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The effect of snow depth on movement rates of GPS-collared moose

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Abstract

During deep snow conditions, wildlife must balance between minimizing movements to conserve energy while seeking high amounts of browse to gain the energy. Knowledge of how snow begins to hinder their movements is therefore vital when predicting their wintertime behavior. We assessed the phenomenon with moose. Movement data from 122 GPS-collared moose were integrated with snow depth data from designated measurement stations. The effects of increasing snow depths on moose movement rates were then modeled with spline regression. The study was conducted in Finland, between 2009 and 2011. The moose were known for their sex and for the presence of calf at heel. On average, the movement rates decreased sharply until snow depths of ca. 30–40 cm, after which further significant decreases were not seen. The movement rates decreased from several kilometers per day to less than 500 m per day. Moose in the northernmost study area with the deepest snow covers moved as much as the moose in the other areas with less snow. Although we saw differences in the movement rates between males and females, differences between individuals were markedly higher than those caused by sex or a calf at heel. Moose are keystone species whose heavy browsing, especially during winter, can have profound effects on vegetation and forest regeneration. As snow covers in large parts of the boreal zone are predicted to decrease due to warming climate, the wintertime movements of moose and how they affect the local vegetation will remain relevant questions.

Keywords Winter · Climate change · Movement · Moose · Ecology · Splines

Background

Movements and range shifts as well as habitat selection of wildlife have gained increased attention due to noted effects of climatic and anthropogenic changes (Singh et al. 2012; Melin et al. 2014, 2019; Tucker et al. 2017). Regardless of climate change or human effects, the changing of seasons is still a major driver of wildlife behavior especially across the boreal zone where the onset of winter and the arrival of snow have a crucial effect on wildlife (Pruitt 1978; Boelman et al. 2019). The effects of snow on boreal mammal communities are noticeable: deep snow prevents access to otherwise preferable food sources, but also directly restricts movements of most mammalian species. To cope with winter, boreal mammals have adopted with various ways. Some mammals,

like the brown bear (*Ursus arctos*), hibernate through winter, while others such as the woodland caribou (*Rangifer tarandus caribou*) migrate to areas with more favorable conditions during winter (Duquette 1988; Boelman et al. 2019). Those who stay are then commonly well adapted to the cold temperatures as well as the deep snow (e.g., a thicker winter coat and the existence of physiological and morphological features that aid moving in snow).

Recently, Boelman et al. (2019) highlighted the need of temporally and spatially representative datasets of snow cover in order to assess the effects that changing snow conditions may have on boreal wildlife. When it comes to species such as ungulates, an equally relevant question is how their reaction to snow affects the way they interact with their surroundings as ungulates, through their browsing followed by urinating and defecating, are often keystone species in their habitats (McInnes et al. 1992; Kielland and Bryant 1998). Therefore, the effect of changing snow conditions may extend beyond the animal itself as a significant change in the movements or habitat use patterns of an ungulate may have cascading effects on the vegetation of the surrounding landscape (Duquette 1988; Nevalainen et al. 2016; Gilbert et al. 2017).

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This is especially true for a large boreal ungulate present across the entire boreal zone: moose (*Alces alces*). In the coldest winter months, an adult moose can consume up to 5–10 kg of dry matter per day (Renecker and Hudson 1985), leading to extremely high local browsing pressure, especially in areas where moose form wintertime herds. In Finland, this behavior of minimizing movements coupled with herding affects the local vegetation and tree species composition especially during winter when moose browsing causes considerable damage in seedling stands and young forests (Heikkilä 1994; Milligan and Koricheva 2013; Wallgren et al. 2013; Nevalainen et al. 2016).

When it comes to moving in snow, moose is comparably well-equipped: it has one of the highest chest heights among boreal ungulates as well as a comparably low foot load on snow (Telfer and Kelsall 1984). Yet, moose behavior during winter suggests the species generally avoids moving in deep snow to conserve energy (Kelsall and Prescott 1967; Ball et al. 2001; Lundmark and Ball 2008; van Beest et al. 2011). In Nova Scotia, Prescott (1968) noted that moose began to concentrate in their preferred wintering areas as snow depths reached ca. 76 cm, while other researchers have noted that snow depths of 40–70 cm will restrict moose movements and those of over 90 cm can be critical for survival (Nasimovich 1955; Kelsall and Prescott 1967; Codey 1974). In the past, the question of how snow depth affects moose movements has been studied with field-based estimates of snow depth, coupled with tracking data. Kelsall and Prescott (1967) estimated moose movements in relation to snow depths via track densities: frequency of local tracks was measured together with snow depths, which was assumed to show the degree of movements as a function of snow depth. More recently, Lundmark and Ball (2008) assessed the question by observing trail-following behavior and sinking depths of radio-collared moose in relation to snow depth. On a wider scale, van Beest et al. (2011) assessed the winter home range sizes of GPS-collared moose in relation to landscape-level estimates of snow depth, while Singh et al. (2012) linked nationwide snow data with location data from GPS-collared moose to assess their migratory behavior in relation to various environmental cues, including snow.

