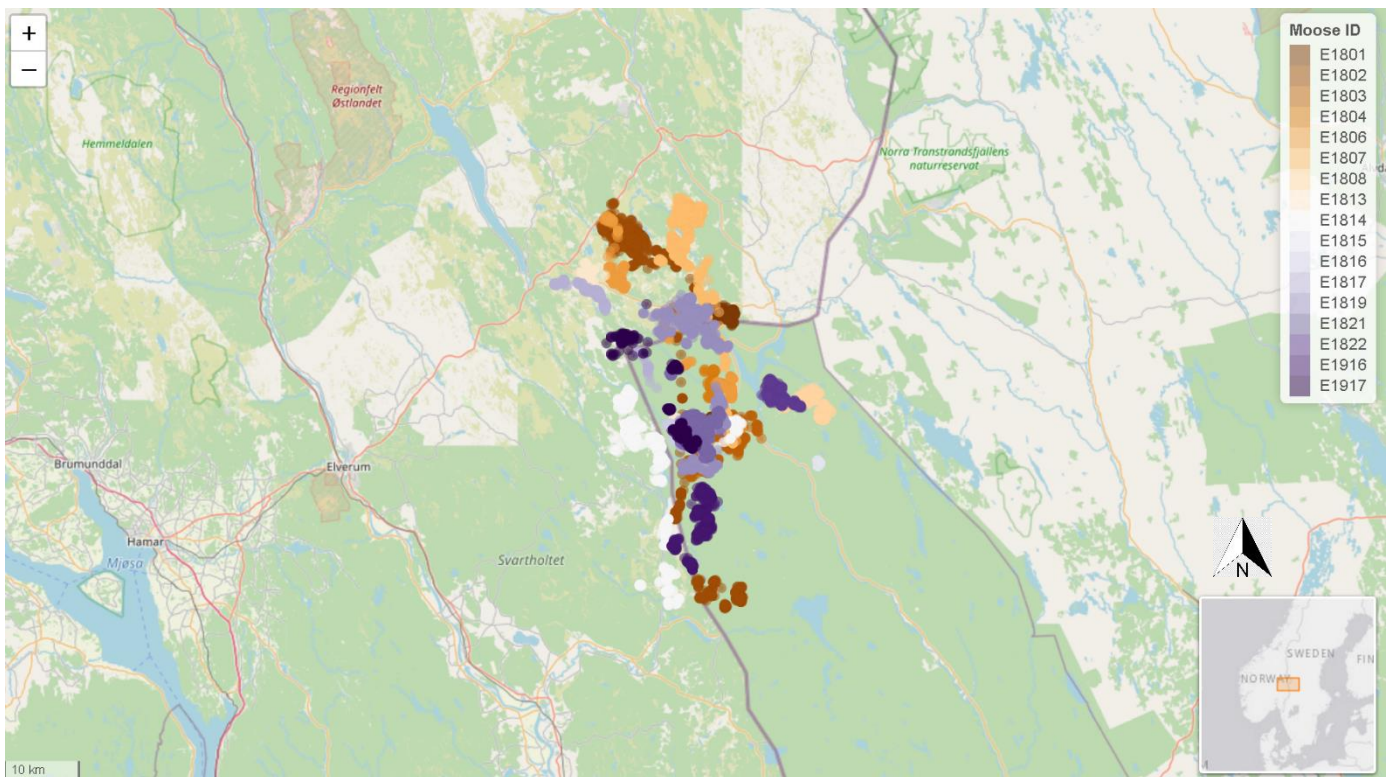


Fig.1. Study area in south-central Scandinavia (map in the lower right corner) where the movement of adult moose ($n=28$) were studied in relation to close proximity with wolves ($n=8$). Circles represent the actual GPS locations ($n=191\ 046$) of moose and the different colors represent the individuals.

south-central Scandinavia is 17 people per km², with large areas within the wolf population range having less than one person per km² (Carricondo-Sanchez et al. 2020; Wabakken et al., 2001; www.scb.se, Sweden; www.ssb.no, Norway). The study area included moose distributed throughout the zone and wolf pack territories that are along the Norwegian-Swedish border (three wolf packs: Varåa, Bograngen and Juvberget).

2.2. Study species ecology

2.2.1. Moose

Moose are the largest species in the deer family and are distributed throughout the boreal zone in Scandinavia and throughout the study area. They are selective herbivores and their diet varies seasonally. In summer, they feed on birch leaves and shrubs like raspberry (*Rubus ideaus*) and bilberry (*Vaccinium myrtillus*), and during spring and fall, they mostly browse on heather (*Calluna vulgaris*) (Wam & Hjeljord, 2010). During winter, they browse on both deciduous species and Scots pine, although the latter is quantitatively the most important food source for moose (Cederlund et al. 1989). The calving period is one of the most critical life stages for moose and moose cows typically give birth to calves in end of May and beginning of June (Tremblay et al. 2007). Main predators of moose in Scandinavia include humans, wolves and bears (*Ursus arctos*) (Jonzén et al. 2013).

2.2.2. Wolf

Wolves are the largest species in the *Canidae* family and in Scandinavia are mostly present in south-central Sweden, as well as along the south-eastern Norwegian border. Their diet is composed mainly of moose, but also roe deer (*Capreolus capreolus*), beaver (*Castor fiber*), badger (*Meles meles*) and other small rodents and birds species (Müller, 2006; Sand et al. 2006, 2008). Other competitive carnivores in the area include brown bear, lynx (*Lynx lynx*), wolverine (*Gulo gulo*) and red fox (*Vulpes Vulpes*).

