Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
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Grimsö Wildlife Research Station

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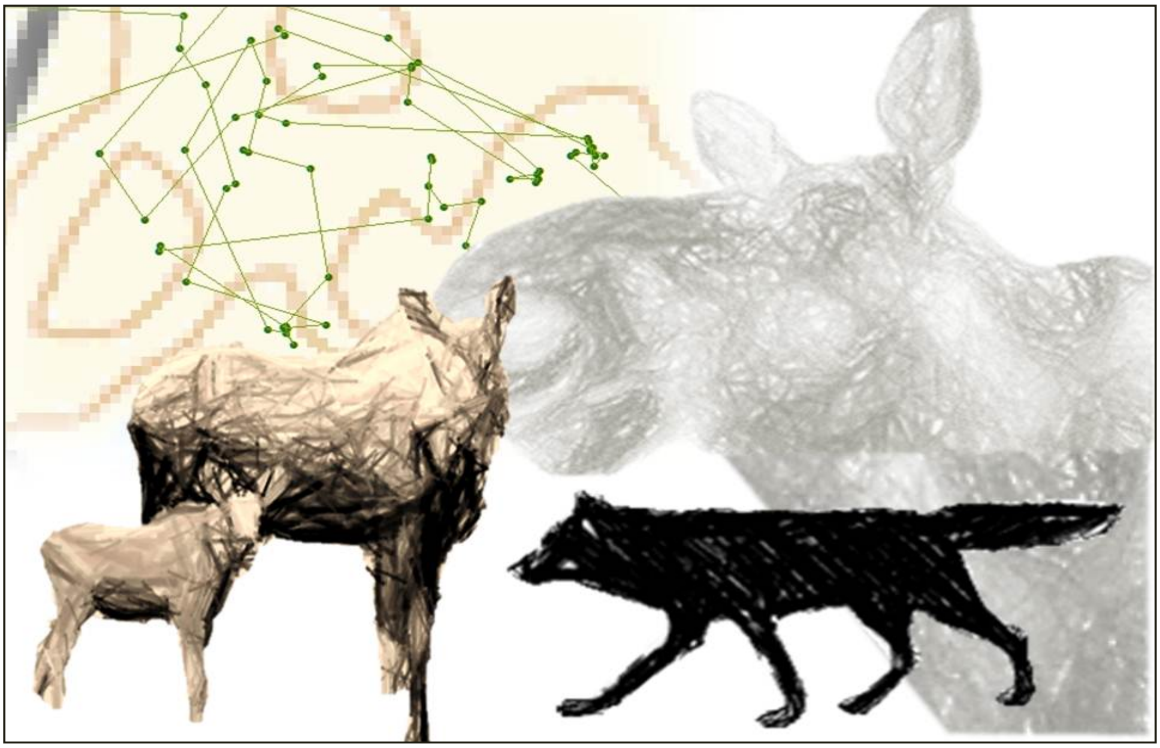
Gyöngyvér Balogh



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ABSTRACT

In a predator-prey system, prey species may adapt to the presence of predators with behavioral changes such as increased vigilance, shifting habitats or changes in their mobility. Across North America, moose (*Alces alces*) have shown to adapt to their re-colonizing predators, the wolves (*Canis lupus*) but such anti-predator behavioral responses have not yet been found in Scandinavian moose. The more than a century long absence of wolves in Scandinavia and the current re-colonization since the 1980s provide unique conditions to further detail our knowledge of their effect on moose. I analyzed travel speed, linearity of movement and seasonal home range size of GPS collared female moose within the same moose population but with spatial (inside- / outside wolf territories) and temporal (before- / after the re-establishment of wolves) differences in the exposure to wolves. Differences in seasonal home range size of female moose in the study area correlated with exposure to wolves, as home ranges tended to be larger in areas of the wolf territory with a more frequent presence of wolves. Travel speed and linearity of movement were mostly affected by seasonal changes and differences in reproductive status. Travel speed was highest during the calving (May – Jul.) and post-calving (Aug. – Oct.) seasons, and was generally lower for females with calves than females without calves in all seasons. Related to presence of wolves, a generally suppressed travel speed was observed inside the wolf territory compared to outside, but an elevated mobility was seen in certain, more intensively used areas of the territory. The linearity of movement was mostly affected by reproduction, as more concentrated movement was observed at females with calves at heel, during the calving season. Overall, the results supported that mobility of female moose was more strongly influenced by external factors and reproductive status, than by the return of their long absent natural predators. This can be due to a combination of several factors including e.g. lower wolf densities, higher moose:wolf ratios and more intensive hunting harvest of the moose population than observed in North America.

Key words: Moose, *Alces alces*, wolf, *Canis lupus*, movement pattern, mobility, home range size, GPS

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INTRODUCTION

Movement links together many ecological processes from reproduction through resource use to competition, therefore studying how animals move has been a focus of research for decades (Phillips et al. 1973, Cederlund et al. 1987, Cederlund & Sand 1992, Turchin 1998, Moorcroft & Lewis 2006, Zimmermann et al. 2007, Cagnacci et al. 2010, Bunnefeld et al. 2011). Analyzing animal movement allows us to have an insight into habitat preference (Phillips et al. 1973) or space use (Fortin et al. 2005, Moorcroft & Lewis 2006). Movement of animals refers to the process by which animals are displaced in space over time (Turchin 1998). These movements are often concentrated within a home range, defined as the area traversed by an animal during foraging, mating, searching for refuge or any other activities (Burt 1943). The behavior and movement pattern of animals reflect responses to their surroundings, and to inter- and intraspecific interactions (Jonsen et al. 2003). With the use of global positioning system (GPS) technology, frequent and precise location data can be acquired on large mammals, enabling us to reconstruct their movement paths (Johnson et al. 2002).

In predator-prey systems behavior of prey species can be influenced by the presence of predators (Stephens & Peterson 1984, Fortin et al. 2005), but also change due to food availability (Phillips et al. 1973, Cederlund 1989) or reproductive status (Cederlund & Sand 1994, van Beest et al. 2011). In this thesis, I studied behavioural changes of prey, focusing on movement patterns of moose (*Alces alces*) in relation to the presence of a recently re-colonized predator, the wolf (*Canis lupus*).

Prey species are shown to change their movement behavior (Main 1987) and speed of movement (Gilliam & Fraser 2001) in presence of predators. On the other hand, predators can synchronize their activity patterns with prey species in order to increase hunting success (Jenny & Zuberbühler 2005). Moose have shown to shift their spatial activity pattern as a response to wolf predation (Stephens & Peterson 1984, Fortin et al. 2005). Such anti-predator behavior includes increased vigilance levels (Berger 1999), females relocating their calving site if they have lost their calf to wolf predation the previous year (Berger et al. 2001) or showing aggressive behavior towards wolves (Mech & Boitani 2003). Furthermore, in moose populations where hunting harvest is the main mortality factor, moose decrease their movement in order to avoid exposure to hunters (Baskin et al. 2004).

