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Living in Snowy Environments: Quantifying the Influence of Snow on Moose Behavior

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Abstract

We investigated the effects of snow and environmental variables on the depths to which moose sank in snow, and the extent to which moose followed in the tracks of other free-ranging moose in the mountains of the subarctic areas of northernmost Sweden. We tested a method to combine the variables that affect snow quality (e.g. density and hardness) into a single variable that is easier to measure in the field. We also studied the snow conditions in the summer and winter ranges of migrating moose. First, we performed correlation analyses that revealed that sinking depths of moose decreased with increasing snow quality, snow depth, altitude, and air temperature. Next, we next used the Akaike information criterion (AIC) to determine the best model of sinking depth, which indicated that the important variables were snow quality, altitude, and snow temperature. For trail-following behavior, the best model included air temperature only. Regarding seasonal ranges, winter ranges had considerably less snow than the summer ranges that these individual moose left, but snow quality did not differ. Overall, our new method to index snow quality (here, using a dynamometer to measure the force required to press a simulated moose foot down in the snow to the depth of a moose footprint) shows promise, and we suggest that future studies of ungulate winter ecology investigate it further.

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Introduction

Snow is one of the most obvious aspects of winter, and it has long been considered one of the main factors shaping the winter adaptations of ungulates. Both quantity (depth) and quality (density and hardness) of snow are important, as they directly influence food availability, the energy cost of walking, and the movements between and within seasonal ranges (Parker et al., 1984; Dailey and Hobbs, 1989; Bunnell et al., 1990; Sæther et al., 1992; Pauley et al., 1993; Klein, 1995; Mysterud et al., 1997; Nicholson et al., 1997; Jones, 1999; Ball et al., 2001; D'Eon, 2001; Johnson et al., 2001; Sabine et al., 2002; Safford, 2004; Doerr et al., 2005; Dussault et al., 2005; Poole and Mowat, 2005; Visscher et al., 2005). These nutritional and environmental factors are thought to present a strong selective pressure on ungulates since more energy is sometimes spent when moving to feed than what is assimilated from ingested food. The properties of the snow vary greatly both spatially and temporally, and depend on the prevailing conditions during deposition and the metamorphic processes that begin immediately thereafter (Coady, 1974; Halfpenny and Ozanne, 1989; Essery et al., 1999; Marsh, 1999). The importance of snow cover also varies within the winter: snow cover during mid to late winter is generally more important in terms of mortality than early winter, because during that period of the year, wintering ungulates are at their lowest body condition (Ballard et al., 1991).

Depth *per se* has long been the most studied aspect of snow in quantitative studies. The depth of the snowpack varies greatly and is affected by many environmental factors, such as the direction and strength of prevailing winds, and the growth form and shape of the vegetation. Snow is nearly always deeper in the open than under closed canopies, as twigs and branches within the forest retain falling snow. In late winter and spring, however, snow may be deeper in sub-canopy areas as it melts faster in the direct sunshine of the open areas (Essery et al., 1999; Teti, 2003; D'Eon, 2004; Winkler et al., 2005).

The quality of the snow is perhaps of even greater importance than snow depth alone, as it affects the depth to which the animals sink. Low density snow provides little or no support, but as density increases, more support is provided (Coady, 1974; Halfpenny and Ozanne, 1989). When studying winter energetics, sinking depth is perhaps the measure of "effective snow depth" that is closest to the animal's point of view, and it has increasingly gained acceptance among researchers studying winter ecology (Coady, 1974; Bunnel et al., 1990; Schmidt, 1993; Ball et al., 2001; Dumont et al., 2005). As an ungulate steps on the snow, a supportive column of compacted snow forms under its hoof, and the shape and size of this column depends on the quality and temperature of the snow, the form and size of the snow crystals, and the depth and hardness of harder layers within the snowpack (Halfpenny and Ozanne, 1989). The supportive capacity of the snow is extremely variable: fresh snow is nearly always less dense than snow which has been on the ground for some time because metamorphosis occurs so quickly (Halfpenny and Ozanne, 1989; Storck et al., 2002). Snow is also generally more dense in the open than under canopies (Pomeroy et al., 2002; Teti, 2003; Gelfan et al., 2004; Winkler et al., 2005), and as for snow depth, it is also affected by wind, radiation, temperature, and humidity (Essery et al., 1999; Roebber et al., 2003).

