



Norwegian University of
Science and Technology

Cost of migration in moose (*Alces alces*) with regard to mortality risk and locomotion

Zandra Margareta Tollefsen

Biology

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Supervisor: Bernt-Erik Sæther, IBI

Co-supervisor: Erling J. Solberg, NINA

Ivar Herfindal, IBI

Christer M. Rolandsen, NINA naturdata

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Summary

1. Migration is present in all animal taxa and is defined as a periodic movement pattern between given ranges. Migratory individuals generally move more directional and with higher speed than stationary individuals during the migration seasons. It is suggested that migratory individuals in these periods encounter more risk factors, and therefore experience a higher mortality.

2. I studied the variation in the speed of movement and the number of times migratory and stationary moose were crossing elements associated with mortality risk, i.e. water bodies, roads and railroads, in Central Norway. This was done by examining the movement pattern of 121 GPS-collared moose. I also examined whether realized mortality differed between the two movement strategies.

3. The results only partly supported my hypothesis that migratory moose experience higher costs of movement and are confronted with more risk elements than stationary moose. As predicted, migratory moose moved faster than stationary moose, particularly during the migratory season. However, stationary moose had higher densities of risk elements within their home ranges, and crossed risk elements more frequently than migratory moose. For a given density of risk elements, migratory moose crossed more frequently, supporting the hypothesis that migratory moose are less risk adverse. This pattern was present throughout the year, suggesting that the behavior is not only related to higher movement during the migratory period.

4. I found no effect of movement strategy on the mortality rates, but the sample size was low. However, the trend of realized mortality was opposite of what I expected, with migratory moose having a lower mortality rate than stationary moose.

5. My results suggest that migratory moose experience a higher risk of mortality by their movement strategy compared to stationary moose. However, this varies between individuals. By considering individual differences in costs of migration, it is possible to increase our understanding of partial migration. Increased human induced risks such as roads, will most likely increase the number of road crossings. The differences between the two movement strategies in number of crossings will most likely decrease as risk density increase, resulting in a high crossing frequency of risk factors performed by moose.

Introduction

Migration is a phenomenon occurring in all animal taxa. Examples are birds that seasonally migrate between continents (Cox 1985), large ungulates such as the caribou *Rangifer tarandus* of north America (Ferguson and Elkie 2004), the large herds of wildebeest *Connochaetes taurinus* in Serengeti (Thirgood et al. 2004), fish utilizing different parts of the sea between seasons (Misund et al. 1998) and insects moving south to escape harsh winters (Brower and Malcolm 1991).

Overall, it is hard to give a general and precise definition of migration due to differences in behavioral traits among taxa and that there is often a continuous scale of movement pattern from stationary via nomadic to highly migratory individuals (Bunnefeld et al. 2011). Moreover, different external factors such as climate conditions and forage opportunities influence movement behavior (Dingle 1996). However, it is suggested through a survey of a broad array of organisms that four different, but overlapping concepts of migration can be used to distinguish it from other forms of movement (Dingle and Drake 2007). First, migration concern a type of locomotory activity that is persistent, undistracted by resources that would normally halt it and it is straightened out (in contrast to stationary behavior where a lot of turning or backtracking may occur). Second, it contains a movement of longer duration with a distinct departing and arriving behavior and a relocation of greater scale than normal daily activity. Third, it involves seasonal movement between two regions with alternatively favorable and unfavorable conditions, both for foraging and breeding. Last, it includes movement leading to redistribution of individuals within a spatially extended population (Dingle 1996, Dingle and Drake 2007).

It is assumed that individuals migrate to obtain a fitness benefit (Stearns 1992, Clobert 2001). Benefits with respect to foraging are one reason to migrate since there is often seasonal variation in spatial distribution and quality of forage. For instance, rain season is an important factor influencing the migrations at the Serengeti plains (Holdo et al. 2009), while large temperate ungulates such as moose *Alces alces* and roe deer *Capreolus capreolus*, often undergo seasonal altitudinal migrations (Myserud 1999, Rolandsen et al. 2010). These ranges from lowland areas occupied during winter to high elevation areas occupied during summer (Fryxell and Sinclair 1988, Myserud 1999, Myserud et al. 2001, Rolandsen et al. 2010). Timing and duration of migration are most likely determined by environmental differences between years more than by individual character (Bunnefeld et al. 2011). Migratory individuals benefit by a prolonged period of newly emergent forage, giving them an

advantage over stationary individuals seen from a nutritional point of view (Mysterud et al. 2001). Ungulates in temperate regions often experience harsh winters, and by migrating to lower elevations they can seek shelter from heavy weather and find areas with less snow and thereby more accessible forage (Lundmark and Ball 2008). From this perspective, it seems like seasonal and spatial variations in food quality and availability are very important factors selecting for migratory behavior (Fryxell and Sinclair 1988, Mysterud et al. 2001). In addition, migrating individuals can be less exposed to predation because predators tend to be territorial and not follow migratory prey over long distances (Fryxell et al. 1988, Fryxell and Sinclair 1988, Hebblewhite and Merrill 2007, 2009).