In Scandinavia the wolf population was reduced by the middle of the 19th century and went functionally extinct by the 1960s (Wabakken et al. 2001). Since the 1980s a re-colonization has started and the current (2010/2011 winter) Scandinavian population counts 289-325 individuals (Wabakken et al. 2011). Moose is the most important prey species for wolves in south-central Sweden all year round, as it can constitute over 90% of the wolf diet in biomass (Sand et al. 2008). Predation risk is highest on calves and yearlings (Sand et al. 2005, 2008). Despite the high hunting success of Scandinavian wolves (Sand et al. 2006b) and a considerable predation risk in wolf territories, hunter harvest remains the main mortality factor in most areas (Wikenros 2011). Since wolves had been absent for many decades in Scandinavia and hunter harvest have replaced this predation risk, moose may have adjusted their behavior to this change in the predator-prey system. Ungulate prey species are able to adapt to re-colonizing wolves (Stephens & Peterson 1984, Berger et al. 2001, Laundré et al. 2001, Fortin et al. 2005), however in Scandinavia, earlier studies have revealed that moose seems to lack the ability to learn how to avoid wolf predation (Sand et al. 2006a). For example, no decrease in hunting success over time after the establishment of wolf territories (Sand et al. 2006a), nor desynchronized daily or seasonal activity patterns (Eriksen et al. 2011) have been evident. Furthermore, no effect has been found on moose home range location in relation to establishment of wolf denning area (Eriksen et al. 2009).

In addition to the presence of predators prey animals have to adapt to a changing resource availability and environmental conditions, induced by seasonality, and so their movement and activity patterns may also show variation following this scale. In general, moose show reduced mobility during the winter with females also reducing mobility during the calving season (Eriksen et al. 2011). During winter, moose move less, move over smaller areas, and spend more time ruminating on the lower quality food (Vander Wal & Rodgers 2009). Movement and activity rates increase as the summer unfolds and a peak can be observed over the July-August period (Vander Wal & Rodgers 2009, Eriksen et al. 2011). Pronounced differences can be observed between sexes during the rutting period, in which male move more intensively than females (Phillips et al. 1973).

In general, females have smaller home ranges than males (Cederlund & Sand 1994) and in both sexes, winter home ranges are reduced in size compared to summer home ranges. The movement pattern and mobility of female moose is also dependent on their reproductive status. Females with calves tend to reduce their movements compared to females without calves and females that had lost their calves. Reproductive status is also shown to be the most influential variable to explain differences in summer home range size of female moose on an individual level (van Beest et al. 2011), although findings on how reproductive status affects home range size differ between studies (Cederlund & Okarma 1988, Cederlund & Sand 1994, van Beest et al. 2011).

In this study, my aim was to examine the effects of a re-colonizing predator, the wolf, on the movement patterns of their main prey, the moose. More specifically, I studied mobility and space use of moose by using GPS-collared female moose within the same moose population but where moose females experienced a spatial difference in the exposure to wolves (inside- / outside wolf territories). Additionally, I used individuals from this population to analyze the temporal differences in their movement patters in relation to the presence of wolves (before and after the re- establishment of wolves). While investigating the effect of wolf presence on mobility and home range size of female moose, I also included season and reproductive status as explanatory variables.

METHODS

Study Area

The study was conducted in the Grimsö Wildlife Research Area (59–60°N, 15–16°E), located in the boreal zone (south-central Sweden, Figure 1.). The topography of this rugged plateau is characterized by various features such as flat ridges, boulders and swampy areas with the elevation ranging between 100-150 m (National Land Survey of Sweden). The main land cover type in the area is forest (72%), but bogs (18%), lakes and rivers (7%) as well as meadows (3%) are also important components of the landscape (Björkhem & Lundmark 1975). Intensive forest management dominates the area, with average stand rotation periods of 80-100 years. The main tree species are Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*), and birches (*Betula pubescens* and *Betula pendula*) (Månsson et al. 2007). The climate is typical of inland central Sweden with mean daily temperatures of -4 ºC in January and 16 ºC in July, snow cover present from December to March with snow depth between 25-30 cm (in February), and an annual average precipitation of 670 mm (Swedish Meteorological and Hydrological Institute, Alexandersson & Andersson 1995, Vedin 1995).

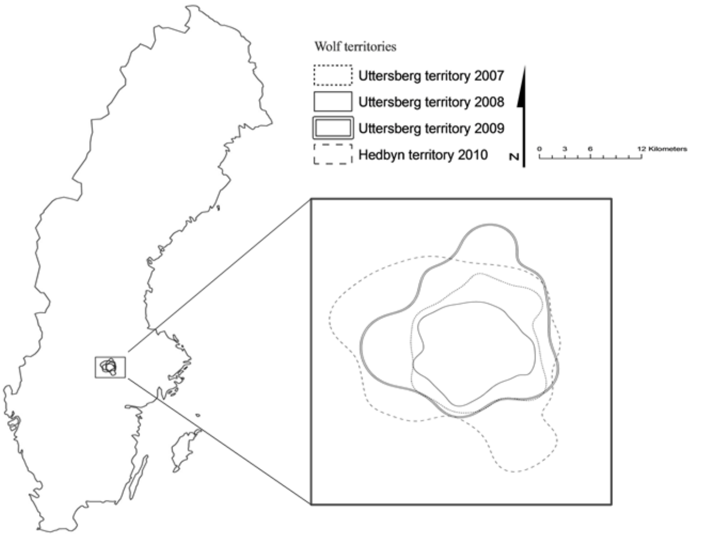

Figure 1. The map of Sweden. The enlargement shows the research area with annual wolf home ranges (n = 4) of two wolf territories, estimated with 95% Kernel method.

The density of moose was estimated to 1.2 moose/km^2 in 2002 and 0.8 moose/km^2 in 2006 by aerial surveys (Rönnegård et al. 2008). The moose population in the area shows high fidelity to the established home ranges and is considered non-migratory (Cederlund & Okarma 1988). Other ungulate species are roe deer (*Capreolus capreolus*), with population densities between 1-5/km^2 (Rönnegård et al. 2008), red deer (*Cervus elaphus*) which occur in very low densities (<0.1/km2) and wild boar (*Sus scrofa*) also in low densities, compared to other areas (Jansson, pers.comm.).

During the study period (2007-2010), wolves were continuously present in the area. The Uttersberg pair established its territory during the winter of 2003/2004 (Wabakken et al. 2004). Reproduction was confirmed each year from 2004 until 2006 and then again in 2008. During the snow tracking in the winter of 2008/2009 a pack of 4-5 wolves were still confirmed in the territory, but no new reproduction was detected in 2009 as only the alpha male could be found. During the following winter (2009/2010), a new scent-marking pair (named Hedbyn) established in the area, including a great part of the former Uttersberg territory in their territory (Wabakken et al. 2010) (Figure 1).

GPS collar data

I used GPS locations from collared female moose (n= 30) and wolves (n = 4) in the two territories. Both wolves and moose were immobilized by darts from helicopters (see Sand et al. 2006b; Cederlund et al. 1989 for details). The alpha male wolf of the Uttersberg territory was collared first in 2005, than again in 2007. The female was fitted with a GPS collar in 2006. Both the female and the male of the Hedbyn territory were collared in 2010. The collar of the Uttersberg male stopped working in October 2009 whereas the collar of the Hedbyn pair were available from February 2010, therefore wolf locations from this period are missing. Locations were acquired from the female wolf of the Hedbyn territory until February 2011(Appendix 1). Female moose were fitted with GPS collars in March 2007 (n=20). One female was recaptured and collared again, along with 10 new individuals in 2010 (Appendix 2). Wolf collars were programmed to take locations with 12 hour intervals, whereas the GPS collars of the moose took locations every 2nd hour. In some cases there are longer intervals between consecutive positions due to missing locations. For my analyses I used locations of both species from four consecutive years (2007-2010).