2.3. Animal capture and handling

Adult wolves (the male and female of the reproductive pair, n = 8) were captured from 3 different packs (Varåa, Bograngen and Juvberget) between 2017 and 2020. Capture and handling of wolves were in accordance with the ethically-approved immobilization protocol for gray wolves in Scandinavia (Arnemo et al. 2004). Wolves were immobilized from a helicopter and darted with 500mg tiletamine-zolazepam using a remote drug delivery system. Animals not down within 15 minutes were re-darted with a full dose. Helicopter pursuit was to not exceed 30 minutes total per individual to avoid extreme stress and physiologic side effects (hyperthermia). Several samples were collected including hair, blood, temperature and measurements samples. Wolves were fitted with a GPS collar (GPS-Plus, VECTRONIC Aerospace GmbH, Berlin, Germany) that took positions at hourly or four-hourly intervals.

A total of 28 adult moose were captured and collared between 2018 and 2020. Capture and handling of moose were in accordance with the ethically-approved immobilization protocol for moose (Evans et al. 2012). Moose were immobilized from helicopter and darted with a mixture of 75mg xylazine, 3.37mg etorphine and 15.0 mg acepromazine. Samples such as hair, blood, and body measurements were collected, and individuals were fitted with collars. Collars (GPS Survey with Iridium link, VECTRONIC Aerospace GmbH, Berlin, Germany) took positions at hourly or two-hourly intervals.

2.4. Data analysis

All data analyses were done using the software R version 3.5.1 (*R Core Team*, 2018) and Microsoft Excel (*Microsoft Corporation*, 2020). All moose that were never closer than 1500m from a wolf, and wolves that were never within 1500m from a moose were removed from the study (n=11 moose and n=1 wolf). All days where field personnel approached moose cows to monitor reproduction and calf survival were removed from the dataset to avoid biases due to human disturbance (n=75 days). Date and time were given as GMT +1.

2.4.1 Close proximity events

Close proximity events were defined as simultaneous positions of a wolf and a moose within 1500m of each other. We then intersected the GPS fix time and coordinates of both species. We chose 1500 m as our close proximity threshold since previous studies showed that it is unlikely for wolves to be able to detect moose beyond that distance (Mech et al. 2015; Oates et al. 2019; Whittington et al. 2011) and to be able to have a continuous variable. We tested anti-predator behavioral response of moose by comparing movement rates and daily home range sizes of moose before and after close proximity with a wolf. Henceforth, we refer to those events as 'close proximity event'.

2.4.2. Moose – wolf interactions (distance, speed calculations)

GPS fix time and coordinates were intersected and for each match we determined the distance between the wolf and the moose using SWEREF99 coordinates. Each close proximity event within 1500m was given an individual ID. For each close proximity event, we included simultaneous positions 48h before and after an event, in order to properly analyze changes in behavioral patterns over a time interval. We compromised and chose the 48h time interval after analyzing which period of time allowed us to observe a significant change in behavior that was not too short (risk of not

seeing any behavioral change) or too long (risk of other events interfering with possible anti-predator behavior).

Several close proximity events had consecutive simultaneous positions within 1500m. We decided to test three different strategies to be able to select only one simultaneous position that best described what we defined as a close proximity event. First, we selected the first simultaneous position below 1500m within a close proximity event sequence ("first subset", containing n = 13 361 observations). Second, we selected the simultaneous position with the minimum distance between a moose and a wolf within a close proximity event sequence ("min subset", containing n = 13 666 observations). Third, we selected the first simultaneous position with a distance that had 50% drop from the previously recorded position within a close proximity event sequence ("drop subset", containing n = 13 491 observations). All three subsets were analyzed separately. Within each subset analysis we then compared models using AIC to determine the best fitted model (Table 1). Within each model, we separately tested both the continuous (48h interval before and after a proximity event) and categorical (before/after) variables representing time in relation to the close proximity event.

Distance in meters between two consecutive simultaneous positions was calculated as the square root of the difference between coordinates to the square (Pythagoras) :

$$Distance = \sqrt{(X_{Moose} - X_{Wolf})^2 + (Y_{Moose} - Y_{Wolf})^2},$$

where X and Y are the coordinates of moose and wolves in the metric coordinate system SWEREF 99. Speed between two consecutive simultaneous positions was calculated as the distance divided by the time between the consecutive simultaneous positions

(*speed = distance/time* in meters per hour).

2.4.3. Home range Minimum Convex Polygon (MCP 100%) analysis

All MCP were done using the *adehabitatHR* package (Calenge, 2006). MCP are calculated by constructing the smallest possible convex polygon around the coordinate locations. The 'encounter' position was not included in any of the two home ranges.

2.4.4. Modelling

We controlled for repeated measures and same origin of the data as there were multiple close proximity events for each moose. To test these different hypotheses, we fitted a linear mixed effect model (LMM) to reflect the relationship between speed and several other factors such as daylight, sex etc. We also fitted a generalized additive model (GAM) to account for the non-linearity of speed in response to time (before/after the close proximity event), and allow for a more flexible, better fitted overall model. Finally, we used an LMM to test different factors that could influence the size of daily home ranges.

2.4.4.1 *Linear Mixed Effects models (LMM)*

We used linear mixed effect models (LMM) to assess shifts in speed of moose in response to close proximity to a wolf. All LMM models were done using the *nlme* (Heisterkamp et al. 2017) and *lme4* (Bates et al. 2015) packages. Speed (log-transformed) and 48-hours home range sizes (log-transformed) were the response (or dependent) variables. Sex, distance between moose and wolf individuals at the time of the close proximity event, daylight state at the time and of the event and at each GPS position (independent of each other) and the time relative to the event were our predictor variables. To reduce pseudo replication and false positives, we identified each close proximity event and each individual moose as random factors. To select the most suitable subset of data based on the proximity definition (see above), we compared coefficient and significant estimates of all three full models. Models based on the subset made up by the closest distance between moose and wolf performed best, and we therefore continued model selection for only this subset. Results for the other models can be found in the appendix.