Migration also involves costs. For instance, moose differ considerably in distance and speed of movement (Bunnefeld et al. 2011). By moving away from familiar surroundings and moving into new environments, migratory individuals expose themselves to unknown ranges. This may lead to increased risk of mortality due to less experience with new potential risks. In addition, directional movements will most likely result in an increased exposure to risk of mortality in form of crossing risk barriers such as water bodies (rivers, lakes, fjords etc.) and mountain ranges.

In a number of large herbivores only part of the population is migratory (Ball et al. 2001, White et al. 2007, Robinson et al. 2010). In moose, for instance, some individuals are relatively stationary all their lives, while other migrate shorter or longer distances between summer and winter ranges (Ball et al. 2001, Rolandsen 2010, Bunnefeld et al. 2011). A relevant question is therefore why not all individuals follow the same strategy, given its assumed advantages. One reason could be the trade-offs between costs and benefits of migration, making the migratory and stationary strategy equal in terms of fitness (Hansen et al. 2010).

Migration behavior is a well known phenomenon, but there is still much knowledge lacking to fully understand the movement patterns of migrants, and how these movement patterns are influenced by the surrounding environment. By understanding why animals migrate, and their migration patterns, conservation of migratory species and their habitats can get more efficient (Bowlin et al. 2010). Where partial migration occurs in the population, there is still poor knowledge of what determines who become migratory and who stay stationary, as well as at which proportion the different strategies occur. Knowledge about individual differences in mortality risks is important for understanding how several strategies can persist within a population.

Moose are large and highly mobile animals that can move over large distances. Some individuals do not seem to show strong fidelity to any area, but rather follow some kind of a dispersing or nomadic strategy (Ball et al. 2001). Andersen (1991) showed that migration routes and winter ranges of moose are traditional, and it may take many generations to evolve a different route even if the browse supply is depleted and by such the benefits of migration has become absent. Migrating moose often move between a highly nutritional summer range with deciduous trees and herbs, and a winter range with lower nutritional value, but with higher browse availability when snow cover limits foraging in the summer area (Månsson 2009). Moose with summer home range within a pine dominated forest will stay relatively stationary and are less likely to migrate (Histol and Hjeljord 1993).

Risk factors can be divided into natural risks and human induced risks. Natural risks are risks that occur in nature and may have been modified by humans, but not been developed by humans, for instance water bodies. Human induced risks include railroads and roads, and these risk layers have been upgraded the last decades (Solberg et al. 2009). The number of traffic accidents involving moose has increased over the last four decades in Norway following the general increase in moose density (Solberg et al. 2009). The numbers of traffic accidents involving moose have increased over the last four decades in Norway following the general increase in moose density (Solberg et al. 2009). Studies suggest traffic volume on roads has a great influence on collision rates with animals (van Langevelde and Jaarsma 2004, Seiler 2005, Litvaitis and Tash 2008, Gunson et al. 2011) indicating that most collisions occur at roads with a higher traffic volume. In addition to traffic accidents, drowning is a known mortality factor of moose and other ungulates. In most cases, drowning occurs when individuals cross lakes with thin ice in fall and spring (Miller and Gunn 1986, Hansen et al. 2010, Rolandsen et al. 2010). Especially migratory individuals may be exposed to this risk of mortality as they show particularly high movement rate in the period with thin ice in autumn and unsafe ice in spring.

A way of measuring risk related to a potential mortality event is to quantify the amount of risk elements within the environment of individuals. An individual with a high density of risk elements within their home range is more likely to have a risk encounter. How individuals behave when encountering a risk element can thus be used as a measure of risk behavior. A risk-prone individual would have more crossings per risk density than a risk-adverse individual. In moose, migratory individuals are assumed to be less risk-adverse than stationary individuals (Neumann 2009) and are expected to cross risk elements more frequently. If the differences in number of crossings between migratory and stationary

individuals are due to a higher movement rate of migratory moose in the seasonal migrations, we would see different crossing patterns between the different seasons of the year. For example, more frequent crossings of rivers and lakes should occur by migratory individuals during spring and fall, while there should be a smaller difference in crossings between migratory and stationary moose during summer and winter. However, if the differences in number of crossings are due to permanent differences between migratory and stationary moose, the differences in the number of risk crossings of the two strategies should be constant over the year. A similar pattern may be observed between sexes. Males are known to be less risk-adverse than females and move more throughout the year (Rolandsen et al. 2010). Therefore, they are also likely to be exposed to more risk elements.

In this study, I will examine the large scale movement (migration) pattern of moose in a Norwegian population with particular emphasis on the costs of migration. I will do this by following GPS-collared individuals to investigate to what extent the movement strategy (migratory vs. stationary) influences costs in terms of locomotion and mortality risk. The migratory strategy is assumed to provide better nutritional feeding opportunities, but these benefits should be affected by increased energetic costs and risk of mortality. According to this, I expect 1) that migratory moose will move at a higher average speed and thus experience higher costs of locomotion, and 2) that the mortality rate is higher among migratory than among stationary moose. However, given the relatively low rate of natural mortality found in Scandinavian moose (Solberg et al. 2005), it can be difficult to show this effect based on the realized mortality alone. I will therefore also focus on the risk of mortality experienced by individuals following the different movement strategies – expecting 3) migratory moose to expose themselves more often to mortality risk elements than stationary moose.