Although snow depth is easy to measure, it is not easy to quantify snow quality. Most methods are rather time-consuming for the short winter days and/or require equipment that is difficult to transport or handle in the field. Some of the methods used currently involves, for example, the use of a Ramsonde penetrometer (a cone-tipped metal rod designed to be driven into the snow; Halfpenny and Ozanne, 1989), or a high resolution penetrometer (a thin flared measuring tip connected to an electric transducer; Schneebeli et al., 1999). Other methods involve digging a vertical shaft in the snowpack and measuring the characteristics of each layer individually (Pielmeier and Schneebeli, 2003), performing compression tests (Lang and Harrison, 1995; Bartelt and von Moos, 2000), or measuring snow-water equivalents either by ground-penetrating radar (Lundberg et al., 2006) or by sampling and subsequent melting in the lab (Halfpenny and Ozanne, 1989). None of these measurements give a fast and at the same time reliable estimate of snow quality, and it would therefore be ideal to combine all the characteristics included in snow quality (density, hardness, and profile lamination) into a single variable that is easier to measure in the field. Thus, one of the aims in this study is to test and evaluate a new method for evaluating snow quality from an ungulate's perspective by analyzing their behavior.

Several studies have identified a number of important behavioral adaptations such as migration, selection of areas with snow of more favorable quality and/or quantity, trail making, and many others (Coady, 1974; Telfer and Kelsall, 1984; Fancy and White, 1985; Ballard et al., 1991; Ball et al., 2001). Ungulates like the moose (*Alces alces*) are known to adjust their behavior according to snow properties at both large (migration between seasonal ranges) and small (within over-wintering ranges) scales (Nicholson et al., 1997; Ball et al., 2001; Dumont et al., 2005; Bruggeman et al., 2006). One of the first indications that an animal has noticed the increment in its cost of locomotion caused by changes in the snow properties (and is doing something about it) is when we observe them placing their feet in the footprints of another animal. Several studies on over-wintering animals have shown that the use of old footprints strongly reduces the cost of locomotion and saves valuable energy (Fancy and White, 1985; Murray and Boutin, 1991; Crête and Larivière, 2003). The increment in energy cost for the first animal on the trail is sometimes more than 80% compared to when walking in snow-free areas, while for the animals following behind the increase is only about 30–40%, a saving of more than half (Fancy and White, 1985).

Seasonal migration has long been known to occur in populations of northern ungulates (Coady, 1974; Ballard et al., 1991; Albon and Langvatn, 1992). Migration patterns have most probably evolved to take advantage of spatial and temporal variations in the environment (Nicholson et al., 1997), and the proportion of migrating animals within a population may vary with changes in habitat suitability and climate severity (Dingle, 1996; Ballard et al., 1991). Animal migration is thus a dynamic process that allows animals to adapt to changing habitats. In our study area, moose commonly move in from the surrounding areas and congregate during winter. Preliminary investigations (Nordengren and Ball, unpublished) indicated that food availability is unlikely to be the main reason for this, as all the browse species are heavily overgrazed and less abundant than on the surrounding summer ranges. Rather, the underlying cause appears to be the snow conditions. The study area lies in a local precipitation shadow, and has considerably less snow (mean snow depth = 55 cm) compared to the surrounding areas where the moose spend their summer (mean snow depth =160 cm; see Nordengren et al., 2003, for data on variation in snow depths within the region).

In this study, we examine a promising way to quantify snow quality and the behavior of free-ranging moose in the mountains of northernmost Scandinavia. As in other observational field studies of complex systems with many variables, we expect at least some of the variables to be somewhat intercorrelated. Hence, we approached our data using the model selection methodology from information theory, which is rapidly gaining acceptance among ecologists (Ngo and Brand, 2000; Anderson et al., 2000; Shtatland et al., 2001; Burnham and Anderson, 2002). We first test if the large number of variables concerning snow quality can be combined into one single variable by using a new method that involves quantifying the force needed to press a simulated moose foot through the snow to precisely the depth of a moose footprint made under the same snow conditions. Second, we examine the quantity and quality of snow, together with other environmental conditions, to quantify the relationships among the abiotic variables before including the biotic variable: the moose. Third, we study moose behavior (i.e. trail-following behavior and sinking depth) in relation to snow (depth, quality, and temperature) and other environmental factors (air temperature, vegetation coverage, and altitude). By quantifying the degree to which moose step in the footprints made by other moose, we hope to be able to index the cost of snow in a way more similar to the way the moose experiences this energetic expenditure. Finally, we also studied snow depths and snow quality in the winter ranges of migratory moose, and in the summer ranges that these individual moose left.