2.4.4.2. *Generalized Additive models (GAM)*

We used a generalized additive model to assess shifts in speed of moose in response to close proximity to a wolf and to account for the non-linearity of the response through time. We hypothesized that moose would travel significantly faster after a close proximity event but would return to a normal speed within 48h. Model diagnostics showed that the data followed a normal distribution. All GAM models were done using the *mgcv* package (Wood, 2011). A smoothing factor was applied to the "time to encounter" independent variable and the speed response variable was log-transformed.

2.5. Ethical note

All experiments complied with the ethical standards of animal manipulation as defined by the European Convention on the protection of animals used for scientific purposes and the Norwegian Animal Welfare Act (ethical permission nr 15170).

3. RESULTS

3.1. Moose – wolf interactions (distance, speed)

We detected 287 unique close proximity events among the 19 individual moose and the 7 wolves. Event distances varied between a minimum of 65.1 meters to a maximum of 1497 meters. Event speed varied between 0 km/h to 3.25 km/h.

3.2. Moose speed before, during and after close proximity to wolves

All subsets were tested and subsequently compared with the significance estimates of the coefficients of the predictor variables to select for the best fitted model.

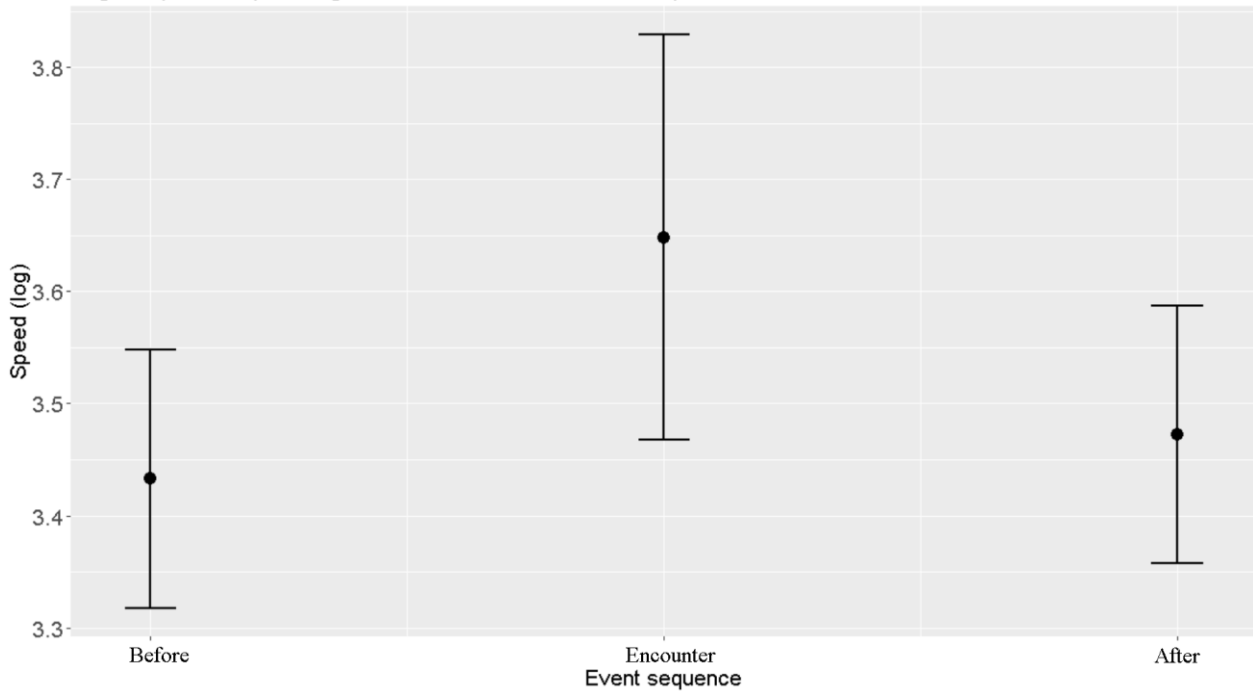
The most parsimonious model used to explain the observed variation in speed of moose between consecutive positions contained the timing in relation to the proximity event as categorical variable (before-during-after), the interaction of the distance between wolf and moose and the day light conditions during the event, and the daylight at the time of the speed measurement (Table 1, model "a2"). Moose moved on average 1.23 times faster during the proximity event than before the event but slowed down again after the event to similar levels as before (Appendix, Fig.5). The ratio of speed during/before or during/after did not change depending on the distance between moose and wolf or the state of daylight. In the end, sex was not retained in the best model as it did not relate significantly to the speed of moose.

Table 1. LMM models to assess the effect of sex (1=Male, 2=Female), distance between the moose and the wolf ("Distance btw moose wolf"), the daylight state at the moment of the close proximity event ("Is Daylight encounter") and the time of the position relative to the time of the event (that describes if the event happens before or after, "Time to encounter") on moose rate of movement (speed). The asterisks refer to an interaction analysis between the items that are before and after. The bold items represent the p-values that are significant. Models within subsets were evaluated based on Akaike's Information Criterion (AIC) value. Overall models were evaluated based on the significance estimate of coefficients of predictor variables.