GPS-data screening

Regarding both wolf and moose GPS data, locations of seven consecutive days, including the day of capture, were removed from the dataset, due to possible effects of the capture on the movement pattern of the animals (Neumann et al. 2011). The dataset of moose locations was screened for error locations with a method developed especially for treatment of large GPS location datasets. The screening is based on removing all highly unlikely movements, defined by travel distances, travel speed and turning angles (Björneraas et al. 2010). In the first step, all locations that were further away than 100 km from the surrounding locations were removed based on the assumption that moose could not have moved this far in a 2 hour interval. In the second step, this distance was refined to 10 km. The third step consisted of identification and removal of such locations in the movement trajectory where the outgoing or incoming speed exceeded 1.5 km/h, and the cosine of the turning angle was less than 0.97. This criterion was based on the assumption that the moose is unlikely to move this fast towards a point further away and then immediately turn back sharply toward the location that it came from (Björneraas et al. 2010). Data screening was done using the package Adehabitat (Calenge 2006) developed for the statistical software R (version 0.95.261, [online] www.r-project.org, accessed on 06.02.2012).

Annual territories and home ranges

I used locations from one individual of the wolf pair at the time, based on the assumption that the movement and activity of a pair is highly synchronized, with the exception of the pup rearing period (Eriksen et al. 2011, Alfredéen 2006). Locations from the male wolf of the Uttersberg territory were used to estimate the territories in 2007- 2009 and of the female wolf in the Hedbyn territory in 2010 (see below description of territory and home range estimations). Annual territories were calculated for wolves (n = 4) and annual home ranges for moose (n = 68).

I calculated the area of overlap between each moose home range and the wolf territory on an annual basis. Values recorded were i) area (km²) of overlap, ii) relative overlap (%) and iii) category of overlap categorized as '*outside*' (0-10% overlap), '*partial*' (11-65% overlap), or '*inside'* (>65% overlap) the wolf territory.

Seasonal moose home range estimations

I divided each year into four seasons to detect changes in the movement pattern of female moose on a finer scale (Cederlund & Okarma 1988; Cederlund & Sand 1994). The seasons used were '*pre-calving'* (1 Feb. - 30 Apr.), '*calving'* (1 May – 31 July), '*post- calving'* (1 Aug. – 31 Oct.) and '*winter*' (1 Nov. – 31 Jan.). Seasonal home range size (km^2) and location was calculated according to these periods. The % overlap values calculated on the annual basis were assigned to all subsequent seasons in any given year (see below description of home range estimations). I excluded all individual seasonal home ranges that represented less than 95% of the given temporal scale, in this case the pre- defined three month seasonal periods (van Beest et al. 2011).

Wolf exposure index

I counted the number of wolf locations from each season in the given year within each individual moose home range (Eriksen et al. 2009). A relative value was calculated by dividing the number of wolf locations by the number of total wolf locations in the given season (see below).

Calculation of territories, home ranges and exposure index

Annual home ranges for wolf and moose, the overlap of these home ranges and the seasonal moose home ranges were estimated using the 95% fixed Kernel (Worton 1987) with the reference technique ("href") to calculate the smoothing factor h (Kie et al. 2010) and the 100% MCP (Mohr 1947) methods. The wolf exposure index was also calculated for the seasonal moose home ranges based on both methods. Calculation of home ranges was done in R library 'AdehabitatHR' (Calenge 2006). For estimating the area of overlap of annual moose home ranges and the wolf territories, I used the intersect tool and the extension Hawths Tools in ArcGIS 9.3.1. (ESRI, Redlands, CA, U.S.A.).

Reproductive status

Female moose were checked for reproduction in the spring (12 May - 04 July), and then again in late summer (26 Aug. - 09 Sep.) and finally at the end of winter the following year (01 Apr. - 29 Apr.). Date of observation and the number of observed calves at heel were recorded. I determined if the female was with or without a calf in each of the four seasons. If the female had lost its calf between two observations but the exact date is unknown, I classified this as an '*unsure*' calving status in the corresponding season. I used both the number of calves in each seasons for each study animals, and a categorical variable with three levels, '*with calf*', '*without calf*' and '*unsure*'.

Mobility

To estimate an index of mobility in each season, I calculated movement variables travel speed (m/h) and linearity. I used i) the straight line distance (m) between consecutive relocations, and ii) the time elapsed between subsequent location. Travel speed and linearity was calculated according to:

$$Travel\ speed = \frac{d_2 - d_1}{t_2 - t_1}$$

$$Linearity = \frac{d_{1-3}}{(d_{1-2} + d_{2-3})}$$

where d is the distance, t is the elapsed time and the subscript (1, 2, 3) represent consecutive locations. The linearity value is always assigned to the second locations of each set of three, and represents a fraction (value between 0-1) which indicates directional movement if it is a value close to 1, and movement concentrated within a smaller area if the value is close to zero (Eriksen et al. 2010). Movement parameters of each study animal were calculated with R library 'AdehabitatLT' (Calenge 2006). In order to meet the assumption of normally distributed residuals, travel speed was transformed by ln(x+1) and linearity by exp(arcsin(√x)).

Statistical analysis

Factors influencing travel speed, linearity of movement and home range size

I used generalized linear mixed models (GLMM) in SPSS Statistics 20.0 (IBM SPSS Inc., Chicago, Illinois, USA) to test for factors that influenced i) travel speed, ii) linearity of movement, and iii) seasonal home range size of female moose. The use of GLMM enables the use of repeated measures on multiple time scales and capable of treating data with unbalanced designs, which occurred due to collar failure, mortality and exclusion of locations.

Two datasets were used in the analysis and both included the same moose individuals. The first 'total' dataset includes all seasonal home ranges and the variables '*reproductive status*' and '*categorical overlap'* both consisted of three levels, *with calf*, *without calf* and *unsure* as well as *inside*, *outside* and *partial*, respectively. Models were also developed using a second, 'reduced' dataset, from which seasonal home ranges with the reproductive status '*unsure*' and the overlap category '*partial*' were removed.

To account for repeated measurements over multiple time scales, year and season were entered as repeated measures with animal ID as subjects. To account for correlations between repeated observations of the same individuals, animal ID was used as a random effect with the default setting of the random effect covariance type. Type of season and reproductive status were included as fixed factors. For the analysis of travel speed and linearity, I accepted the assumptions of the model, but for the analysis of home range sizes, I used the setting "robust estimation of fixed effects and coefficients". In models using the travel speed or linearity of movement as the response variables, I started with including season alone as a fixed factor, and then made the model more complex by adding reproductive status, and finally the wolf effect. Because the three variables; categorical overlap, proportion of overlap, and wolf exposure all express the potential effect of wolves on mobility of moose; these were entered into the model one at the time, exclusive of each other. In the most complex model, season, reproductive status and one of the three wolf presence variables were entered as fixed effects. Using home range size as the response variable, I estimated the effect of the fixed factors season, reproductive status, and wolf presence with the same model structure (Appendix 3). All models were run first with the Kernel estimates than repeated with MCP estimates.

Factors were considered to have a significant effect at the α-level < 0.05 and close to significant at α-level < 0.10. Akaike information criterion (AIC) corrected for small sample sizes (AIC_C) was used to represent the relative goodness of fit of the statistical models. Models with ≤ 2 ΔAIC_C received strong support, models having $4 \leq \Delta AIC_C \leq 7$ had considerably less support, while models with > 10 ΔAIC_C received no support (Burnham & Anderson 2002).