Moreover, we may expect females with calves to be more risk adverse than males and also to move less through the year than males because of the generally lower mobility of the smaller calves, as well as the higher risk involved when calves are crossing intersecting obstacles (e.g. rivers, lakes). According to this, I will expect 4) to see generally higher movement rates of males than females with calves, and similarly that males are willing to take more risks to achieve their goals than do females.

Methods and materials

Study area

My study area is the county Nord-Trøndelag in the central parts of Norway, as well as the municipalities Bindal and Grane in the county of Nordland, and the municipalities Rissa, Osen, Malvik and Selbu in the county of Sør-Trøndelag. It also includes some areas in Jämtland in Sweden (Figure 1). The study area is located within 63° and 65.5° N and 10° and 16° E.



Figure 1. The study area includes central Norway and parts of Jämtland in Sweden.

The study area ranges from coastal areas in the boreonemoral zone to alpine zones. It is dominated by coniferous forest which is mostly used for commercial forestry. The main tree species are Norway spruce *Picea abies*, Scots pine and downy birch *Betula pubescens*. In the area there are also many bogs with sparse or no tree vegetation, creating a heterogeneous forest landscape. Cultivated land, mainly used for grass or grain production, is found at lower

altitudes (Moen et al. 1999). Scots pine is an important forage source for moose, but is less preferred than rowan *Sorbus aucuparia*, willow *Salix* ssp. and aspen *Populus tremula* (Månsson et al. 2007). When the forage availability of preferred forage species increase, the browsing pressure on Scots pine decrease (Månsson 2009). The preferred tree species are less abundant than Scots pine, and also shed their leaves during the winter. Moose therefore select for deciduous forest when available in spring, summer and fall, while pine forests are selected for in winter (Bjørneraas et al. 2011).

Data collection

Location data of moose were collected by the project “Elgundersøkelser I Nord-Trøndelag, Bindal og Rissa, 2005-2010”, conducted by NINA naturdata (Rolandsen et al. 2010). The location data included information about moose ID, geographic coordinates and the time of sampling. In total, data were sampled from 169 GPS-collared individuals, but the lack of distinct movement strategies or individuals with data for less than a full year reduced the sample size to 121 individuals. For several individuals data were available for more than one year, generating a sample of 186 moose-years with data.

The location points were collected by GPS-collars manufactured by Vectronic Aerospace GmbH and Followit Lindesberg AB. The sampling intervals were set to collect a position every hour to every second hour. The locations were sent to NINA as an SMS over the GSM network, for every fifth or sixth position recorded, depending on manufacture. If the collars lost connection with the GSM network, the positions were sent when connection was retrieved. Obvious location errors were removed by a method developed by Bjørneraas et al. 2010.

Roads, railroads and open water were considered to be risk elements. For Norway, map layers were provided by the Norwegian Mapping Authority whereas Swedish data was obtained from the Swedish Mapping Authority. Roads were classified into private and public roads, where private roads include for instance forest and tractor roads. Public roads include larger roads owned by the government, such as highways.

Spatial analyses

Annual home ranges were created by merging monthly minimum convex polygons (MCP) for each moose each year. By this method, overestimations of the home ranges were reduced. A moose year was set to start in April and end in March the year after. This was to correct for

different starting times in migration, where spring migration starts more or less at the same time for all animals, with only few exceptions (Rolandsen 2010). Fall migration varies much more. However, by setting the end of year to March all migratory moose were back in their winter area. To examine the seasonal pattern in crossing frequency, I made a season variable based on when migration mainly occurs, i.e: i) winter (December – March), ii) spring (April-May), iii) summer (June-September) and iv) fall (October-November).

For roads and railways, risk density within home ranges was defined as meters of road or railroad per km², whereas for water it was m² water per km². This generated monthly and seasonal estimates of risk density for each moose. Similarly, I calculated the number of crossings of roads, railroads and open water for each moose on a monthly and seasonal basis. Number of crossings compared to risk density was then used as a measure of risk prone behavior.

The Swedish map layers for water were of lower resolution than the Norwegian. Rivers in Sweden were represented by lines, whereas in the Norwegian map layers rivers were represented by polygons. To be able to calculate density of Swedish water, I assumed a mean width of 30 meters for Swedish rivers. The mean width for Swedish rivers was set after visual comparison with Norwegian rivers.

Migratory and stationary categories

Migratory moose was defined as any moose where a distinct spring- and fall migration pattern can be seen. The spring- and fall migration pattern was based on change in the net displacement from 1st of April within the individual home range of the moose. The net displacement for each individual was calculated as the distance between the location at 1st of April to the location in question. Stationary moose are moose that use more or less the same area throughout the year, without ranging between distinct summer and winter ranges. Here I defined stationary moose as individuals lacking a directional movement pattern between two seasonal ranges, whereas migratory moose were individuals with a directional movement pattern towards seasonal ranges (Rolandsen 2010). Starting at 1st of April, migratory individuals moved away during the spring migration, stayed in a the summer area before moving back to the winter range. This movement pattern generated a distinct pattern in the net displacement (Figure 2). Stationary individuals had no variation in net displacement during the year.