Despite the past studies on the topic, the details of how and at what depths snow begins to hinder and guide moose movements have not been thoroughly studied by observing movements of individuals. The demand for this kind of information is foreseen to increase due to the effects of climate change on the duration of winter and snow cover (Ruosteenoja et al. 2016; Boelman et al. 2019), especially since the behavior (and even calf survival) of moose is affected by snow depths and wintertime temperatures (Renecker and Hudson 1986; Mech et al. 1987; Broders et al. 2012). For Finland, the predicted effects point to warmer winters with increased precipitation (Ruosteenoja et al. 2016), which especially in southern parts

of the country mean shorter winters with less snow, while in northern regions, they may mean more difficult snow conditions: thinner snow covers, but which due to the increased precipitation will be denser (Ruosteenoja et al. 2016; Turunen et al. 2016). To study how moose movement rates depend on snow depths, this study integrates data from a nationwide network of snow depth measurement stations with movement data from 122 GPS-collared moose, at a daily level. The aim is to model moose movements in varying snow depths and especially to analyze whether moose show a threshold in relation to snow depths beyond which their movements no longer decrease. In addition, the potential effects of geographic region, sex, and the presence of calf at heel are examined.

Materials and methods

Study area

The study was conducted in three separate regions in Finland that differ considerably in relation to winter conditions (Fig. 1).

In north, permanent snow (i.e., snow that does not melt until spring) typically arrives between mid-October and early November. In south and west, this happens between late November and early January. Maximum snow depths in the study areas range from 50 to 100 cm in north, 25 to 75 cm in west, and 10 to 60 cm in south (Table 1).

The moose densities in the study areas ranged from 3–4 moose/1000 ha in south and west to 2–3 in north (Pusenius et al. 2017). Predators were virtually non-existent in the south area. A small number of brown bears (*Ursus arctos*) were present in north and west, and at the time the main predator of moose, the gray wolf (*Canis lupus*) was present only in the south-eastern parts of the north area (Luke (Natural Resources Institute Finland) 2018).

Data on snow depths and moose movements

Data on snow depths were obtained from the Finnish Meteorological Institute (FMI). The data contained information on daily snow depths from 272 measurement points located across Finland (Fig. 1). The daily snow depths are read manually from a fixed measurement pole. The locations of the snow depth measurement points are such that they would be as reliable as possible in representing the snow conditions of the wider landscape (e.g., an airport would be too open, and potentially more subjected to winds that can carry away the snow). On average, the nearest snow depth measurement stations were ca. 13–25 km away from the locations of our moose (13 km in south, 20 km in west, 25 km in north).

Moose location data were provided by Natural Resources Institute Finland (Luke). The GPS collars (Vectronic) installed on the moose stored positions on an hourly basis and