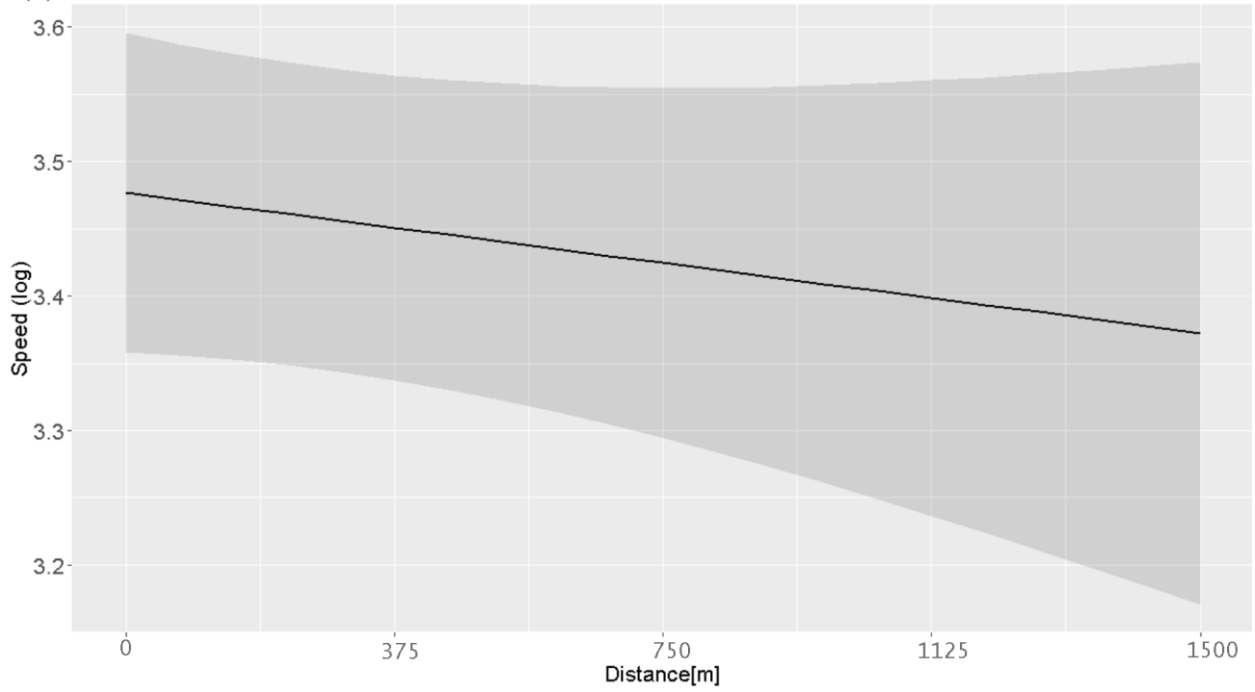
Subset	Model	n	Predictor variable	Estimate	SE	P	AIC
min	a1	13361	Sex[2]	-0.059393	0.13829070	0.6737	31799.64
			Distance btw moose wolf	-0.000001	0.00000265	0.5990	
			Is Daylight encounter	0.227807	0.05548824	0.0001	
			Time to encounter	-0.015531	0.01073302	0.1479	
	a2		Distance btw moose wolf	-0.000008	0.00000349	0.0188	31790.99
			Is Daylight encounter	0.113296	0.06525544	0.0838	
			Before_After (before)	-0.214812	0.07595057	0.1128	
			Before_after (encounter)	-0.175408	0.07541006	0.0200	
			Is Daylight	0.101400	0.02506768	0.0001	
	a3		Is Daylight encounter * Distance btw moose wolf	0.000014	0.00000504	0.0046	31800.28
			Sex[2]	-0.046934	0.13873861	0.7398	
			Distance btw moose wolf	-0.000008	0.00000350	0.0188	
Is Daylight encounter		0.112800	0.06530468	0.0854			
Before_After (before)		-0.039388	0.02484939	0.1130			
Before_after (encounter)		0.175356	0.07541061	0.0201			
Is Daylight		0.101270	0.02506881	0.0001			
Is Daylight encounter * Distance btw moose wolf	0.000014	0.00000504	0.0047				

Results of model "a2" (Table 1) show that moose were moving significantly faster during a close proximity event ($P = 0.0002$) than after but there were no significant differences in speed before and after the event ($P = 0.1128$, Fig.2 A). Moreover, distance at the time of close proximity resulted in significant differences in terms of speed before or after an event ($P = 0.0188$, Fig.2B). Moose were moving significantly faster if they were encountering the wolf at close distance. Furthermore, moose moved significantly faster during daytime ($P = 0.0001$, Fig.2C) than during nighttime. However, there was no significant difference in speed if the close proximity event happened during the day or at night ($P = 0.0838$, Fig.2D).