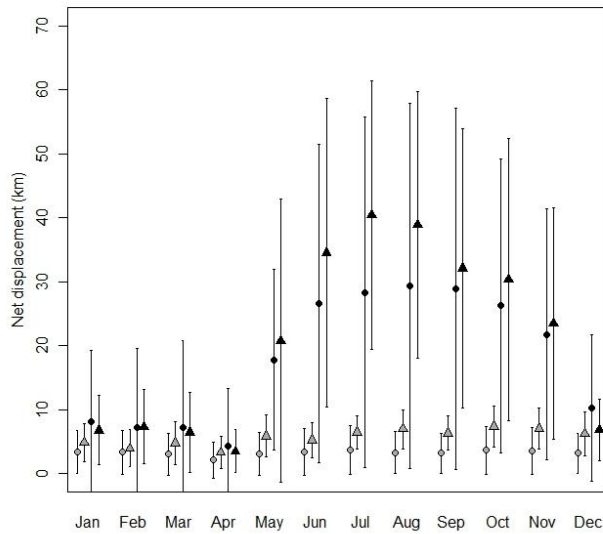


Figure 2. Mean net displacement throughout the year. Grey represent stationary moose, while black represent migratory moose. Females and males are represented with circles and triangles respectively. Bars indicate ± 1 standard deviation.

This method involved some subjective decisions because of the interpretation of directional movements, as well as the visual considerations made from the positions on the map. Some individuals were difficult to classify to either migratory or stationary. The analyses only include moose that were either stationary or migratory, while moose without clear movement strategy were excluded from the analyses.

Statistical analyses

The variables of risk density and number of crossings were ln-transformed to reduce heteroscedasticity. By so doing, it was possible to test if the crossing frequency increased proportionally to an increase in risk density within individual moose home ranges. A proportional increase in $\ln(\text{crossing})$ with $\ln(\text{density})$ would give a slope of one. Some home ranges did not have one or several of the risk elements within their home range, giving a density of 0. These were excluded from the analyses of that particular risk element. I only included home ranges with risk elements present in my analyses since these were the only ones where crossings were possible. One was added to the number of crossings to allow ln-transformation of individuals that did not cross risk elements.

The risk elements were analyzed separately. I tested if the frequency of crossing of risk elements was related to their density, while also considering strategy, season and sex in a

multiple linear model. Strategy, season and sex were treated as categorical variables whereas density was added as a continuous variable. In addition, I expected the relationship between crossing and density to differ between season, sex and strategy, which were tested for by adding two-way interactions between all explanatory variables. I also expected that the effect of season on the density-crossing relationship would differ between the two strategies, which were represented by a three-way interaction between the variables. A difference between males and females among seasons are expected in the relationship of risk density and crossings. This leads to a three-way interaction between season, sex and density was included. Finally, I included a three-way interaction between sex, strategy and season. For description of the full models, see Table 1.

The importance of the explanatory variables and their interactions on the crossing frequency of risk elements was evaluated using the Akaike's Information Criteria (AIC) corrected for low sample size (AICc; Burnham and Anderson 2002). The AICc value is based on the principle of parsimony to find the best fitted model while avoiding over-parameterization, and models differing with $\Delta\text{AICc} \leq 2$ were considered to have similar empirical support by the data (Burnham and Anderson 2002). AICc weights were interpreted as probability that the model is best for the given data and models (Burnham and Anderson 2002).

For survival analyses, I used the Cox proportional hazards analysis. For this analysis, 94 adult females were included with 10 mortality events. The highest risk of mortality of males is hunting in fall, so as a measure of natural mortality causes, females give a better overview due to little hunting pressure on adult females (Solberg et al. 2006). Individuals were censored when GPS-collars failed, or when individuals were shot for various reasons.

All analyses were run in R version 2.12.1 (R Development Core Team 2011).

Results

Movement speed

Movement speed varied over the year, and differed between migratory and stationary moose (Figure 3). During winter, migratory and stationary moose moved with relatively low speed and I found a trend towards males moving faster than females. In May, the differences in speed increased, with migratory moose moving faster than stationary, and males moving faster than females. These differences persisted through the summer and early fall. The larger intersexual differences occurred in June, September and October (Figure 3).