Moose mobility before and after the establishment of wolves

I analyzed effects of wolf establishment on the mobility and home range size of three female moose that had their home ranges 100% outside of the wolf territory during one year (2008) and then 100% inside the wolf territory during one year (2010).

The response variables seasonal home range size (km^2), travel speed, and linearity of movement were analyzed using a general linear model with repeated measures (GLM repeated measures). Years were included in the model as a within subject factors, while season was used as a between subject factor. Simple contrast was used for comparing the year, and the interaction of year and season.

RESULTS

The number of seasonal home ranges used in the statistical analysis constituted 73% (n = 180) of the total number of seasonal home ranges (n = 245). 27% of the seasonal home ranges were removed due to low number of moose locations (n = 58), and lack of wolf exposure data due to collar failure (n = 7). From these 180 another 36 of the seasonal home ranges were removed due to corresponding reproductive status '*unsure*' and the overlap category '*partial*', resulting in a reduced dataset (n = 144). Due to these exclusions the total number of female moose used in the analysis was reduced to 26. Of all the seasonal moose home ranges (n = 180), 76% (74%) were '*inside*', 8% (7%) were '*partially inside* 'and 16% (19%) were '*outside*' of the wolf territory, depending on the home range estimation method (100% MCP shown in brackets). For 133 seasonal home ranges the females had calves, 48 were from females without calves, and 19 were of unknown reproductive status. The proportion of wolf locations that was located within individual seasonal home ranges ranged 0-16% with 95% Kernel estimates, and 0-13% with 100% MCP estimates. Reproductive status of three females used in the analysis of movement variables before and after wolf establishment (with 24 seasonal home ranges), was '*with calves'* in 15, *'unsure'* in one and '*without calves'* in eight seasonal home ranges.

Travel speed

Effect of wolves

Based on the 95% Kernel estimates, categorical ($F_{3,174} = 3.53$, $p = 0.031$) and proportional overlap ($F_{1,175} = 4.36$, $p = 0.038$) both indicated that travel speed of females was significantly lower inside than outside of the wolf territory (model A4 and A5; Table 1), however this effect was non-significant when reproductive status was included the models (model A10 and A11; Table 1). Models including proportional overlap had low ΔAIC_C values, indicating that this variable explained little variation in travel speed (Table 1). Results were similar when the models (model A4, A5, A10 and A11; Table 1) were tested on the reduced dataset (n=144). Analyses also (model A12; Table 1) indicated that travel speed was higher ($F_{1,173} = 6.15$, $p = 0.014$) in home ranges where the wolves were present more often (higher exposure), but there was no significant effect of wolf exposure when tested on the reduced dataset ($F_{1,138} = 2.37$, $p = 0.126$). For 100% MCP estimates, only wolf exposure ($F_{1,173} = 5.39$, $p = 0.021$), showed a significant, positive effect on travel speed (model A15; Table 1).

Effect of season and reproductive status

From the 15 tested models (models A1-15; Table 1) dealing with the effects on travel speed, models (model A3; Table 1) including the effect of season and reproductive status had the lowest AIC_C value. The difference (ΔAIC_C) between model A3 and the 2nd ranked model (A2) was only 0.9, indicating that those models were equally good and that a significant amount of variation in travel speed was due to seasonal changes (Table 1). Both season ($F_{3,174} = 121.3$, $p < 0.001$) and reproductive status ($F_{2,174} = 6.56$, $p = 0.002$) had a significant effect on travel speed (model A3; Figure 2, Table 1). Travel speed was highest during calving season (May - July) and lowest during winter (November - January). Females with calves had a reduced travel speed compared to females without calves. Including reproductive categories only as *with calf* and *without calf* (the reduced dataset) gave the same results (Appendix 3). This difference in travel speed due to reproductive status was most pronounced during the calving season.

Table 1. GLMM models to assess the effect of seasons, reproductive status and wolf presence (categorical overlap, proportional (%) overlap and exposure to wolves) on travel speed (m/h), linearity of movement and home range size (km^2) estimated with 95% Kernel and 100% MCP methods. The models were evaluated based on Akaikes Information Criterion (AIC$_C$) values.

Model	**Response variable**	**Fixed factors**	***df***	***AIC$_C$***	***ΔAIC$_C$***
A3	Travel speed	**season + reprod.**	**5,174**	**-17.42**	**0**
A2		season	3,176	-16.55	0.9
A12		season + exposure + reprod. (KER)	6,173	-13.84	3.6
A4		season + cat. overlap (KER)	5,174	-13.80	3.6
A15		season + exposure + reprod. (MCP)	6,173	-13.20	4.2
A10		season + cat. overlap + reprod. (KER)	7,172	-11.85	5.6
A9		season + exposure (MCP)	4,175	-11.19	6.2
A13		season + cat. overlap + reprod. (MCP)	7,172	-10.89	6.5
A6		season + exposure (KER)	4,175	-10.44	7.0
A7		season + cat. overlap (MCP)	5,174	-9.90	7.5
A5		season + % overlap (KER)	4,175	-6.81	10.6
A11		season + % overlap + reprod. (KER)	6,173	-5.39	12.0
A14		season + % overlap + reprod. (MCP)	6,173	-3.96	13.5
A8		season + % overlap (MCP)	4,175	-3.68	13.7
A1		intercept only	-	92.95	110.4
B3	Linearity	**season + reprod.**	**5,174**	**-352.63**	**0**
B13		season + cat. overlap + reprod. (MCP)	7,172	-343.00	9.6
B10		season + cat. overlap + reprod. (KER)	7,172	-342.23	10.4
B15		season + exposure + reprod. (MCP)	6,173	-342.22	10.4
B12		season + exposure + reprod. (KER)	6,173	-341.99	10.6
B11		season + % overlap + reprod. (KER)	6,173	-337.77	14.9
B14		season + % overlap + reprod. (MCP)	6,173	-336.96	15.7
B2		season	3,176	-332.17	20.5
B7		season + cat. overlap (MCP)	5,174	-329.57	23.1
B4		season + cat. overlap (KER)	5,174	-326.27	26.4
B5		season + % overlap (KER)	4,175	-324.60	28.0
B8		season + % overlap (MCP)	4,175	-323.57	29.1
B6		season + exposure (KER)	4,175	-323.10	29.5
B9		season + exposure (MCP)	4,175	-321.21	31.4
B1		intercept only	-	-302.95	49.7
C9	Home range size (95% Kernel)	**season + exposure + reprod.**	**6,173**	**2641.13**	**0**
C6		season + exposure	4,175	2679.49	38.4
C7		season + cat. overlap + reprod.	7,172	2729.51	88.4
C8		season + % overlap + reprod.	6,173	2750.14	109.0
C3		season + reprod.	5,174	2751.95	110.8
C4		season + cat. overlap	5,174	2754.93	113.8
C5		season + % overlap	4,175	2775.49	134.4
C2		season	3,176	2777.45	136.3
C1		intercept only	-	2809.79	168.7
D9	Home range size (100% MCP)	**season + exposure + reprod.**	**6,173**	**2669.18**	**0**
D7		season + cat. overlap + reprod.	7,172	2701.10	31.9
D6		season + exposure	4,175	2705.49	36.3
D8		season + % overlap + reprod.	6,173	2724.62	55.4
D3		season + reprod.	5,174	2726.93	57.7
D4		season + cat. overlap	5,174	2730.02	60.8
D5		season + % overlap	4,175	2754.30	85.1
D2		season	3,176	2756.97	87.8
D1		intercept only	-	2798.50	129.3

Linearity of movement

Effect of wolves

Based on 95% Kernel home range estimates, categorical ($F_{2,174} = 4.24$, p = 0.016) and proportional ($F_{1,175} = 10.21$, p = 0.002) overlap showed that movement of females was more directional outside of the wolf territory than inside. However, significant effect of these factors only appeared in models that did not include reproduction (model B10 and B11; Table 1) and had low support ($\Delta AIC_C = 23.1$ - 31.4), but remained significant when the models were run on the reduced dataset. The wolf exposure index had no significant effect on linearity of movement ($F_{1,175} = 1.99$, p = 0.161) in any of the tested models. Using the 100% MCP estimates gave the same result with categorical ($F_{2,174} = 5.62$, p = 0.004) and proportional ($F_{1,175} = 8.495$, p = 0.004) overlap significant as long as reproduction was not included (model B7 and B8; Table 1) and with exposure to wolves ($F_{1,175} = 0.00$, p = 0.970) not significantly affecting linearity.