Study Area

The study was performed close to Abisko (68°21′N, 18°49′E) in the mountains of Sweden, including Abisko National Park, north of the Arctic Circle. The study area is situated in a local precipitation shadow, with a mean annual precipitation of 320 mm. The mean annual temperature is −0.5 °C, and the ground is generally covered by snow from October to May with a mean snow depth of 55 cm. Climate data refers to the period 1971 to 2000 (Abisko Scientific Research Station). Forested valleys are dominated by mountain birch *Betula pubescens czerepanovii* (Orlova) Hämet-Ahtii in dry to mesic areas, and willow *Salix* spp. in more moist areas. Additionally, aspen *Populus tremula* L., rowan *Sorbus aucuparia* L., and pine *Pinus sylvestris* L. occur as scattered individuals or stands. The field layer is mainly comprised of dwarf shrubs such as bilberry *Vaccinium myrtillius*, lingonberry *V. vitis-idaéa*, crowberry *Empetrum hermaphroditum*, willow *Salix* spp., sedge *Carex* spp., grasses *Poaceæ* spp., and dwarf birch *Betula nana*. The tree line is at 700–800 m a.s.l., and the surrounding mountains reach 1000 to 1700 m a.s.l.

Methods

As a part of a larger project, we immobilized 24 female moose during late winter (February–April) with Ethorphine and Xylazine (Sandegren et al., 1987) using a dart gun (Model 1M, Daninject) from helicopters. Each animal was marked with a radio collar (Televilt International, Lindesberg, Sweden) and unique ear tags. The locations of radio-collared moose were determined by triangulation. The centroids of the home ranges were calculated using the adaptive kerneling (Worton, 1989) option of the program Tracker (Camponotus AB, 1994).

SINKING DEPTHS AND TRAIL-FOLLOWING BEHAVIOR

To measure the behavioral response of moose to variations in snow conditions, we examined very fresh (2–10 min old) footprints from free-ranging moose with radio collars, and from unmarked moose when we were able to observe them directly. We used only back-tracking, so that the behavior of the moose (as evidenced by their footprints) would not be altered by the observer. The proportion of trail-following behavior (i.e. placing their feet in the old footprints made by other moose) was recorded along a minimum of 200 m of each trail, and the properties of the snow were measured immediately adjacent to the footprints. We used a very conservative definition of trail-following behavior: a moose had to put its feet exactly in the footprints of other moose, and not just follow along their trail (which also saves energy, but not as much as when stepping exactly in the footprints of other moose). Clearly, an individual moose that is placing its feet exactly in the footprints of a preceding moose is not doing so by chance alone. By using this strict definition in our test, we hoped to obtain the most "clear-cut" results regarding the behavioral responses. First, we measured the depth of the moose footprint to the nearest centimeter. Second, to assess snow quality, we used a mechanical dynamometer (PIAB model DT/DTN 300, CA Mätsystem AB, Täby, Sweden) attached to a steel extension rod with a replaceable circular disc on the other end of the rod. We were then able to measure the force required to press the disc down through the snow to the depth equal to that of the adjoining footprint. We used a range of disc sizes (1.7, 3.5, 6, and 11 cm) to cover different snow conditions. We could not use a simulated moose foot of natural size, because our field staff was much lighter than a moose and thus unable to push a natural size foot to full depths in the snow. Instead, we used different sized discs so that we could make readings in the middle of the dynamometer's range where it was most accurate (the manufacturer, CA Mätsystem AB, Täby, Sweden, states that inaccurate measurements may result if used below 24% of full scale). Finally, we calculated the force per unit area (kg cm^{-2}) needed to reach the depth equal to the moose footprint. This measurement (force per unit area) is hereafter labeled "snow quality." We hoped that this measure of snow quality (and hopefully "effective snow depth" from the moose's point of view) would relate well to the work the moose itself had to do when walking through the same snow just minutes before. We also recorded the occurrence and location of any harder layers within the snowpack, and total snow depth was measured to the nearest centimeter. We conducted multiple (up to 12) measurements along each 200-m section of the studied moose trails. To avoid pseudo-replication (Hurlbert, 1984), we treated these measurements as subsamples and used their mean in all subsequent analyses. Thus the unit of statistical independence is a 200-m section of a moose trail on a given day under a given set of conditions (hereafter "a moose trail observation"). In addition to snow properties, we also observed altitude, snow and air temperatures, and the vegetation coverage at the site of the moose trails.