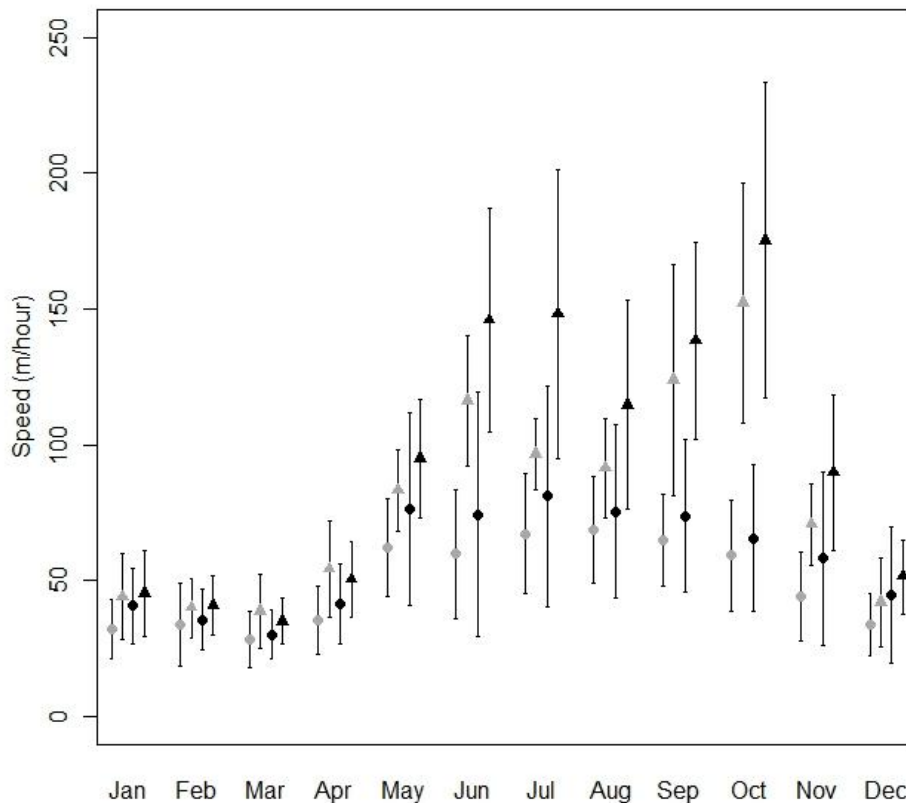


Figure 3. Mean speed of moose through the year, measured as meter per hour. Grey symbols represent stationary while black are migratory. Circles and triangles represent females and males, respectively. Bars indicate ± 1 standard deviation.

Density of risk elements within home ranges

Over all, stationary moose had a higher density of risk elements within home range through the year (Figure 4, left columns). Stationary moose had a significant higher density of

railroads within home ranges compared to migratory moose ($F_{1, 127}=4.17$, $p=0.04$; Figure 4a). There was no difference in railroad density between months ($F_{1, 127}=0.05$, $p=0.83$), nor did monthly densities of railroad differ between the strategies ($F_{1, 127}=0.43$, $p=0.52$). Similarly, stationary moose had a significant higher density of public roads ($F_{1, 1455}=7.89$, $p=0.005$; Figure 4c) and private roads ($F_{1, 1654}=44.76$, $p<0.001$; Figure 4e) within their home ranges compared to migratory moose, and the difference in density of these risk elements between months were also significant (public roads: $F_{1, 1455}=38.29$, $p<0.001$, private roads: $F_{1, 1654}=22.08$, $p<0.001$). Private road density within home ranges between months depended on the strategy ($F_{1, 1654}=12.32$, $p<0.001$), while the density of public roads did not ($F_{1, 1455}=0.25$, $p=0.62$). Water was present at a significant higher proportion in migratory moose home range ($F_{1, 1840}=18.58$, $p<0.001$) than in stationary moose home ranges (Figure 4g). There was a significant difference in the water density between months ($F_{1, 1840}=13.48$, $p<0.001$), where the magnitude of difference varied with the strategy of the moose ($F_{1, 1840}=5.61$, $p=0.018$).

Crossings of risk elements

There was no significant difference between migratory and stationary moose in the number of railroad crossings ($F_{1, 127}=2.89$, $p=0.092$; Figure 4b). The number of railroad crossings varied between months ($F_{1, 127}=5.76$, $p=0.018$), but the difference did not vary between the two strategies ($F_{1, 127}=0.31$, $p=0.58$). Stationary moose crossed roads more often than migratory moose (public roads: $F_{1, 1455}=26.21$, $p<0.001$, private roads: $F_{1, 1654}=16.38$, $p<0.001$, Figure 4 d, f). There was a significant difference in the general number of crossings among months (public roads: $F_{1, 1455}=12.65$, $p<0.001$, private roads: $F_{1, 1654}=10.31$, $p=0.0014$), but the two strategies did not differ in number of road crossings within months (public roads; $F_{1, 1455}=2.78$, $p=0.095$, private roads; $F_{1, 1654}=1.95$, $p=0.16$). There was no difference between strategies in number of crossings of water ($F_{1, 1840}=0.04$, $p=0.84$, Figure 4f). However, there was a significant difference in number of water crossings between months ($F_{1, 1840}=38.16$, $p<0.001$), which was not dependent on strategy of the moose ($F_{1, 1840}=2.83$, $p=0.093$).