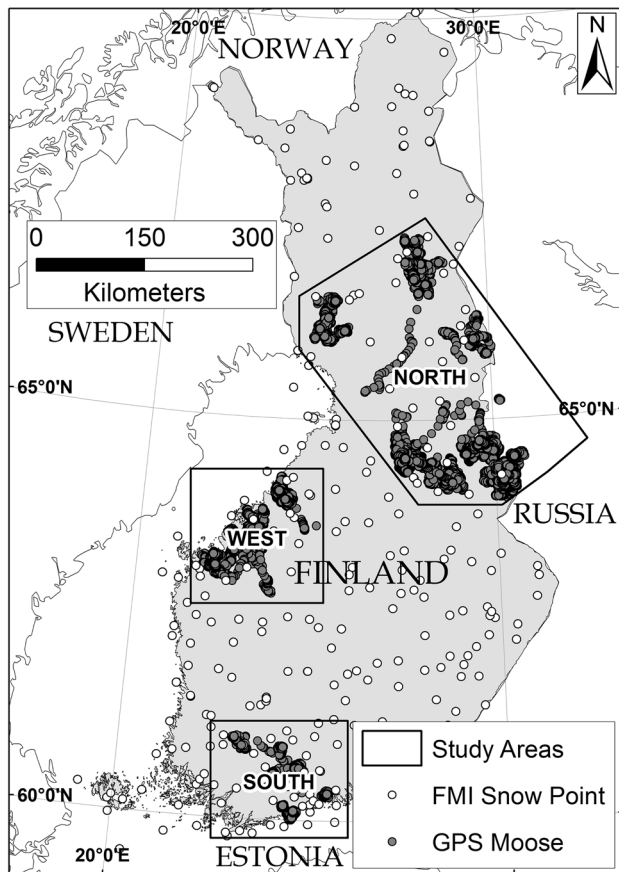


Fig. 1 Finland overlaid with the locations of the GPS-collared moose and with the locations of snow depth measurement points of the Finnish Meteorological Institute (FMI)

sent the data to an external database (WRAM—Swedish University of Agricultural Sciences 2011) every fourth hour via the GSM network (Global System for Mobile Communications). The collars were installed in the winter of 2008–2010 by the Finnish Game and Fisheries Research Institute (now part of Luke), in co-operation with the Finnish Food Authority. For collaring, the moose were located from helicopter and tranquilized with ketamine-medetomidine combination using a dart gun. The average fix rate of GPS positioning was assessed in Melin et al. (2014, 2016a) and it was noted to be ca. 99% (excluding periods of total blackout that occurred

Table 1 Landscape-scale estimates of the arrival dates of the snow and maximum snow depths in the three study areas during the study period

Study area	Arrival dates of permanent snow (dd-mm)*			Maximum snow depths (cm)*		
	2008–2009	2009–2010	2010–2011	2008–2009	2009–2010	2010–2011
North	1.–15.10.	1.–15.10.	15.11.–1.12.	50–75	75–100	50–100
West	15.–31.12.	15.–30.11.	30.12.–15.1.	25–50	50–75	50–75
South	15.–31.12.	1.–15.12.	30.12.–15.1.	10–50	25–50	25–75

*The numbers tell the ranges within the study areas based on statistics of the Finnish Meteorological Institute. For example, in the winter of 2008–2009, maximum snow depths varied between 50 and 75 cm in different parts of the north area

Table 2 The GPS-collared moose data used in the study divided into three groups accordingly

Study area	Number of GPS-collared moose			Total
	Males	Barren females	Females with calves*	
North	35	32	23	67
West	8	25	14	33
South	6	16	7	22

*The amount of females moving with a calf at heel

predominantly during summers). Positioning accuracy of the collars was noted to range from 10 to 30 m, which was quantified by analyzing the positioning deviations of a motionless GPS collar in a forest.

This study focused on data from snow-covered periods between 2009 and 2011. The data consisted of movements of 122 moose (49 males and 73 females) with 44 cases of females with a calf at heel (validated with field observations during and after each autumn’s hunting season, but not during winter). The tracking period of individual moose varied from 6 months to up to nearly 2 years depending on the duration of batteries, GPS failures, or dropped collars. Altogether, the final data consisted of 363,134 moose locations (Table 2).

The movements of moose were described with a metric *Displacement*, which was derived by summing the total displacements (in meters) between consecutive hourly GPS locations from a 24-h period (midnight to midnight). Data on snow depths were linked to moose locations so that each moose location was associated with snow depth data from the FMI data point that was closest to it during the day of positioning.

Statistical analysis

A common hypothesis is that the effect of increasing snow depth on moose movements is non-linear. We chose to test this hypothesis, and to analyze the potential non-linearity with restricted cubic spline regression (Harrel 2015; Mehtätalo and Lappi 2020) that have useful properties for such analyses. Restricted cubic splines offer a flexible way of modeling

curvilinear relationship between the y -variable and the predictor in the context of linear models. In a restricted cubic spline, the regression function is formulated from pieces of third-order polynomials, which are joined at knots so that they have continuous derivatives. Furthermore, the function is forced to be linear at the tails (beyond the last knots). The flexibility is controlled by the number of knots K . Technically, the spline regression is implemented by defining a total of $K-2$ non-linear transformations of the original predictor, which are called the base functions. These base functions are entered into the linear mixed-effects model as predictors in addition to the non-transformed original predictor variable. The models were defined for observation j of moose i in year t as:

$$y_{itj} = x'_{itj}\beta + a_i^{(1)} + a_i^{(2)}\text{snow}_{itj} + b_t^{(1)} + b_t^{(2)}\text{snow}_{itj} + e_{itj}$$

where snow is the snow depth in cm, $(a_i^{(1)}, a_i^{(2)})$ is a bivariate normal random effect for moose, $(b_t^{(1)}, b_t^{(2)})$ a bivariate normal random effect for year, and e_{itj} is the zero-mean residual error with variance

$$\text{var}(e_{itj}) = \sigma^2 \left| \tilde{y}_{itj} \right|^{2\delta}$$

The fixed part $x'_{itj}\beta$ included the binary predictors for sexual status (“Female,” “Female with calf,” and “Male”), a curvilinear function that shows the effect of snow depth, and the interaction between the binary predictors of sexual status and the curvilinear snow cover function. This curvilinear response to snow cover was modeled as

$$\beta_1\text{snow}_{itj} + \beta_2c_{itj}^{(1)} + \beta_3c_{itj}^{(2)} + \dots + \beta_{K-1}c_{itj}^{(K-2)}$$

where the last $K-2$ terms are the truncated power basis functions of form:

$$c^{(k)} = (\text{snow} - t_k)_+^3 - (\text{snow} - t_{K-1})_+^3 \frac{(t_K - t_k)}{(t_K - t_{K-1})} + (\text{snow} - t_K)_+^3 \frac{(t_{K-1} - t_k)}{(t_K - t_{K-1})}$$

where $(\text{snow} - t_k)_+^3$ is zero when $\text{snow} < t_k$ and $(\text{snow} - t_k)^3$; otherwise, t_1, \dots, t_K are the knots that are selected from the range of variable “snow.”

Different options were tested in the selection of the number of knots and their location. These were based on the recommendations of Harrel (2015) as well as on the noted thresholds at which moose movements had changed in past studies. Based on these, a maximum of four knots were allowed in the models to avoid excess complexity. Similarly, models were tested with a minimum of three knots in order to avoid oversimplifying the movement patterns. The models with 3 and 4 knots were then compiled and their fit to the movement patterns was observed and compared against

one another visually and with Akaike Information Criterion (AIC) (Akaike 1974). If the model with four knots did not result in a better fit, the less complicated model (i.e., the spline with three knots) was preferred. The differences in the movement pattern between different classes of sexual status (“Female,” “Female with calf,” and “Male”) were analyzed using conditional F -tests. First, a test was conducted to see whether the group-wise differences were significant, and if so, post hoc tests were conducted to see which of the groups differed from the others in terms of movement rates: males versus barren females, barren females versus females with calves, and males versus females with calves. Modeling was conducted in R (R Core Team 2020) with the package *nlme* (Pinheiro et al. 2018) and figures were drawn with the package *ggplot2* (Wickham 2016).

Results

The spline models chosen to depict the relationships between snow depth and moose movements were built with four knots in all study areas; four knot-splines resulted in lowest AIC among the tested models and showed visually good fit in the data. The knots were placed at 5th, 35th, 65th, and 95th quantiles of the range of snow depth values in each study area as suggested in Harrel (2015). Snow depth caused significant decreases in moose movements, and the movement patterns themselves were non-linear in relation to the accumulation of snow. The three moose groups differed significantly from one another in relation to their movement patterns: barren females were different from females with calves ($p=0.03$), barren females were different from males ($p<0.001$), and males were different from females with calves ($p<0.001$). In addition, significant variation between individuals was present among all the three groups (Table 3).

Depending on the region, the movement-decreasing effect of snow continued until the depths of approximately 30–40 cm beyond which further increments in snow depth did not cause additional decreases in movements. In south, males moved the most, followed by barren females and females with calves. In west, females with calves moved the most, followed by barren females and males, but the differences were smaller than in south. Similarly, in north, the movement patterns between the three groups were not as high as in south. In north, the snow depths reached 100 cm, but this did not cause additional declines in the movement rates of any of the moose groups (Fig. 2). The moose movement patterns in relation to snow were significantly different between the three study areas (DFn=24, DFd=23901, F -value=7.93, $p<0.001$).