Table 2. Parameter values of the models with the lowest AIC_C values (according to Table 1.) for the response variables travel speed (m/h), linearity and seasonal home range size (km^2). Models were tested on the 'total' dataset (n = 180).

Model	**Response variable**	***n***	**Fixed factors**		**β**	**SE**	**P**
A3	Travel speed	180	intercept		3.605	0.063	**< 0.001**
			season	pre-calving	0.116	0.043	**0.008**
				calving	0.661	0.041	**< 0.001**
				post-calving	0.581	0.037	**< 0.001**
				winter	0	0	
			reproduction	unsure	-0.133	0.058	**0.023**
				with calf	-0.128	0.052	**0.015**
				without calf	0	0	
B3	Linearity	180	intercept		3.043	0.018	**< 0.001**
			season	pre-calving	0.033	0.016	**0.035**
				calving	-0.072	0.017	**< 0.001**
				post-calving	0.036	0.011	**0.001**
				winter	0	0	
			reproduction	unsure	-0.061	0.022	**0.006**
				with calf	-0.080	0.020	**< 0.001**
				without calf	0	0	
C9	Home range size (95% Kernel)	180	intercept		929.161	115	**< 0.001**
			season	pre-calving	-246.012	71.802	0.664
				calving	-36.391	83.556	0.164
				post-calving	-107.852	77.087	**0.001**
				winter	0	0	
			reproduction	unsure	-226.934	69.057	**0.001**
				with calf	-265.423	33.751	**< 0.001**
				without calf	0	0	
			wolf exposure		175.958	22.307	**< 0.001**
D9	Home range size (100% MCP)	180	intercept		929.878	125.452	**< 0.001**
			season	pre-calving	-184.457	62.288	**0.003**
				calving	33.745	85.855	0.695
				post-calving	116.307	106.304	0.275
				winter	0	0	
			reproduction	unsure	-450.806	103.977	**< 0.001**
				with calf	-314.996	113.456	0.006
				without calf	0	0	
			wolf exposure		116.683	26.192	**< 0.001**

Effect of season and reproductive status

Among the 15 tested models (models B1-15, Table 1) on linearity of movement, the model (B3; Table 1) including the effect of season and reproductive status had the lowest AIC_C value. In contrast to the result on travel speed, the model that included only season (model B2; Table 1) had substantially less support, suggesting that linearity of movement was more affected by reproductive status than was travel speed (Table 1). Seasons explained a significant amount of variation in the linearity of movement ($F_{3,174} = 31.17$, $p < 0.001$) with female moose having the lowest value of linearity during the calving season and this value being significantly different from all the other seasons (Table 2). Reproductive status ($F_{1,139} = 23.95$, $p < 0.001$) revealed that females without calves moved significantly more directional in all seasons than females with calves (Figure 3). Movements with a low degree of linearity during the calving season were pronounced for females with calves, while females without calves showed no such movement pattern (Figure 3). Analysis of the reduced dataset with the same model (model B3; Table 1) showed that seasonal differences in linearity were significant ($F_{3,139} = 24.86$, $p < 0.001$) although not all seasons differed from each other (Appendix 3). The difference in linearity due to reproductive status ($F_{1,139} = 45.49$, $p < 0.001$) also remained significant (Appendix 3).

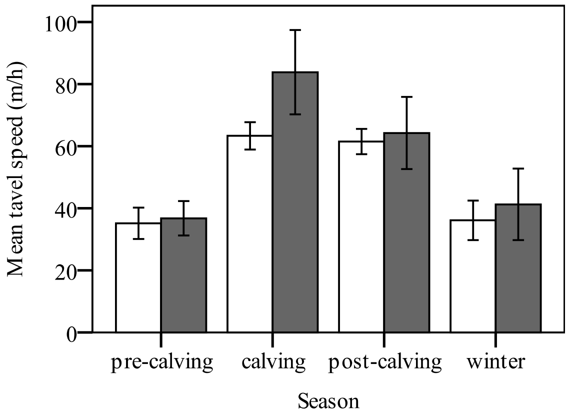

Figure 2. Seasonal variation of mean travel speed (±95% CI) of female moose (n = 26) with calves (white bar) and without calves (grey bar). Values represent the original, non-transformed data.

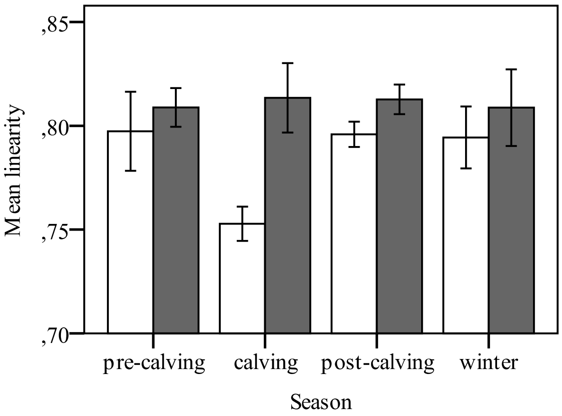

Figure 3. Seasonal variation of mean linearity (±95% CI) of female moose (n = 26) with calves (white bar) and without calves (grey bar). Values represent the original, non-transformed data.

Seasonal home range size

Effect of wolves, season, and reproductive status

Categorical overlap showed no significant effect on seasonal moose home range size (model C4; Table 1) neither for the total dataset ($F_{2,174} = 0.93$, $p = 0.397$) nor for the reduced dataset ($F_{1,139} = 0.150$, $p = 0.484$) using the 95% Kernel estimates. Using the 100% MCP estimates (model D4; Table 1), seasonal home range sizes significantly differed between overlap categories ($F_{2,174} = 6.37$, $p = 0.002$), whereas the reduced dataset showed that home ranges inside and outside of the wolf territory did not differ in size (F $_{1,139}$ = 0.14, p = 0.70). The proportion of overlap showed no significant effect on seasonal home range size in any of the models that included this variable. In contrast, exposure to wolves (model C6 and D6; Table 1) showed a significant positive correlation with seasonal home range size using both the 95% Kernel (F $_{1,175}$ = 43.91, p < 0.001) and 100% MCP (F $_{1,175}$ = 15.96, p < 0.001) estimates and in both cases the reduced dataset confirmed this effect (Appendix 3).