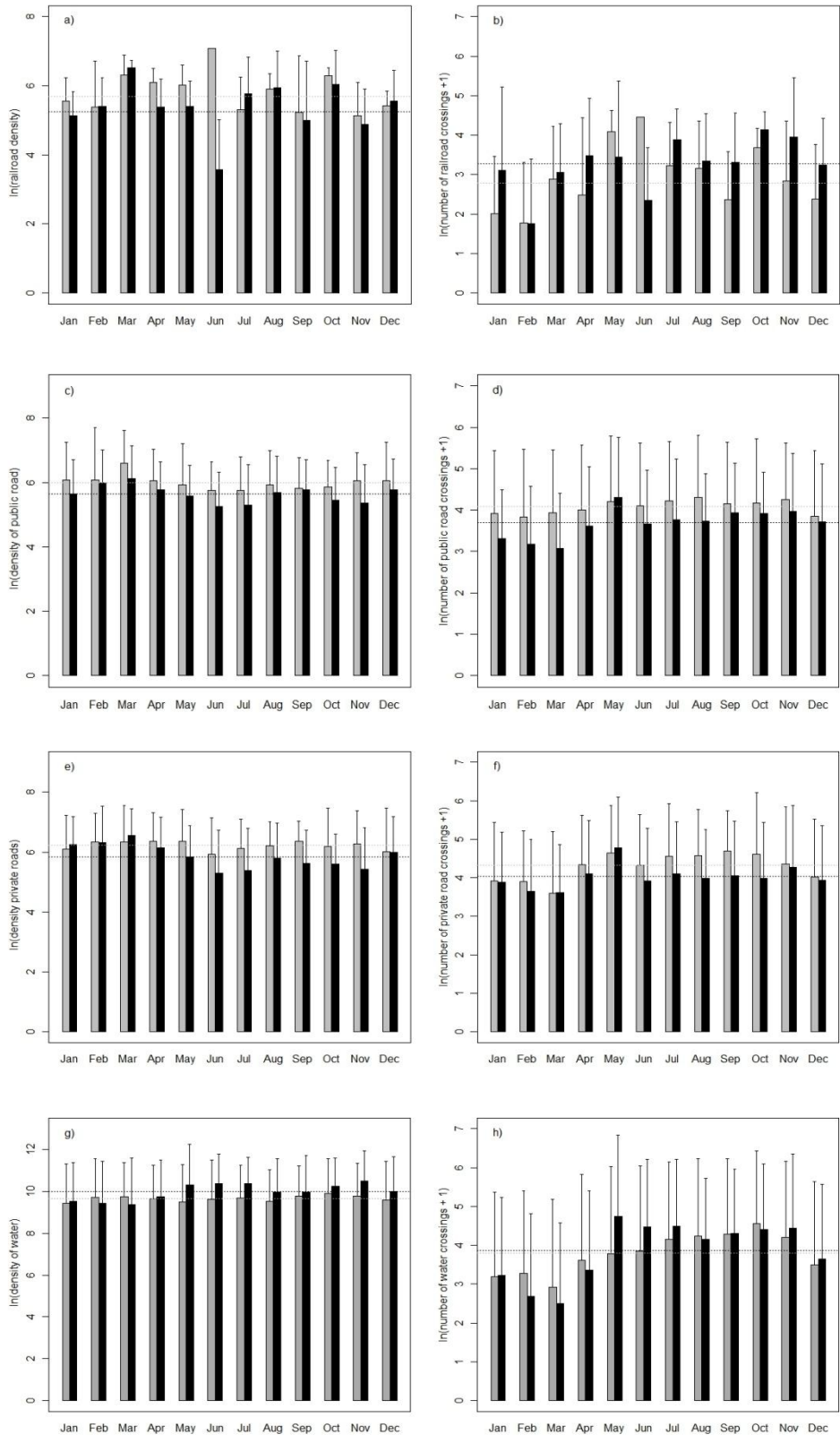


Figure 4. Mean density of risk elements within moose home ranges (left panels) and frequency of crossings (right panels) separated by month and strategy (gray = stationary, black = migratory). Bars represent standard deviation of the means. The dashed lines give the annual mean values. Panel a and b show railroad, c and d show public roads, e and f show private road while g and h show water. Bars indicate one standard deviation.

Risk crossing in relation to risk density

The AICc-based model selection indicated that the most parsimonious model explaining the number of crossings of railroad, included railroad density and movement strategy as explanatory factors (AICc weight = 0.33, Table 1). The second best model also included an interaction between the density and sex, and had a ΔAIC of 1.97 compared to the highest ranked model (Table 1). The frequency of railroad crossings increased with railroad density within the home range, and for a given density of railroads, migratory moose cross railroads more often than stationary moose (Figure 5a-d). Since sex was not included in the most parsimonious model for railroad, the differences between males and females in the relationship between railroad density and railroad crossings is not considered further.

The best model explaining the frequency of crossings of public roads included density, strategy, sex and season, as well as the interactions between density and strategy, strategy and season, and sex and season (AICc weight = 0.20). The second best model did not include the interaction between sex and season and had a $\Delta AICc$ of 1.56 (Table 1). According to the highest ranked model (Table 1), frequency of crossing of public roads increased with the density of public roads within the home range (Figure 5e-h). However, this increase was steeper for stationary ($\beta = 1.21 \pm 0.06$) compared to migratory ($\beta = 0.76 \pm 0.07$) moose. This lead to a higher crossing frequency for a given density for migratory moose compared to stationary moose at low public road density, whereas at high public road density there were less differences in the crossing frequency between the two strategies (Figure 5e-h). There were also a difference in number of crossings between males and females among seasons, with the largest differences in summer and fall (Figure 5g and h).