SNOW CONDITIONS IN SEASONAL RANGES

Some of the moose initially marked were killed by hunters or vehicles, others migrated beyond our ability to find them, or their radio collars failed, so the number of moose for which we could compare their individual summer vs. winter range conditions was reduced. To best quantify the snow conditions in the ranges *per se* (and not at a particular moose trail), we measured snow depth and snow quality at regular intervals along the 1.5 km sides of a triangle centered on the centroid (Manly et al., 1993) of the home ranges of 9 of the radio-collared moose (mean measuring points per range = 73). We were thus not able to evaluate snow quality adjacent to the footprints of real moose, so instead of pressing the simulated moose foot to the depth equal to that of a moose footprint, we pressed it to a depth of 27 cm (based on preliminary observations).

STATISTICAL METHODS

Pearson correlation analysis was used to analyze the relationship between snow conditions, vegetation, and environmental variables, and also for initial tests on trail-following behavior and sinking depths. As in other studies of complex systems with multiple variables, we expect that some of the variables may not be completely independent. To avoid the pitfalls of performing multiple bivariate analysis, we therefore also approached our behavioral data using the model selection approach from information theory (Anderson et al., 2000; Shtatland et al., 2001; Ngo and Brand, 2000). In systems where more than one hypothesis is possible because of multiple variables, model selection has many advantages compared to the traditional null hypothesis testing and provides a more clear-cut method to identify the best model among several competing models (Anderson et al., 2000; Anderson and Burnham, 2002; Johnson and Omland, 2004; Richards, 2005). We used the Akaike information criterion (AIC) (Akaike, 1973) to assess the effect of environmental factors on sinking depths and trail-following behavior of moose, and to reduce the number of possible models (Anderson et al., 2000; Richards, 2005). The model with the best fit (i.e. the lowest value of AIC) is the one with the smallest expected difference between the model and the truth and should be considered as the model with the most biologically reasonable variables (Richards, 2005). AIC values by themselves are, however, relatively uninformative, so we therefore also calculated the difference in AIC values between the models (Δ) as well as their Akaike weights (W) (Anderson et al., 2000; Richards, 2005). Δ demonstrates the difference in the AIC value of the current model (M) from the minimum AIC value (AIC_{min}) of all models ($\Delta_M = AIC_M - AIC_{min}$), and models with $\Delta < 2$ are all likely to be the best model. The Akaike weight (W) is a measure of the relative likelihood of the current model, and represents the ratio of Δ-values for each model relative to the whole set of candidate models (R). The weights are conveniently normalized to sum to 1, as

$$W = \exp(-\Delta_M * 0.5) \Big/ \sum \exp(-\Delta_R * 0.5). \quad (1)$$

W can be interpreted as the approximate probability that the current model is the best of those considered: a higher value of W thus indicates a "better model." Differences in snow conditions between summer and winter ranges of individual moose were analyzed using the Wilcoxon Matched-Pairs Signed Rank test (Siegel, 1956), with the means of each range as the unit of independence. All tests were done using the SAS statistical package (SAS Institute Inc., 2000).