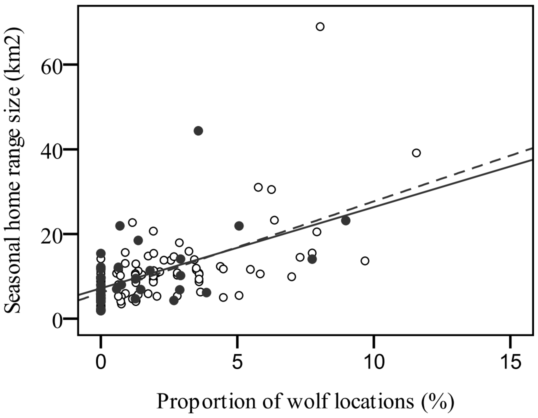

Figure 4. Proportion of wolf locations in relation to the size (km^2) of seasonal home range of female moose with calves (white dots, dotted line R^2= 0.,379) and without calves (grey dots, solid line R^2= 0.268). Home range sizes were estimated with 95% Kernel method.

The model with the strongest support for explaining variation in both 95% Kernel (model C9; Table 1) and 100% MCP (model D9; Table 1) seasonal home range estimates included exposure to wolves, season, and reproduction status. Model C9 (Table 1) showed that wolf exposure (F $_{1,173}$ = 62.22, p < 0.001) had a positive correlation with home range size, indicating that seasonal moose ranges were larger in areas most often used by wolves (Figure 4). Home range size also showed significant seasonal variation (F $_{3,173}$ = 12.52, p <0.001) with seasonal home range size in the pre-calving season (8.5 km^2 ± 1.1) being significantly lower than during winter (11.0 km^2 ± 1.3) and during the calving season (10.6 km^2 ± 1.0). Reproductive status influenced (F $_{2,173}$ = 31.09, p < 0.001) seasonal home range size and the reduced dataset confirmed that females with calves had significantly smaller seasonal home ranges than females without calves. Females with calves showed the largest reduction in home range size of all moose categories during the calving season.

The best model (model D9; Table 1) for 100% MCP seasonal home range estimates also showed that home ranges were significantly smaller during the pre-calving season compared to other seasons, but unlike the 95% Kernel estimates (model C9; Table 1), home ranges were largest during the calving and post calving season, (F $_{3,173}$ = 3.35, p= 0.020). Seasonal home range size was larger for females without calves than females with calves (F $_{1,138}$ = 9.40, p= 0.003) and this difference in home range size during the calving season was more pronounced than in model C9 (Table 1). Exposure to wolves showed a strongest effect (F $_{1,173}$ = 19.85, p < 0.001), with larger seasonal home ranges in areas most intensively used by wolves (Table 2).

Mobility and home range size before and after establishment of wolves

Travel speed of moose (n=3) decreased between 2008 (range: 38.8 – 76.8 m/h) and 2010 (range: 31.7 – 73.1 m/h) by average 8.09 m/h and this was statistically significant (Table 3). The interaction term "Year * Season" showed that there is a significant difference between the two years depending on the season. The highest travel speed was observed during the post calving season, while the lowest was in the pre-calving season. The average travel speed increased from 34 m/h in the pre-calving season to 71 m/h in the calving season and then decreased from 73 m/h (post calving) to 35 m/h in winter (Figure 5). Although average travel speed differed between the seasons, there was no significant difference between winter (range 32 – 39 m/h) and the pre-calving season (range 27 – 44 m/h), or between calving (range 69 – 73 m/h) and post calving (range 70 – 77 m/h) seasons (Figure 5).

Table 3. Results from GLM with repeated measures of female moose (n=3) home range size (km^2), travel speed, (m/h) and linearity of movement in response to before and after wolf establishment (Year, n=2) and time of the year (Season, n=4).

Response variable	**Effect**	***df***	***F***	***P***
Home range size (95% Kernel)	Year	1	0.49	0.504
	Season	3	1.56	0.273
	Year:Season	3	1.61	0.262
Home range size (100% MCP)	Year	1	0.02	0.894
	Season	3	2.82	0.107
	Year:Season	3	0.57	0.652
Travel speed	**Year**	**1**	**21.18**	**0.002**
	Season	**3**	**27.82**	**< 0.001**
	Year:Season	**3**	**8.41**	**0.007**
Linearity	Year	1	0.62	0.453
	Season	3	3.39	0.074
	Year:Season	3	0.84	0.509

There were no significant differences in the linearity of movement between before and after the establishment of the wolf territory (Table 3). The main effect of season on linearity indicated a close to significant difference (Table 3), but there was a slight reduction during the calving season compared to the preceding and the following seasons (Figure 6).

Home range size (95% Kernel) of the three females did not change in relation to the establishment of wolves and did not vary significantly between seasons. The interaction of years and season also revealed that there was no significant difference in the seasonal home range sizes in response to wolf establishment (Table 3). The same was shown using the 100% MCP method (Table 3).

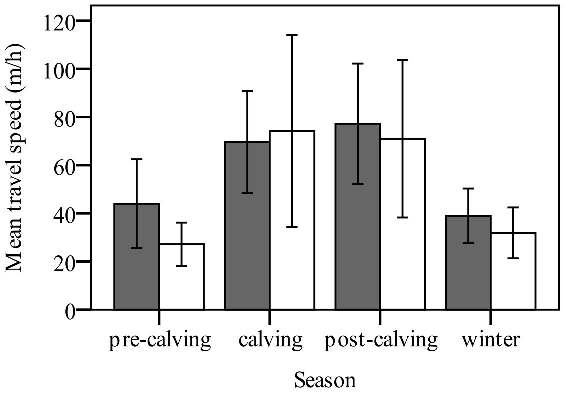

Figure 5. Seasonal variation of travel speed of female moose (n = 3) (±95% CI) before (grey bar) and after (white bar) the inclusion into the wolf territory. Values represent the original, non-transformed data.

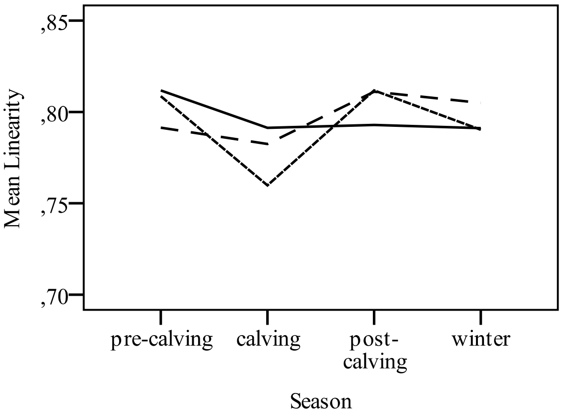

Figure 6. Seasonal variation of linearity (±95% CI) of female moose (n = 3) F07005 (solid line), F07010 (dotted line) F07011 (dashed line) (Appendix 2). Values represent the original, non-transformed data.

DISCUSSION

Seasonal home range size

I found that seasonal home size was related to wolf presence, since the best model indicated variation in home range size due to variation in the exposure to wolves, reproductive status, and seasons. Moose home ranges tended to be larger in areas of the wolf territory where wolves showed a higher presence frequency. The fact that this effect was pronounced using both 95% Kernel and 100% MCP home ranges estimates, indicated that this increase in relation to exposure to wolves was significant, irrespective of home range estimation method. This can be controversial to what is presented by Fraker & Luttbeg (2012). These authors state that smaller movement range may limit the availability to more profitable habitats but increases the probability of spotting other animals, and as the movement range increases the ability of visually detecting other individuals decline. My results showed that in a moose population, known to show little adaptation to re-colonizing wolves (Sand et al. 2006a, Eriksen et al. 2009, 2011), home ranges which were more intensively used by wolves were larger, possibly due to increased mobility induced by wolves. However, comparing years with and without wolf presence for the same female moose, I could not detect an increase in seasonal home range size following the establishment of wolves. Possibly this subsample of three individuals included in this analysis did not capture the above described effect of the wolves. This is possible, considering that the effect of wolves may be highly dependent on the location of the moose home range within the wolf territory (Eriksen et al. 2009). Furthermore, this analysis did not take the degree of exposure to wolves into account, but only considered the general absence or presence of wolves (based on home range overlap). This may explain why I did not find larger home ranges of these three female moose in more intensively used areas within the wolf territory.