The best model explaining number of private road crossings included density, strategy, sex and season, with interactions between density and strategy, density and sex, density and season, and sex and season (AICc weight = 0.14). The next best model also included an interaction between strategy and sex, and had a ΔAIC of 0.73 (Table 1). According to the highest ranked model, there was a positive relationship between the density of private roads within moose home range and number of private road crossings. Stationary moose had a steeper increase ($\beta = 0.97 \pm 0.15$) in number of crossings as density increased than migratory moose ($\beta = 0.75 \pm 0.13$). This indicates a higher crossing frequency for a low density of private road for migratory moose compared to stationary, whereas at high public road density there were less difference in the crossing frequency among the two strategies (Figure 5i-l). There was a difference in crossing frequency at a given road density among seasons with a

weaker relationship between road density and crossings in spring (winter: $\beta = 0.97 \pm 0.15$, spring: $\beta = 0.72 \pm 0.14$, summer: $\beta = 1.03 \pm 0.14$, fall: $\beta = 1.04 \pm 0.12$), indicating a higher crossing frequency at low road densities in spring. Moreover, the crossing frequency was higher among males compared to females at low densities of private roads within moose home range, but as private road density increased the difference decreased (Figure 5i-l).

To explain crossing of water, the best model based on AICc selection included density, strategy, sex and season, as well as an interaction between density and strategy, density and sex, and density and season. There was also an interaction between strategy and sex, and a three-way interaction between density, strategy and sex (AICc weight = 0.38). The second best model did not include the interaction between density and season ($\Delta\text{AICc} = 1.24$, Table 1). According to the highest ranked model (Table 1), the number of water crossings increased with the density of water within moose home range (Figure 5m-p). However, migratory moose had a steeper increase ($\beta = 0.71 \pm 0.12$) in number of crossings per density compared to stationary moose ($\beta = 0.16 \pm 0.17$). Thus, stationary moose had a higher number of water crossings at low density of water, but as water density increased, the difference in number of water crossings between the two strategies decreased.

Males and females differed in number of water crossings, with females having a steeper increase with density of water ($\beta = 0.65 \pm 0.14$) than males ($\beta = 0.16 \pm 0.17$). Moreover, whether the males and females were stationary or migratory also affected the relationship between water density and number of crossings (Figure 5m-p). The effect of density on crossing frequencies differed between seasons, where the largest difference was found between winter and summer (winter: $\beta = 0.16 \pm 0.17$, spring: $\beta = 0.37 \pm 0.16$, summer: $\beta = 0.41 \pm 0.18$, fall: $\beta = 0.36 \pm 0.18$).

Table 1. The AICc-based ranking of models explaining the variation in number of crossings. Variables included in the candidate models are marked by an X. Δ AICc refer to the difference in AICc between the best model and the candidate model. Only models with Δ AICc ≤ 2 are presented in the table.

<i>Risk factor</i>	Density	Strategy	Sex	Season	Density * Strategy	Density * Sex	Density * Season	Strategy * Sex	Strategy * Season	Sex * Season	Density*Strategy*Sex	Density*Strategy*Season	Strategy*Sex*Season	Δ AICc	AICc weight
<i>Railroads</i>	X	X												0.00	0.327
	X	X			X									0.97	0.122
<i>Public roads</i>	X	X	X	X	X				X	X				0.00	0.198
	X	X	X	X	X				X					1.56	0.091
	X	X	X	X	X	X			X					1.58	0.090
	X	X	X	X	X	X		X	X					1.70	0.085
	X	X	X	X	X			X	X	X				1.75	0.083
<i>Private roads</i>	X	X	X	X	X	X	X			X				0.00	0.141
	X	X	X	X	X	X	X	X		X				0.73	0.098
	X	X	X	X	X		X			X				0.79	0.095
<i>Water</i>	X	X	X	X	X	X	X	X			X			0.00	0.384
	X	X	X	X	X	X		X			X			1.24	0.207