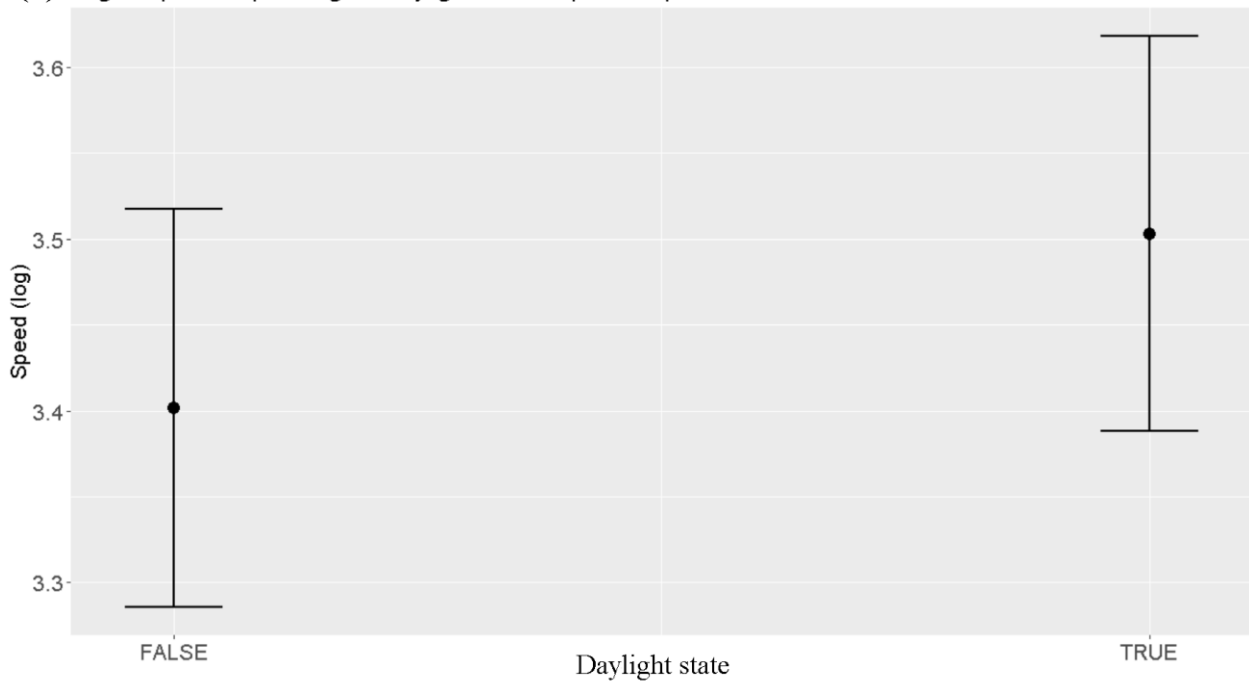
(A) Log of speed depending on before or after encounter predicted values



(B) Log of speed depending on the distance predicted values



(C) Log of speed depending on daylight at each position predicted values



(D) Log of speed depending on daylight at encounter predicted values

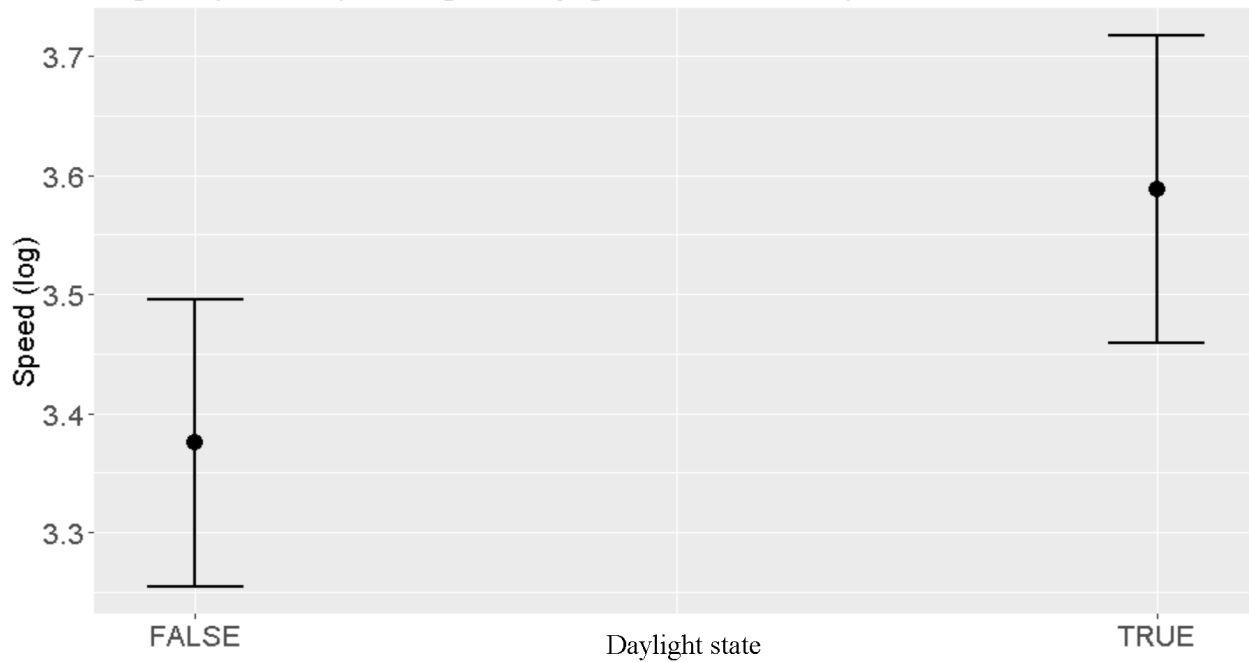


Fig.2. Speed of GPS-collared moose in proximity of GPS-collared wolves in Scandinavia. Mean confidence intervals for speed are predicted from mixed-effect models that relate moose speed to (A) the event sequence (before, during and after), (B) the close proximity event distance between moose, (C) the daylight state at each position and (D) the daylight state at the time of the event.

The GAM model revealed no significant difference in the time relative to the time of the close proximity event ($P=0.0847$, Fig. 3B). However, the analysis showed this model was not appropriate for our data, as there seemed to be too much variation for this test to distinguish a pattern. This reinforced our decision to use the categorical variable "Before_After" instead of the linear variable of time for our modeling.