Home range size of female moose without calves was larger than females with calves, and this was most pronounced during the calving season. van Beest et al. (2011) also showed that females with calves reduce seasonal home range sizes compared to alone females during the summer. In contrast, other studies found no difference in home range sizes respective of reproduction status (Cederlund & Okarma 1988) or show that females with calves have significantly larger home ranges during the autumn (Cederlund & Sand 1994). Concerning changes in home rage size between seasons, the estimation method was important, since the two methods yielded slightly different results. According to both estimations, the smallest seasonal home ranges were observed during pre-calving season and this is also shown in other studies (Phillips et al. 1973, Cederlund & Okarma 1988, van Beest et al. 2011). The 95% Kernel home range estimates indicated that seasonal home range size was largest during winter for both reproductive categories. I did not find evidence that this was described earlier, although Phillips et al. (1973) reported restricted movements of moose cows during the rut, followed by an increase in movement rates and also larger home range size during late fall and early winter (September to December), compared to late winter (January- April). The 100% MCP method showed that home ranges were the largest during the post calving season and smaller in the winter, which was similar to what was described by Stenhouse et al. (1995) and Cederlund & Sand (1994) although only for females with calves. In older studies, VHF transmitters are used for tracking the movement of moose, therefore minor differences in results of later studies applying GPS technology are not surprising and may be due to the increased precision and accuracy provided by these innovative devices (Cagnacci et al. 2010, Kie et al. 2010). Additionally, differences in home range size estimated with the 95% Kernel and the 100% MCP methods may come from the different principals of the two approaches. The Kernel method is based on the intensity of area utilization, allowing to identify multiple centers of activity and excluding unused areas form the estimation (Worton 1989, Hemson et al. 2005), while the MCP method includes all locations, connecting the outermost ones and not differentiating between how intensively different areas are used by the animal (Kenward 1987, Lawson & Rodgers 1997).

Travel speed

For travel speed, factors that represented the effect of wolves were not included in the best model, indicating that other external factors were generally more important for moose travel speed than the re-establishment of wolves. Nonetheless, I found that female moose had lower travel speed inside than outside the wolf territory, which may indicate that moose suppressed their movements in areas with wolf presence. Such a reduction of activity levels if predators are present in the area can be a beneficial anti-predator behavior, given that a moving animal can be detected by a predator more easily than an inactive animal (Lima and Dill 1990). On the other hand exposure to wolves showed increased travel speed with the amount of wolf locations in the individual moose home ranges. Increased movement rates could also be an advantageous behavior in order to escape predators

(Mitchell & Lima 2002). Comparing speed between the years with and without wolf presence revealed that the three female moose reduced their travel speed after the inclusion into the wolf territory. These findings provided basis for the assumption that moose females generally reduced their travel speed in relation to establishment of wolves, but showed elevated mobility in areas with a high exposure to wolves, i.e. with increased probability of encounters with wolves. Generally lower travel speed inside the wolf territory can be due to increased vigilance (Berger 1999, White and Berger 2001) and suppressed mobility (Lima and Dill 1990) when predators are present in the area. Increased travel speed in areas with higher level of wolf presence can be due disturbance and close encounters with wolves (Gude et al. 2006).

Travel speed was most affected by seasonal changes and reproductive status. I found that travel speed of females was highest during the calving season and the post calving season, while it was reduced during the pre- calving and the winter season. The analysis of travel speed before and after the establishment of wolves also showed a significant seasonal variation, although these three females had the highest mobility during the post calving and the lowest during winter. This can be explained by only minor differences found in travel speed between calving and post calving or between winter and pre calving seasons and possibly by high individual variation in movement responses to the changing of seasons (Vander Wal & Rodgers 2009). Findings of former studies also report that variation in movement rates follow seasonal changes because activity patterns are highly correlated with food quality and availability (Reisenhoover 1986, Cederlund et al. 1989). As more and higher quality forage is available in the spring, moose move more and utilize as much of it as possible, while in the autumn, the decrease in availability and quality of food results in reduced movement rates and gradual switching to less nutritious diet (Renecker & Hudson 1986, Cederlund 1989). Previous studies indicate that movement rates peak in May (Cederlund 1989, Eriksen et al. 2011) or June-July (Vander Wal & Rodgers 2009) and again in August and September (Eriksen et al. 2011, Cederlund 1989). Movements are gradually reduced from October-November (Eriksen et al. 2011) and are lowest around February (Cederlund 1989). In my study, I included May, June and July in the calving season therefore the observed increase in travel speed during calving season was consistent with findings of former studies. Season designations used in the cited studies differ from each other and also from my study, which made it difficult to compare between studies but may explain some of the differences seen in results.

Both reproductive categories of female moose showed elevated travel speed during the summer and autumn whereas females without calves had a more pronounced increase during the calving season. It is expected that females with calves move less intensively during calving season due to the restricted mobility of the calves (van Beest et al. 2011). In this study, females with calves increased their travel speed more moderately during the calving season, compared to females without calves. Inter-seasonal change of travel speed was more pronounced than the differences due to reproductive status, with the exception of the calving season. Season alone explained most of the variation in travel speed, but the distinct differences observed between females with and without calves during the calving season also showed that movement patterns are affected by reproductive status.

Linearity of movement

I found that the directionality of female moose movement did not differ in relation to the presence of the wolves or between before and after the establishment of wolves. Although research in North America showed that as a response to wolf presence, female moose with calves are likely to reduce their foraging in order to increase vigilance (Berger 1999, Berger et al. 2001), behavioral adaptations that can affect linearity of movement have not been observed in Scandinavia (Eriksen et al. 2011).

I found that female moose changed between concentrated and directional movements mostly according to seasons and reproductive status. Female moose accompanied by calves moved less directional. This difference in linearity was most pronounced during the calving season and explained most of the seasonal variation, considering that no such reduction was seen in females without calves. Females without calves generally travelled more directional in all seasons with a lower variance in this movement pattern. Foraging movements are generally characterized by an increased variety of turning angles and shorter steps in the movement path, while if not foraging, animals move in a more direct manner (Fryxell 2008). If this is linked to resource availability, more concentrated movement can be expected when a lot of food is available and longer, more directional movements as resources get scarcer (Fryxell 2008). The fact that this reduction of linearity was only seen in females with calves, indicated that this was a result due to the limited movement abilities of their young (Eriksen et al. 2011), and increased vigilance (Berger 1999, White and Berger 2001). Eriksen et al. (2011), also observed minimal variation in linearity of female moose between seasons, except for a reduction in June which they explained as restricted movements due to taking care of their young.