Results

GENERAL SNOW CONDITIONS

Snow quality (including properties of density and hardness) increased with increasing snow depth ($p < 0.01$, $r_{324} = 0.31$, where 324 is the sample size), air- and snow temperatures ($p^{air} < 0.01$, $r_{308} = 0.21$; $p^{snow} < 0.01$, $r_{273} = 0.22$), and in less vegetated areas ($p < 0.01$, $r_{325} = -0.16$). Snow was deeper at higher altitudes ($p = 0.03$, $r_{369} = 0.11$). Air- and snow temperatures were strongly correlated ($p > 0.01$, $r_{307} = 0.94$). The number of harder layers within the snowpack was too low to be analyzed statistically, so we do not discuss it further in this study.

At the sites of the moose trail observations, mean snow depth was 55.68 cm, air and snow temperatures −0.3 and −1.1 °C, respectively (Table 1), mean vegetation coverage 40%, and mean altitude 472 m a.s.l. (Table 1). Snow quality (as indexed by the

TABLE 1

Summary table showing the variables included in the analyses of sinking depths and trail-following behavior: snow depth, snow quality, snow and air temperatures, sinking depth, altitude, and vegetation coverage. Mean, maximum and minimum values, standard deviations (STD), coefficients of variation (CV), and number of observations (N) are shown in the table.

	Mean	Min	Max	STD	CV	*N*
snow depth (cm)	55.68	2.00	245.00	41.58	74.66	390
snow quality (kg cm^{-2})	1.63	0.04	10.97	2.09	127.80	325
snow temp (°C)	−1.12	−16.00	11.00	4.74	−421.32	365
sinking depth (cm)	21.68	1.00	70.00	12.78	59.00	392
air temp (°C)	0.29	−21.00	12.00	5.65	1966.73	365
altitude (m a.s.l.)	472	340	660	81	17	376
coverage (%)	40	0	1000	26	66	397

force needed to press a simulated moose foot down to the depth of the moose footprint, was highly variable, with a mean value of 1.63 kg cm^{-2} (Table 1).

SINKING DEPTHS AND TRAIL-FOLLOWING BEHAVIOR

In shallow snow, moose may sink all the way to the ground, which could potentially affect our measurements. We therefore first performed regression analysis of sinking depths vs. the amount of snow left under the moose footprint. This was done to test if we could detect a "critical minimum snow depth" where the amount of snow would start to affect sinking depths because of a column of compressed snow building up under the hoof. The regression analysis showed a strong linear relationship ($r = 0.96$, $p < 0.0001$, $N = 104$). The intercept was 20.13 cm, thus indicating the cut-off point when the column of compressed snow between the hoof and the ground started to affect our readings of sinking depths (Fig. 1). Data points with snow less than this critical depth were therefore eliminated from further analyses.

In total, we studied 200 m sections along the trails of 56 different moose during 99 moose trail observations (some moose were observed under different snow conditions) for a total of 345 extremely fresh footprints (only 2–10 minutes old). We then used the mean values for each 200 m section made at a given time (i.e. each moose trail observation) to make each observation the unit of statistical independence [mean number of footprints investigated during each moose trail observation = 4.50 ± 2.78 (STD)]. As the number of observations (*N*) was high in relation to the number of model parameters (*K*), we were able to use the original version of AIC instead of the one corrected for small sample sizes AIC_c (Burnham and Anderson, 2002).

On average, sinking depths of moose were 21.68 cm (Table 1). Correlation analyses showed that sinking depths varied with snow quality ($p < 0.01$, $r_{83} = -0.44$; Fig. 2), snow depth ($p < 0.01$, $r_{93} = -0.30$; Fig. 2), altitude ($p = 0.02$, $r_{89} = -0.25$; Fig. 2), and air temperature ($p = 0.01$, $r_{88} = -0.27$; Fig. 2). AIC analyses revealed that snow quality was the single most important variable predicting sinking depths of moose (Table 2a). When comparing models using the all the attributes included in the AIC analyses (AIC values, differences in AIC Δ, and Akaike weights *W*), sinking depths could best be explained by a combination of snow quality, altitude, and snow temperature (Table 3a).

To predict trail-following behavior, bivariate correlation analyses showed that trail-following behavior decreased in warmer air temperature ($p = 0.05$, $r_{88} = -0.24$). Similarly, AIC analyses also suggested that the single most important variable was the temperature of the air (Tables 2b, 3b).