When comparing the movements of different moose groups across the three study areas (Fig. 3), the movement patterns of males are most similar. Apart from the sudden

Table 3 The parameter estimates of the final spline regression model. For better visualization and comparison, the results area displayed by study areas

	North		West		South	
	Coefficient	Std. error	Coefficient	Std. error	Coefficient	Std. error
Fixed effects						
Intercept	1861.55	76.29	1791.52	81.64	1612.22	113.95
SnowDepth	- 31.86	4.36	- 35.99	4.83	- 37.02	6.50
Female + Calf	- 135.04	129.19	325.55	286.66	- 659.37	189.25
Male	64.58	110.79	- 23.62	219.24	330.90	256.39
SplinePart 1	0.01	0.00	0.01	0.00	0.01	0.00
SplinePart 2	- 0.01	0.01	- 0.02	0.01	- 0.02	0.01
SnowDepth: Female + Calf	- 1.47	8.07	- 16.77	16.61	31.29	12.35
SnowDepth: Male	- 9.02	6.04	10.58	12.98	- 8.62	14.97
SplinePart 1: Female + Calf	0.00	0.00	0.00	0.01	- 0.01	0.01
SplinePart 1: Male	0.00	0.00	- 0.01	0.01	0.01	0.01
SplinePart 2: Female + Calf	- 0.01	0.01	0.00	0.03	0.03	0.02
SplinePart 2: Male	0.00	0.01	0.03	0.02	- 0.03	0.02
Random effects						
var($a_i^{(1)}$)	0.04 ²					
var($a_i^{(2)}$)	0.0006 ²					
cor($a_i^{(1)}, a_i^{(2)}$)	- 0.908					
var($b_i^{(1)}$)	0.047 ²					
var($b_i^{(2)}$)	0.001 ²					
cor($b_i^{(1)}, b_i^{(2)}$)	- 0.962					
var(e_{ij})	0.15 ² $\left \tilde{y}_{ij} \right ^{2 * 1.29}$					

drop of male movements in south, there are no clear differences as to where males would move clearly the most or the least. On contrary, females with and without calves both move clearly less in south than in the other two study areas. For females with calves, the movement rates in south are the smallest of all the groups, regardless of region.