Conclusions

My results showed that the re-establishment of wolves in Sweden may to some extent affect the movement patterns of female moose. In conclusion, I found that differences in seasonal home range size of female moose in the study area correlated with exposure to wolves and that travel speed and linearity of movement was mostly affected by seasonal changes and differences in reproductive status. By applying the method of model selection (Burnham & Anderson 2002), I discovered that the generally suppressed travel speed and the more elevated mobility observed in certain, more intensively used areas was related to presence of wolves. Overall, my results supported that mobility of females was more strongly influenced by external factors and their reproductive status, than the return of their long absent natural predators.

Former studies investigating the possible effect of the re-establishment of wolves on Scandinavian moose found that moose do not adapt to this predator (Berger et al. 2001, Sand et al. 2005, 2006, Wikenros 2011, Eriksen et al. 2009, 2011). Overseas, prey species e.g. elk (*Cervus elaphus*), bison

(*Bison bison*), and moose show strong behavioral adaptation towards the re-establishment of wolves with changes in habitat selection (Stephens & Peterson 1984), increased vigilance (Berger 1999, White and Berger 2001, Berger et al. 2001, Laundré et al. 2001), shift in feeding and birthing sites (Berger et al. 2001) or aggressive behavior (Mech & Botiani 2003). These anti-predator behavioral responses have not yet been found in Scandinavian moose (Berger et al. 2001, Sand et al. 2005, 2006, Wikenros 2011, Eriksen et al. 2009, 2011) and it remains an interesting question if they ever will be. There are major differences between the two continents regarding predator-prey history. In Scandinavia, predators were absent for a much longer period than in North America (Sand et al. 2006a), and during most of this time the moose population was intensively harvested by humans (Lavsund & Sandegren 1989), in contrast to no or a very low hunting pressure overseas (Orians et al. 1977, Peterson et a. 1984). In Scandinavia, human harvest have completely replaced predation and even remained the main mortality factor after the re-establishment of wolves (Wikenros 2011). With increased density of wolves, prey species may invest more in anti-predator adaptations, balancing the cost with reducing predation risk (Creel et al. 2005). A combination of factors such as larger wolf territories (Fritts & Mech 1981, Hayes & Harestad 2000), lower densities of wolves, high moose:wolf ratios (Pedersen et al. 2005), intense current and past hunting harvest (Lavsund & Sandegren 1989, Cederlund & Sand 1991, Wikenros 2011) and a more homogenous landscape (Cederlund & Okarma 1988, van Beest et al. 2010 Olsson et al. 2010) may alone or in combination contribute to wolves using individual moose home ranges less intensively in Scandinavia and may possibly explain why behavioral adaptations of moose to wolves are not as uniform and extensive as found in North America.

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Appendix 1. GPS collar IDs, sex, birth year, as well as dates of captures and last locations acquired from GPS collared wolves.

Collar ID	Sex	Territory	Birth year	Date of capture	Last GPS location
M1347	male	Uttersberg	2001	2005/03/16	2006/02/07
M1345[1]	male	Uttersberg	2001	2007/03/09	2009/10/07
F2159	female	Uttersberg	1999	2006/01/27	2008/07/05
M7571	male	Hedbyn	2007 or 2008	2010/02/11	2010/04/13
F7572	female	Hedbyn	2007 or 2008	2010/02/11	2011/02/15

[1]same individual as M1347

Appendix 2. GPS collar IDs, sex, birth year, dates of captures and last locations acquired from GPS collared moose as well as the number of estimated seasonal home ranges. Females excluded from the analysis due to low number of locations are shown in *italics*. Females used in the analysis of movement variables before and after wolf establishment are shown in **bold.**

Collar ID	Sex	Birth year	Date of capture	Last GPS location	Seasonal home ranges (n)
F07001	female	1997	2007-03-05	2012-01-10	14
F07002	female	2004	2007-03-05	2012-01-10	14
F07003	female	2002	2007-03-06	2009-10-23	7
F07004	female	2006	2007-03-08	2007-12-12	2
F07005	**female**	**2000**	**2007-03-08**	**2012-01-10**	**14**
F07006	female	2001	2007-03-08	2011-11-26	14
F07008	female	1997	2007-03-09	2007-08-23	1
F07009	female	2005	2007-03-09	2009-08-29	9
F07010	**female**	**2002**	**2007-03-09**	**2012-01-10**	**14**
F07011	**female**	**2005**	**2007-03-09**	**2011-07-19**	**14**
F07014	female	2006	2007-03-10	2007-09-22	1
F07014a[1]	female	2006	2010-03-31	2012-01-10	3
F07015	female	2002	2007-03-10	2009-08-31	9
F07017	female	1997	2007-03-10	2011-12-11	6
F07018	female	1999	2007-03-11	2008-01-30	3
F07019	female	2002	2007-03-11	2009-08-09	8
F07020	female	1991	2007-03-11	2010-12-15	12
F07021	female	2002	2007-03-11	2009-11-14	10
F07022	female	2006	2007-03-11	2008-01-03	2
F07023	*female*	*2006*	*2007-03-12*	*2007-07-11*	*0*
F07024	female	2003	2007-03-12	2009-07-03	8
F10001	female	2008	2010-03-30	2010-11-18	2
F10002	*female*	*2004*	*2010-03-30*	*2010-07-22*	*0*
F10004	female	2007	2010-03-30	2012-01-09	3
F10008	female	2006	2010-03-31	2010-12-23	2
F10009	female	2001	2010-03-31	2012-01-10	3
F10010	*female*	*2007*	*2010-03-31*	*2010-06-30*	*0*
F10012	female	2006	2010-03-31	2010-09-29	1
F10013	*female*	*2005*	*2010-03-31*	*2010-06-27*	*0*
F10014	female	1999	2010-03-31	2010-08-17	1
F98015	female	1998	2010-03-31	2012-01-10	3

[1]same individual as F0714

Appendix 3. Parameter values of the models with the lowest AIC_C values (from Table 1.) for the response variables travel speed (m(h), linearity and seasonal home range size (km^2). Models were tested on the 'reduced' dataset (n = 144).

Model	Response variable	*n*	Fixed factors		β	SE	P
A3	Travel speed	144	intercept		3.623	0.061	**< 0.001**
			season	pre-calving	0.063	0.061	0.300
				calving	0.681	0.051	**< 0.001**
				post-calving	0.596	0.047	**< 0.001**
				winter	0	0	
			reproduction	with calf	-0.153	0.039	**< 0.001**
				without calf	0	0	
B3	Linearity	144	intercept		3.068	0.022	**< 0.001**
			season	pre-calving	0.003	0.023	0.911
				calving	-0.087	0.020	**< 0.001**
				post-calving	0.023	0.017	0.171
				winter	0	0	
			reproduction	with calf	-0.089	0.013	**< 0.001**
				without calf	0	0	
C9	Home range size (95% Kernel)	144	intercept		985.933	128.734	**< 0.001**
			season	pre-calving	-206.608	98.996	0.039
				calving	-9.761	71.254	0.891
				post-calving	-131.143	71.776	0.070
				winter	0	0	
			reproduction	with calf	-253.438	27.107	**< 0.001**
				without calf	0	0	
			wolf exposure		136.587	9.465	**< 0.001**
D9	Home range size (100% MCP)	144	intercept		1093.183	144.527	**< 0.001**
			season	pre-calving	-202.968	144.776	0.079
				calving	82.344	99.545	0.410
				post-calving	122.778	98.480	0.215
				winter	0	0	
			reproduction	with calf	-336.544	71.296	**< 0.001**
				without calf	0	0	
			wolf exposure		71.124	12.105	**< 0.001**