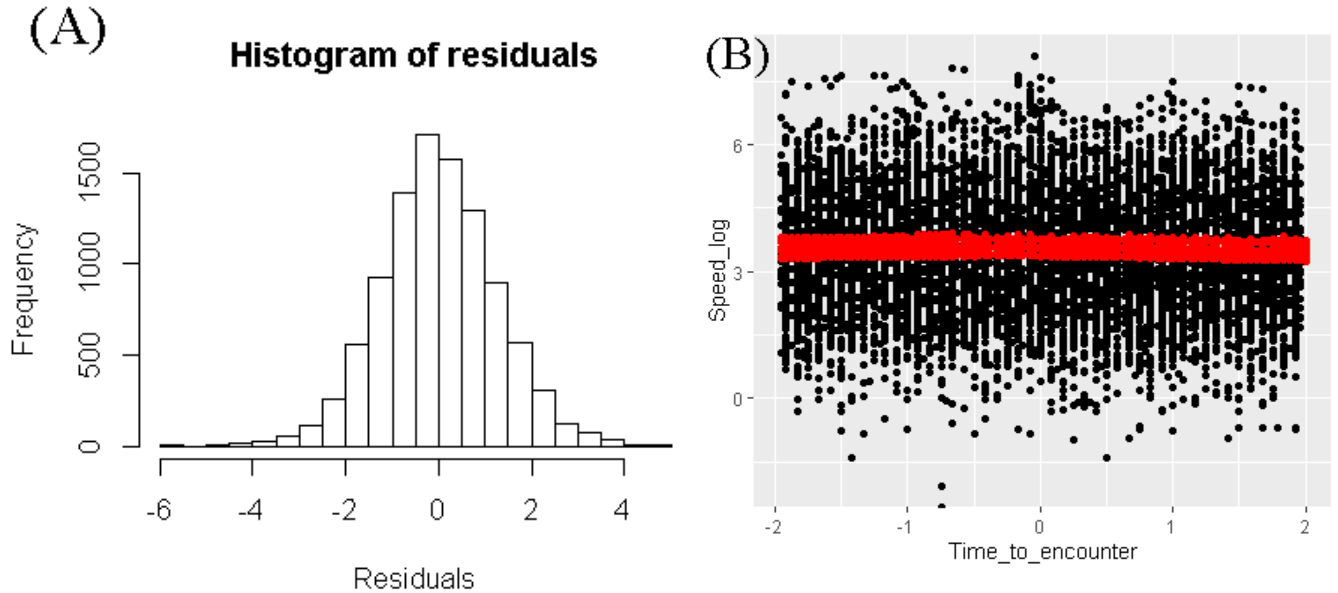


Fig.3.(A) Histogram representing the distribution of residuals for the GAM model. (B) Predicted values of speed in relation to the time of each position relative to the time of the close proximity event (linear variable).

3.4. Home range MCP analysis

Table 2. LMM models to assess the effect of distance between moose and wolf, the daylight state at the moment of the close proximity event and the time of the position relative to the time of the event on moose home range area size. The asterisks refer to an interaction analysis between the items that are before and after. The bold items represent the p-values that are significant.

Model	Model type	n	Response variable	Predictor variable	P
d1	LMM	13354	Home range area	Is Daylight encounter	0.0353
				Encounter distance	<0.0001
				Before_After (before)	<0.0001
				Encounter distance *	<0.0001
				Before_After	

Home range MCP analysis (see Table 2) revealed that moose generally had significantly larger 48-hours home ranges before the proximity event than after the event ($P = <0.0001$, Fig.4). Furthermore, 48-hours home ranges were significantly larger during the day than during nighttime ($P=0.0353$). Additionally, daily home ranges were significantly smaller when the event happened at close range rather than longer distances ($P < 0.0001$).

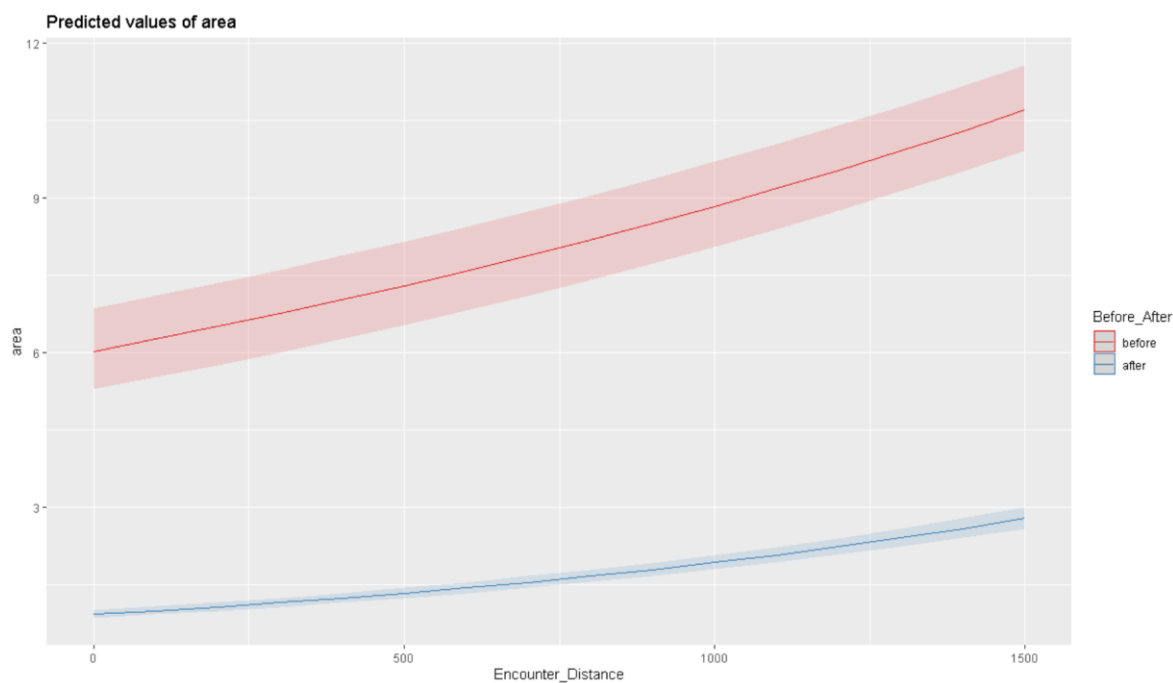


Fig.4. 100% MCP area of GPS-collared moose in proximity of GPS-collared wolves in Scandinavia. Mean confidence intervals for home range area are predicted from mixed-effect models that relate moose home range size to the close proximity event sequence (before, during and after).