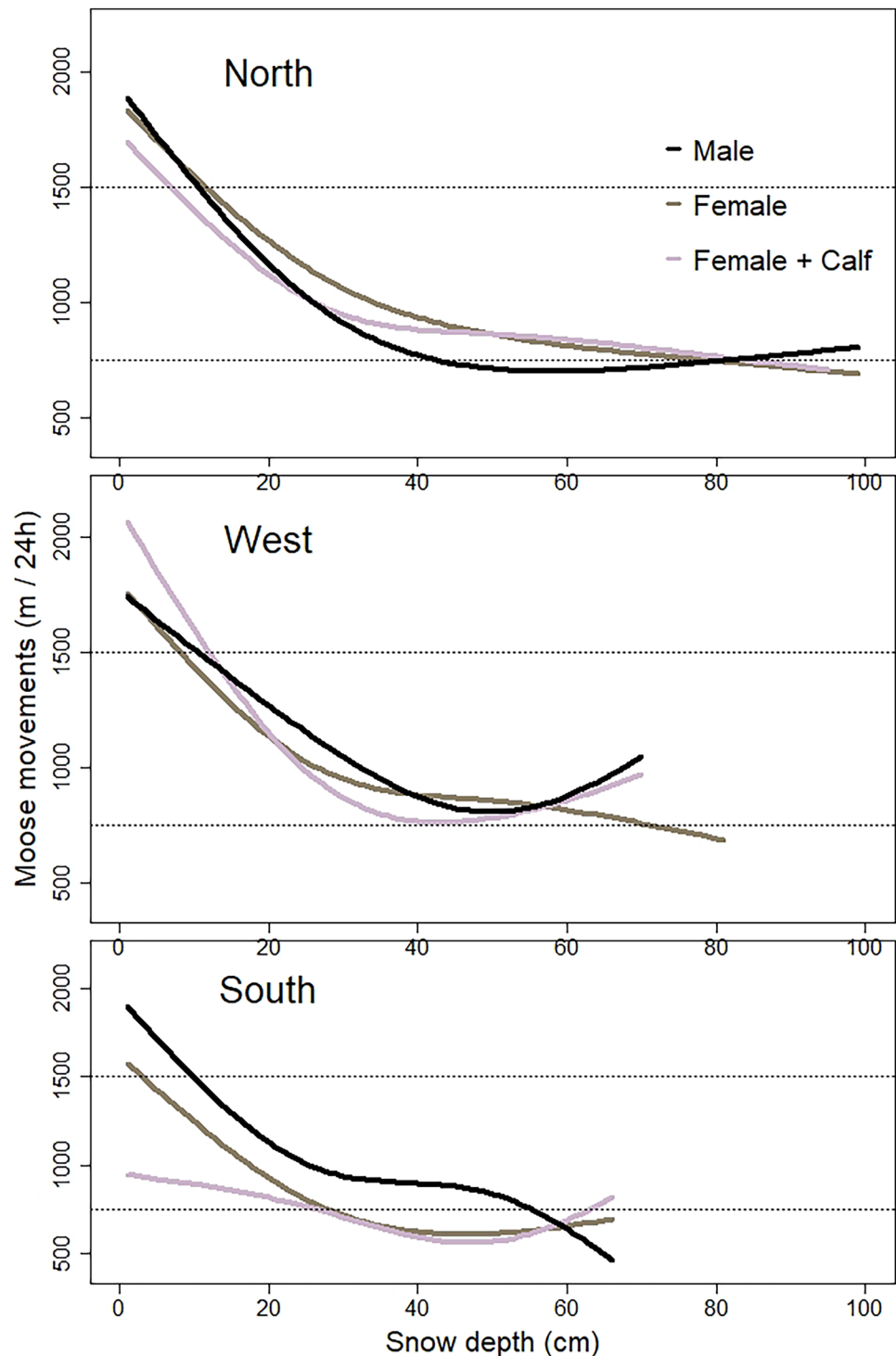
Discussion

Compared to earlier studies, our results gave more detailed views on how and at what depths snow begins to impede moose movements. A factor that we were not able to assess due to lack of data was that of snow density. While snow density is related to the carrying capacity of snow and therefore also to how deep moose sink in the snow, it is also a variable that is hard to quantify (Telfer and Kelsall 1984; Lundmark and Ball 2008; Johnson and Marks 2004). Furthermore, there is undoubtedly uncertainty in estimating the snow depth itself at the exact moose location. We did not have the chance to verify how the snow depths gained from the nearest FMI snow measurement points matched with those prevailing at the locations of moose. While there

is a degree of uncertainty, the method of using nationwide snow depth data has been found useful in the past as well. Van Beest et al. (2011) used data from a single weather station to assess the effect of snow depth on moose home range size in a study area of 1733 km². Similarly, in assessing moose movement and migratory behavior, Singh et al. (2012) also used landscape-level estimates of snow depth provided by the Swedish Meteorological Institute. The earliest field-based studies (Kelsall and Prescott 1967, for example) did neither measure the snow depth at moose locations but assessed at what snow depths moose moved away from a specific site. Therefore, while there is variation in snow depths within any landscape, the use of the FMI data was the only feasible method to link daily estimates of snow depths to each moose location at least in the near vicinity.

The results from our analysis agreed with those of earlier studies on the general phenomenon, but with differences in how the deep snow affects moose. While there were minor differences in the movement rates themselves, the general effect of snow depth decreasing movements was found among all the groups (male, female, female with calf). Depending on the region and sex, a threshold seemed to occur at snow depths between 30 and 40 cm beyond which