SNOW CONDITIONS IN SEASONAL RANGES

The winter ranges of moose had significantly less snow than the summer ranges that these moose left ($p < 0.01$). Mean snow depths were 80.04 ± 18.40 (STD) cm in winter ranges, and 56.18 ± 4.75 cm in summer ranges. Snow quality did not differ between seasonal ranges ($p = 0.37$).

Discussion

If moose behavior in snow is adaptive, it must involve some positive change in the moose's energy budget. Moose and other ungulates should therefore adjust their behavior in response to

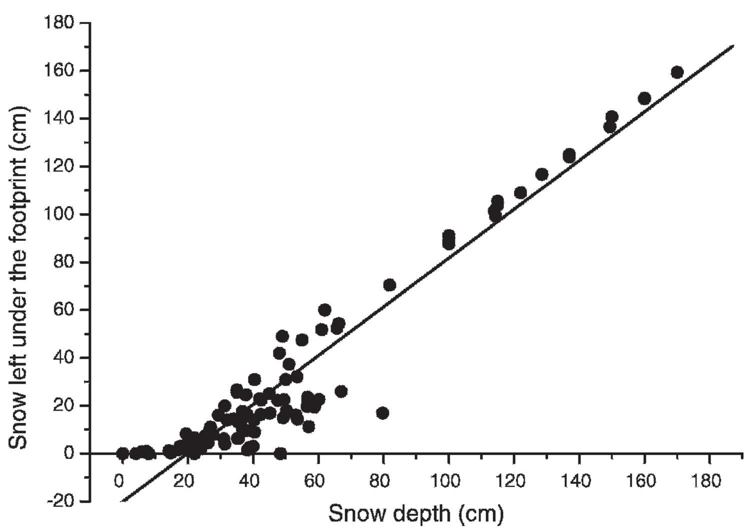

FIGURE 1. The amount of snow left under the moose footprint in relation to snow depth for moose. The regression line shows the cut-off point when shallow snow may start to affect sinking depths of moose, as viewed by the intercept at 20.13 cm of snow.

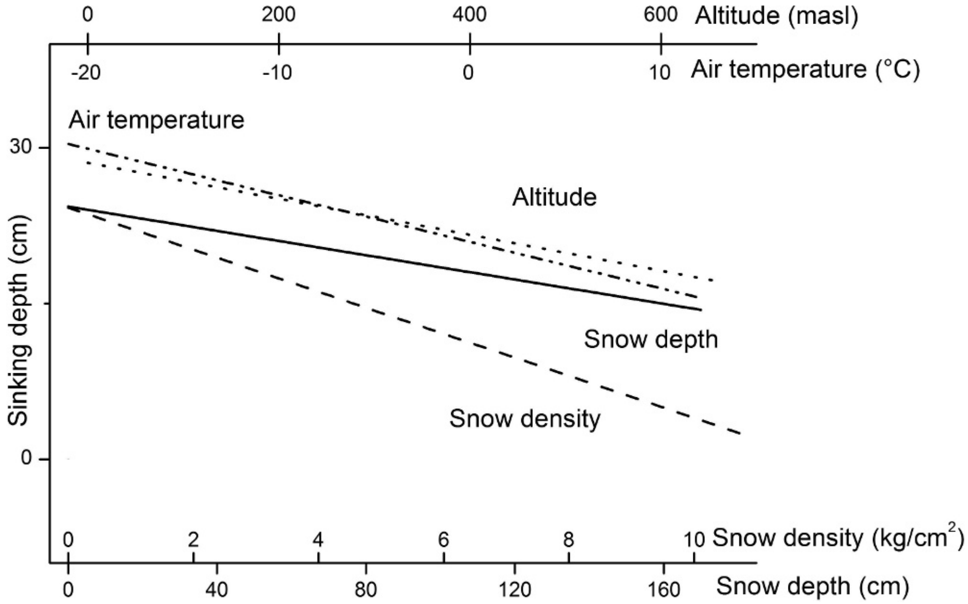

FIGURE 2. Bivariate plots of multiple variables vs. sinking depths. Moose sinking depths decreased with increasing snow quality ($p < 0.01$, $r_{83} = -0.44$), snow depth ($p < 0.01$, $r_{93} = -0.30$), altitude ($p = 0.02$, $r_{89} = -0.25$), and air temperature ($p < 0.01$, $r_{88} = -0.27$).