4. DISCUSSION

In this study, moose appeared to exhibit some anti-predator strategies when in close proximity to wolves. In line with our first hypothesis, our findings show that moose moved significantly faster when the proximity event occurred at close range. Moreover, moose were moving the fastest during the event compared to before and after. There were no significant differences in speed depending on if the close proximity event occurred at night or during the day, but moose moved significantly faster during daytime than nighttime. The analysis of daily home ranges showed that moose had smaller home ranges after close proximity compared to before, which is in contrast with our hypothesis. Moose also had smaller home ranges after an event had occurred at close range. Lastly, moose had larger home ranges if close proximity occurred during the day compared to night, independent of whether the close proximity event occurred before or after.

Some of our results are in line with previous literature about the ecology of moose. Indeed, moose are diurnal animals and are most active during dawn and dusk, which could explain the increased movement rates (Eriksen et al. 2011). However, in relation to the findings of other studies on moose and wolf in Scandinavia, our results appear to differ. Although some studies reported an increase in speed after an close proximity event or other disturbances due to wolf or dogs (Ericsson et al. 2015; Latombe et al. 2013), more recent studies showed no significant differences in speed (Wikenros et al. 2016). Moreover, Ericsson et al. (2015) observed that moose had a larger home range after the disturbance caused by dogs compared to before, which is in contrast with our results. A possible hypothesis to explain this pattern could be that moose move in a less linear way to either increase the probability of success successfully escaping or to find a more suitable and safer habitat in close range. Surprisingly, the home range size was also negatively correlated before a close proximity event, although we expected it not to be affected by the event distance. A possible hypothesis could be that for some of the close proximity events, the way we subsetted our data might not account for wolves being already close to moose before the minimum event distance. This would mean that the change of behavior is occurring before the time we used as our close proximity event. Another hypothesis could be that moose that have smaller home ranges before also have smaller home ranges after a close proximity event, compared to moose with larger home ranges.

Because we found that moose moved significantly faster during a close proximity event than before or after, it is possible that moose choose to move slower in a reduced home range as an anti-predator strategy. Indeed, reduced activity can be beneficial as the probability of detecting a moving animal is higher than that of a relatively inactive individual (Lima & Dill, 1990). Lower speed in a smaller home range could also be reflective of the use of other anti-predator strategies such as increased vigilance (Berger, 1999; White & Berger, 2001).

In addition, Scandinavian moose appear to behave very differently than their American counterparts (Sand et al. 2006). In terms of anti-predator behaviors, American moose was observed to exhibit increased rates of vigilance and movement (Wirsing & Ripple, 2010) as well as habitat selection for denser forests (Boyce et al., 2003; Hebblewhite et al. 2005). Several factors can explain the difference in behavior between American and Scandinavian moose. For instance, wild game management differs between America and Scandinavia, as there is much higher hunting pressure on Scandinavian moose than there is on American moose. Scandinavian hunters account for over 90% of moose mortality compared to <5% for the wolves (Sand et al. 2006). This may lead to an altered anti-predator behavior that is making moose more exposed to being killed by wolves. For example, if moose stand their ground in front of hunters, they make an easier target and increase the probability of them getting shot. It is thus more adaptive for them to choose to flee, which is often the behavior observed in studies (Wikenros et al. 2009). Fleeing however, might increase the predation success of wolves and moose should have higher chances of surviving if they stand their ground (Wikenros et al. 2009). As prey species often choose the anti-predator strategy that corresponds to their most abundant predator, it would make sense that Scandinavian moose remain more reactive to humans rather than wolves. They may develop a set of new behaviors that are useful to avoid being shot, but not necessarily useful to avoid getting killed by natural predators. Future studies should aim to investigate whether the development of anti-predator strategies towards wolves compromises moose survival when being hunted by human hunters, and vice versa.

In addition, wolf densities in Scandinavia are much lower than in in the US. This could contribute to a lower encounter rate with a wolf in Scandinavia. Furthermore, the added pressure of increased human hunting to the lower densities of wolves could contribute to the high cost of investment in an anti-predator strategy specific to wolves for any moose individual. This would make investing

in anti-predator strategies against hunters much more beneficial as the encounter rate is much higher, and would, ultimately, contribute to increasing the probability of individual moose survival towards hunters (Kujiper et al. 2016; Sand et al. 2006).

Several limitations impeded our study. For example, the temporal resolution of the GPS collars (fixes every 1-4h and differing depending on the species) was likely a contributing factor to the difficulty in pinpointing the exact time and distance of the close proximity events. Additionally, as it is a very large interval, we likely missed many close proximity events which occur at a much finer scale. In addition, the sex ratio of the animals used in this study was very skewed towards females (n=4 males, n=13 females) and could be contributing to the fact that we did not find any significant differences in sex.

Moreover, future additions to this study will include a habitat analysis aiming at characterizing the types of habitats moose travel across after encountering a wolf, and whether those habitats differ from those moose occupied prior to close proximity. Furthermore, we wish to include an additional variable in our analysis, which is the presence of calves, to investigate whether female moose with calves respond differently to close proximity to a wolf compared to males and female moose without calves. We also wish to study the linearity of moose movement before and after close proximity to a wolf, to investigate why moose have smaller home range but higher speed after an event. Future studies should also aim to investigate whether the development of anti-predator strategies towards wolves compromises moose survival when being hunted by human hunters, and vice versa. Indeed, the anti-predator strategy towards wolves is opposite to that of towards humans.