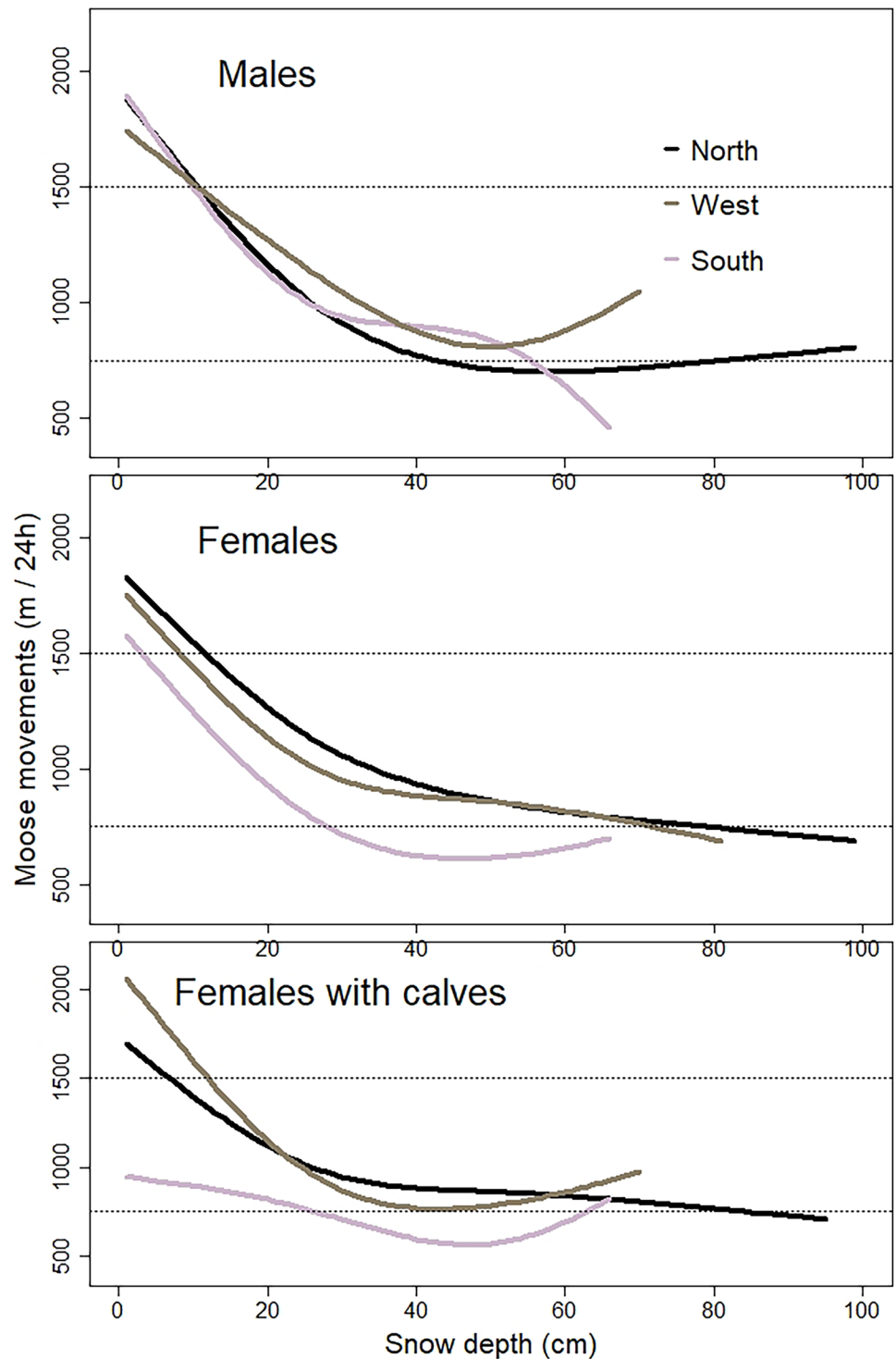
Fig. 2 Fitted spline regression curves showing the response of moose movement rates to snow depths in the three study areas. The two horizontal lines are drawn at movement rate values of 750 m and 1500 m



movement rates did not decrease significantly despite increasing snow depths (Figs. 2 and 3). Kelsall and Prescott (1967) saw moose movements being impeded (based on observed track densities) at snow depths of ca. 70 cm and to cease almost completely after 90 cm. Nasimovich (1955) suggested that depths of 60–70 cm will impede the movements of Eurasian moose significantly and that depths of

100 cm are critical. Similarly, Codey (1974) stated that snow depths of > 40 cm will have a mild restricting effect on movements, depths of 60–70 cm will restrict movements, depths of over 70 cm will impede movements, and those of over 90 cm can even increase mortality. Our results indicated that movements began to decrease already at much lower snow depths: this threshold was ca. 30–40 cm for all of the

Fig. 3 Fitted spline regression curves showing the response of moose movement rates to snow depths in the three groups (males, females, females with calves). The two horizontal lines are drawn at movement rate values of 750 m and 1500 m



study areas (Figs. 2 and 3). Furthermore, our results showed no further significant decreases in moose movements regardless of increasing snow depth, not even in the north area where snow depths reached 100 cm. Interestingly, the moose in north, even during the deepest snow conditions, moved just as much as, or even more than, the moose in the other areas with less snow. A probable cause of this phenomenon

is that in the north vegetation is more sparse, meaning that the lower quality food needs to be searched more intensively, as well as from larger areas—even during the deep snow conditions (DeGiudice et al. 1997; Edenius 1991; Schwartz et al. 1987). Here, the moose of the northernmost study area move, on average, ca. 500–1000 m each day even when snow depths were above 70 cm.