snow conditions, including how deep they sink into the snow. Our analysis revealed that trail-following behavior did not seem to be strongly affected by snow depth, snow quality (as measured by our simulated moose foot), or sinking depths (measured from tracks made by real moose). Instead, moose seemingly responded to air temperature, presumably because temperature influences snow metamorphosis (snow quality varied significantly with increasing air and snow temperatures). It thus seems necessary to combine several variables to explain trail-following behavior of moose. Although we studied extremely fresh footprints, snow properties did not emerge particularly strongly in the model: snow depth was only the third most important variable, and snow quality the fifth. Thus, our analyses are (unfortunately) in agreement with findings by other researchers: snow quality is notoriously difficult to quantify, especially in late winter when the snow cover approaches the melting temperature (Johnson and Marks, 2004). Snow of high density, and/or snow with harder layers within the snowpack may also add to the energy cost of locomotion by increasing the drag on the legs, and by causing the animal to lift its legs higher (Fancy and White, 1985). This paradoxical importance of snow quality (reducing the energy cost in some cases, but in others increasing it by forcing the animal to work harder) may partly explain why we did not detect strong evidence for the importance of snow quality when considering it independently from other variables. Note also that in this initial test, we used a very strict definition of trail-following behavior: the moose had to put its feet exactly in the footprints of other moose, and not just follow along their trail. Further studies of trail-following behavior in relation to snow should perhaps also study the phenomenon with a less strict definition, i.e. when the studied animals are simply following along the trails of those in front.

TABLE 2

Akaike information criterion (AIC) table for single individual variables used to model (a) sinking depths, and (b) trail-following behavior. Variables are sorted by Akaike weights (*W*). The tables also show AIC values (AIC), differences in AIC values (Δ), and *r*-values (*r*) for the variables: snow depth, snow quality, snow temperature, sinking depth, air temperature, vegetation coverage, and altitude.

(a) Sinking depth				
AIC	**Δ**	***r***	***W***	**Variables in Model**
298.75	0.00	0.41	0.37	snow quality
298.85	0.10	0.40	0.35	altitude
299.40	0.66	0.39	0.26	snow depth
305.23	6.48	0.28	0.01	snow temp
307.70	8.95	0.21	0.00	air temperature
309.27	10.52	0.14	0.00	coverage
(b) Trail-following behavior				
AIC	**Δ**	***r***	***W***	**Variables in Model**
397.27	0.00	0.22	0.33	air temp
398.84	1.57	0.14	0.15	altitude
399.17	1.91	0.14	0.13	snow depth
399.20	1.93	0.14	0.13	snow temp
399.82	2.55	0.00	0.09	snow quality
399.83	2.57	0.00	0.09	coverage
400.02	2.75	0.00	0.08	sinking depth

The large scale behavior (seasonal migration) of moose appeared to be affected by snow depth, as moose moved to winter ranges with considerably less snow than the summer ranges they just left. Our results thus support the numerous reports on the importance of snow depths for migration of moose (Coady, 1974; Andersen, 1991; Ballard et al., 1991; Albon and Langvatn, 1992; Sæther, 1992). We found no difference in snow quality between summer and winter ranges. Some previous studies have, however, emphasized its importance for seasonal movements of northern ungulates (Kelsall and Prescott, 1967; Bunnell et al., 1990), and some have also found that snow quality differs between ranges of migrant and resident moose (Ball et al., 2001). In our study area, the large differences in snow depth between summer and winter ranges appear to be the main factor regarding migration. So far, the importance of snow quality for seasonal migration is far less studied than the importance of snow depth, perhaps due to the difficulties in quantifying it, and we hope that other ecologists may investigate it further with the method we have tested here.

Sinking depths of moose appeared easier to quantify than trail-following behavior: there were more significant bivariate correlations (snow quality, snow depth, altitude, and air temperature). Evaluation by AIC indicated that three explanatory variables were needed to predict sinking depths (snow quality, altitude, and snow temperature). Here, snow quality (and not

TABLE 3

AIC table for (a) sinking depths, and (b) trail-following behavior. Models are sorted by Akaike weights (*W*). The tables also show AIC values (AIC), differences in AIC values between the models (Δ), and *r*-values (*r*) of the variables used in the model: snow depth, snow quality, snow temperature, sinking depth, air temperature, vegetation coverage, and altitude.