5. CONCLUSION

In conclusion, this study found that the re-establishment of wolves in Scandinavia has influenced the behavior of moose when in close proximity to wolves. Scandinavian moose in this study were observed to exhibit higher rates of movement during a close proximity event with a wolf, as well as when the event occurred at a closer range. Home range analysis showed that home ranges were smaller when close proximity occurred at a closer range. Further study on the Scandinavian moose population are needed in order to provide us with more details on the intricate prey-predator relationship and could contribute to making management programs more efficient.

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APPENDIX

Table 3. LMM models with subsets "First" (first simultaneous position within a close proximity event sequence) and "Drop" (first simultaneous position with a distance that had 50% drop from the previously recorded position within a close proximity event sequence) to assess the effect of sex, distance between the moose and the wolf ("Distance btw moose wolf"), the daylight state at the moment of the close proximity event ("Is Daylight encounter") and the time of the position relative to the time of the event (that describes if the event happens before or after, "Time to encounter") on moose rate of movement (speed). The asterisks refer to an interaction analysis between the items that are before and after. The bold items represent the p-values that are significant. Overall models were evaluated based on the significance estimate of coefficients of predictor variables.

First	b1	13666	Sex	0.3957	33547.65
			Distance btw moose wolf	0.2939	
			Is Daylight encounter	0.0119	
			Time to encounter	< 0.0001	
First	b2	13666	Distance btw moose wolf	0.1467	33593.43
			Is Daylight encounter	0.0152	
			Before_After (before)	0.0006	
			Before_after (encounter)	0.0410	
			Is Daylight	< 0.0001	
			Is Daylight encounter * Distance btw moose wolf	0.0964	
First	b3	13666	Sex	0.4385	33597.08
			Distance btw moose wolf	0.8135	
			Is Daylight encounter	0.0152	
			Before_After (before)	0.0006	
			Before_after (encounter)	0.0409	
			Is Daylight	< 0.0001	
			Is Daylight encounter * Distance btw moose wolf	0.0964	
Drop	c1	13491	Sex	0.4678	33204.41
			Distance btw moose wolf	0.9320	
			Is Daylight encounter	0.0003	
			Time to encounter	0.0001	
Drop	c2	13491	Distance btw moose wolf	0.1692	33254.79
			Is Daylight encounter	0.1500	
			Before_After (before)	0.0008	
			Before_after (encounter)	0.0057	
			Is Daylight	< 0.0001	
			Is Daylight encounter * Distance btw moose wolf	0.0100	
Drop	c3	13491	Sex	0.5156	33258.64
			Distance btw moose wolf	0.0073	
			Is Daylight encounter	0.1600	
			Before_After (before)	0.0008	
			Before_after (encounter)	0.0057	
			Is Daylight	< 0.0001	
			Is Daylight encounter * Distance btw moose wolf	0.0102	

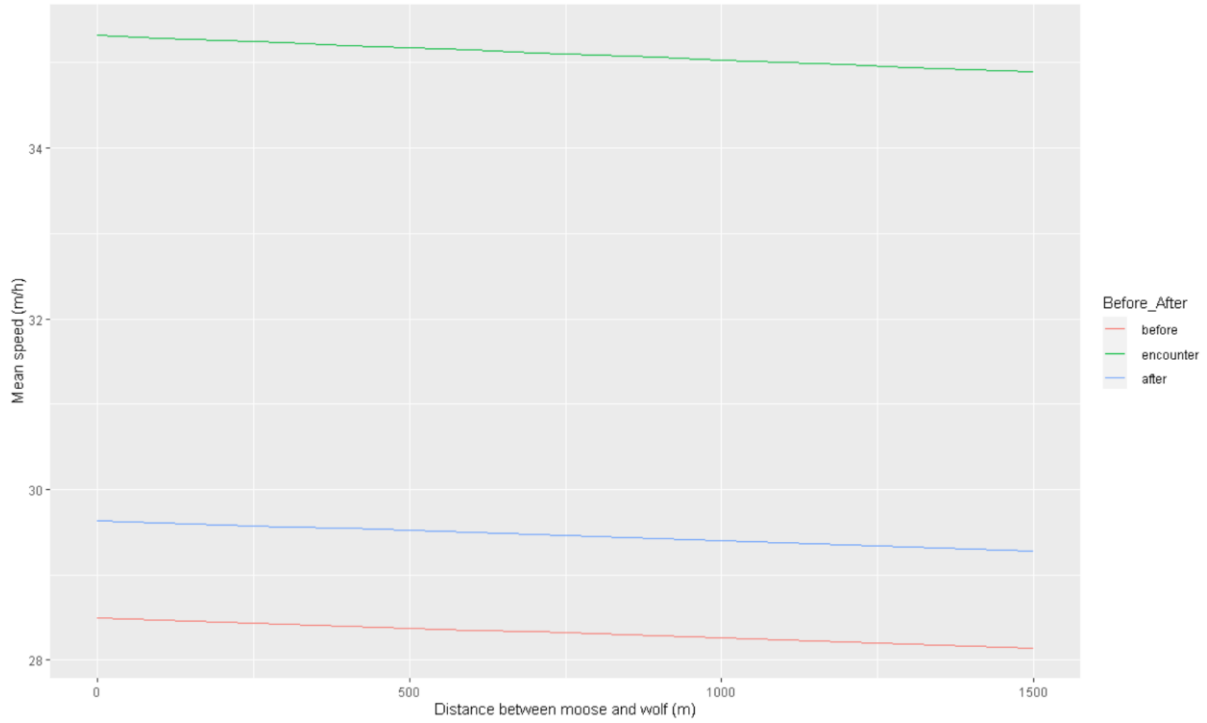


Fig.5. Speed of GPS-collared moose in proximity of GPS-collared wolves in Scandinavia. Mean confidence intervals for speed are predicted from mixed-effect models that relate moose speed to the event sequence (before, during and after and the close proximity event distance between moose).