Earlier studies have not thoroughly assessed differences between sexes nor the effect of calf, but it has been noted that from many boreal ungulates the moose shows the least sexual dimorphism in relation to how their movements respond to snow (Telfer and Kelsall 1979, 1984). Our results, for the most parts, agree on this assumption: the depicted movement patterns of each group in Figs. 2 and 3 show that while in some cases the group-wise responses to snow do differ, there are no systematic patterns where females with calves, for instance, would always be different from the other groups. Instead, a clear result was that individual-level variation in movement rates as well as in responses to snow depths was very high (Table 3). Similar results were gained also by Wattles (2011), who showed that the home range sizes and movement rates of moose during different seasons varied significantly between individuals regardless of their reproductive status. The only exception was the considerably low movement rates of females with a calf at heel in south—whether compared to other moose groups, or to females with calves in west or north (Fig. 3).

In general, just how the changing snow conditions affect keystone species such as boreal ungulates has been of wide interest in recent research. Boelman et al. (2019) discussed how the changes in the seasonality of the snowscapes will have cascading effects on a wide range of wildlife species: ones for which the snow provides cover during the time when they have white winter coats, and species that use snow for digging nests and burrows, as well as migratory birds to which the timing of snowmelt is a clock against which egg-laying and incubation begins (Boelman et al. 2019 and references therein). For moose, snow depth is known to affect not only the movements but also the availability of browse (Visscher et al. 2006), and changes in snow cover due to climate change may thus have interactions with the role of moose as regulator of tree species composition (Vuorinen et al. 2020). Furthermore, as our results show (Fig. 2), the movement-impeding effect of snow is clear and thus, the diminishing snow covers may allow the moose to move more also during the winter. This is of crucial importance for browsing damage on Scots pine, which (in Finland) moose use excessively during the winter (Lavsund 1987; Heikkilä and Härkönen 1993). The excessive use of Scots pine is related to its availability—not because it would be the most preferred browse species—and moose is known to select winter habitats also based on how much browse they can offer so that the animal can minimize movements in the deep snow (Heikkilä and Härkönen 1993; Histøl and Hjeljord 1993; Melin et al. 2016a). Now, if the role of deep snow as a restricting factor diminishes in the future, moose may be able to move more during winter in search of more optimal browse—potentially decreasing the wintertime browsing pressure that a single site or a single tree species (the Scots pine) would otherwise face. Indeed, Histøl and Hjeljord

(1993) found moose browsing pressure to increase towards the end of the winter with both resident and migrant moose, which suggests that the accumulation of snow results in even more localized moose and thus more localized browsing pressure. After all, our results here show that during the deepest snow conditions, the moose moved no more than ca. 750 m per 24 h while earlier results with GPS-collared moose and remote sensing data have confirmed that towards the end of the winter, moose (regardless of their sex or reproductive status) begin to utilize areas that offer more shrub-level vegetation (Melin et al. 2016b).

Winters in the Fennoscandian region are warming more rapidly than in other parts of the world (Mikkonen et al. 2015; Ruosteenoja et al. 2016) and in large parts of Central and Southern Finland, snow covers have already decreased due to warming climate. This could even have a positive effect on moose as decreased snow cover would result in better movement abilities and in improved access to food otherwise covered by snow. However, the increase in temperatures would also cause additional heat stress: earlier studies have shown moose's sensitivity and intolerance against both high summer and winter temperatures (Renecker and Hudson 1986; Dussault et al. 2004; Broders et al. 2012; Melin et al. 2014; Montgomery et al. 2019). While moose is among the best-equipped ungulates to move in deep snow, it is also the most ill-equipped one against warming temperatures. As their movements and habitat use are so heavily affected by snow and temperature, future research will show whether moose begin to show range shifts or changes in habitat use in accordance with the evidently shifting thermal and snow regimes. As said, moose are keystone species of boreal forests, and their heavy browsing especially during winter has profound effects on vegetation and forest regeneration. Therefore, the relationships of snow conditions and moose ecology during winter will remain a highly topical question.

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Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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