(a) Sinking depth				
AIC	Δ	*r*	*W*	Variables in Model
288.94	0.00	0.57	0.39	snow quality, altitude, snow temp
289.85	0.91	0.58	0.25	snow quality, altitude, snow temp, snow depth
290.02	1.08	0.54	0.23	snow quality, altitude
291.69	2.75	0.58	0.10	snow quality, altitude, snow temp, snow depth, air temp
293.68	4.73	0.58	0.04	snow quality, altitude, snow temp, snow depth, air temp, coverage
298.75	9.80	0.16	0.00	snow quality

(b) Trail-following behavior				
AIC	Δ	*r*	*W*	Variables in Model
397.27	0.00	0.22	0.43	air temp
398.18	0.92	0.26	0.27	air temp, snow temp
399.23	1.96	0.28	0.16	air temp, snow temp, altitude
400.72	3.45	0.30	0.08	air temp, snow temp, altitude, sinking depth
401.85	4.58	0.33	0.04	air temp, snow temp, altitude, sinking depth, snow depth
403.52	6.26	0.33	0.02	air temp, snow temp, altitude, sinking depth, snow depth, snow quality
405.41	8.15	0.33	0.01	air temp, snow temp, altitude, sinking depth, snow depth, snow quality, coverage

merely quantity) proved to be important, and it also emerged as the single best predictor variable, an observation completely in agreement with what has been suggested by numerous previous studies (Bunnel et al., 1990; Sæther et al., 1992; Ball et al., 2001). Although snow quality measurements were highly variable, it still proved to be important for sinking depth of moose, which further highlights its likely importance. The effects of air temperature (in correlation analyses) and snow temperature (in AIC analyses) may again be explained by their effects on snow metamorphosis. Regarding the effects of altitude on sinking depth, our results showed that areas situated at higher elevations had more supportive snow, thus indicating an indirect effect on sinking depths. Snow depth was the third important single variable in affecting sinking depth, and it did not emerge in the best model. Although snow depth has long been known to be of great importance for the winter survival of ungulates, our analyses further indicates that it should not be the only variable considered, but rather together with other factors (as also noted by Likhatskii et al., 1995).

Conclusions

We tested the effect of snow quality on trail-following behavior and sinking depths of moose. The analyses supported our predictions regarding sinking depths, although it was not as clear for trail-following behavior. A more simple and direct method to estimate the effects of snow would greatly help in increasing our knowledge about winter ecology and the behavioral adaptations to snow, and our analyses suggest that our method of measuring snow quality (by the force required to press a simulated moose foot down to the depth of a footprint) could be a step in the right direction.

In this study, we detected one especially important variable regarding sinking depth: snow quality—which we suggest is likely related to the energy expended in locomotion by moose in winter. The behavior of free-ranging ungulates reflects trade-offs between a wide range of factors, such as foraging and digestive efficiencies, food availability and quantity, environmental variations, and changes in body mass and condition. Ungulates traveling in snow carefully adjust their behavior in response to these factors to spend as little energy as possible. By examining trail-following behavior, we can use ungulate behavior as evidence that the animal has noticed the changes in energy cost and is doing something about it. As our study shows, it is possible to conduct this kind of study using free-ranging animals, as long as they can be observed so that the snow can be investigated when it is in the same condition as when the animal was there. In this initial investigation, we used extremely fresh footprints (<10 min), but we believe that investigating the footprints within three hours would still be adequate for ecological studies, as long as the weather conditions do not change dramatically. If trails are older than that, studies of sinking depth or trail-following behavior should perhaps be restricted to measuring snow depth and sinking depth alone. We encourage other ecologists to consider further evaluation of our method of measuring the force required to push a simulated ungulate foot down to the depth of the footprints. Perhaps this new snow quality variable (combining several snow quality aspects) will prove to be a step forward in understanding the winter ecology of ungulates in a way that is closer to what is experienced by the animal.

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