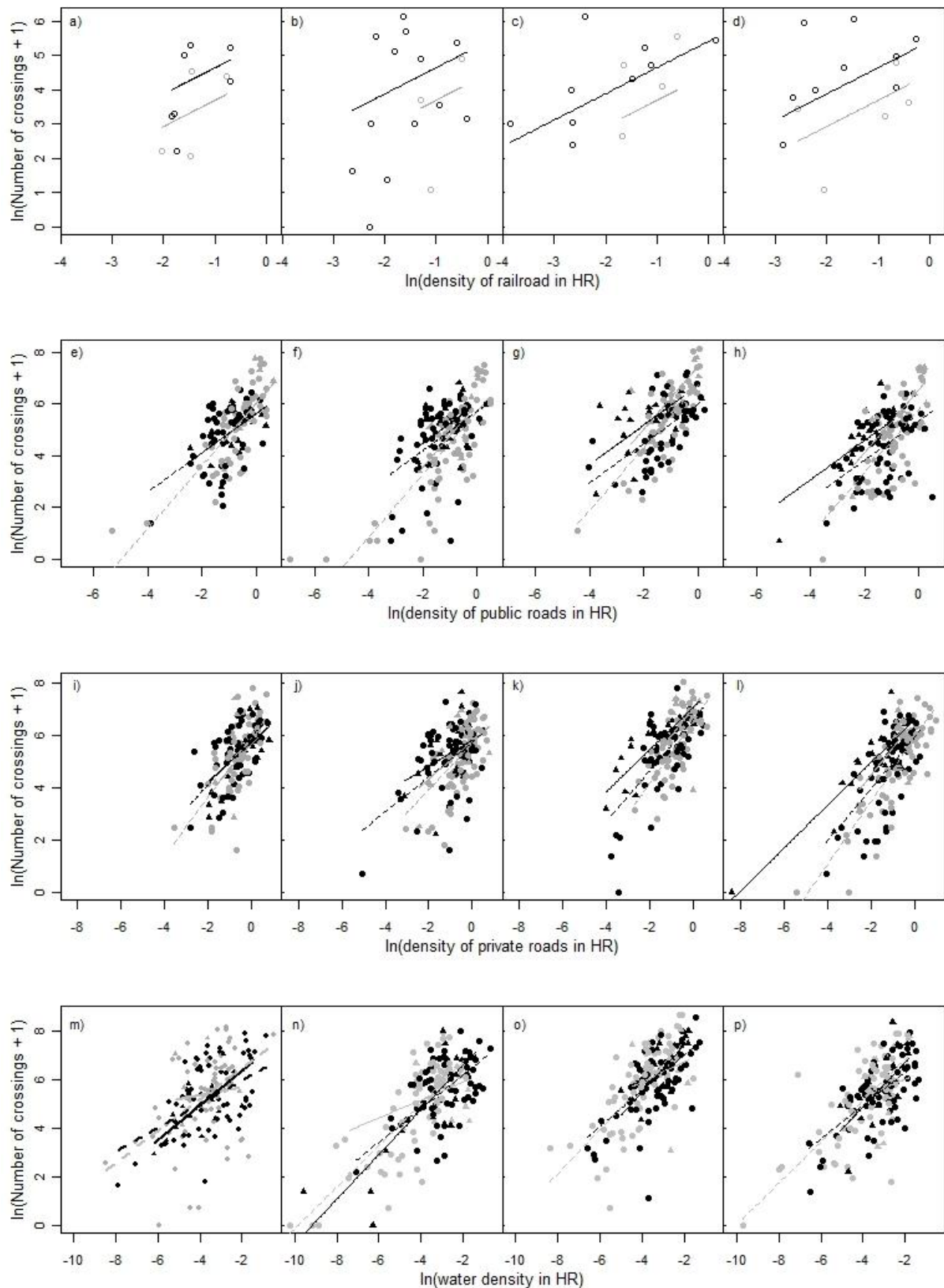


Figure 5. The relationship between risk density and number of crossings of risk elements in different seasons (from left: winter, spring, summer and fall) separated by strategy (gray=stationary, black=migratory) and sex (circles/dashed lines=females, triangles/solid lines=males). In the relationship between railroad density and number of railroad crossings, only strategy of the moose is presented. Panel a-d show railroad, e-h show public roads, i-l show private roads and m-p show water.

Realized mortality

The Cox regression with movement strategy (stationary vs. migratory) indicated that migratory females had a 39% reduced weekly hazard of dying compared to stationary females, but this difference was not significant (Figure 6, $p=0.45$).

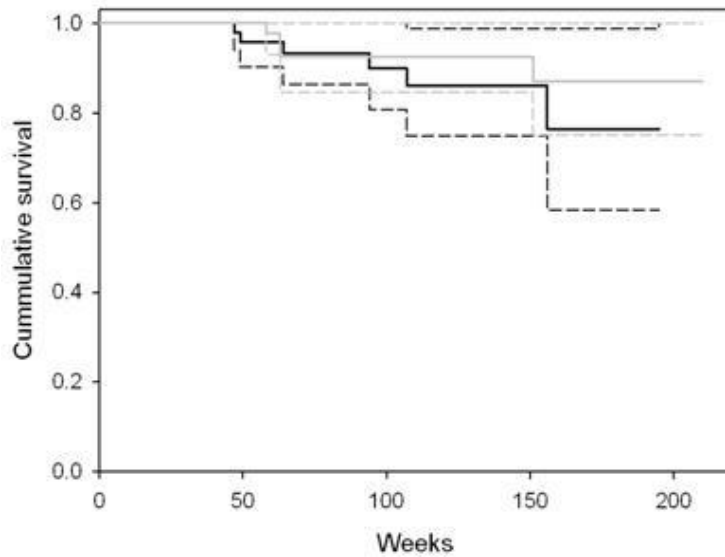


Figure 6. Estimated cumulative weekly survival (\pm 95% CI) for stationary (black line) and migratory (gray line) female moose. The broken lines show the point-wise 95-percent confidence envelope around the survival function for stationary and migratory female moose.

Discussion

By using an extensive dataset on moose movement, I documented distinct differences between individual moose in potential costs of movement throughout the year. These differences were closely related to the movement strategy of the individual moose. Firstly, migratory moose moved faster, particularly during spring, summer and fall (Figure 3), probably involving a higher energetic cost of the strategy. Second, stationary moose had on average a higher density of risk elements within their home ranges (Figure 4, left columns), except for water, where migratory moose had on average a higher density. Third, the number of crossings of risk elements differed between the two movement strategies (Figure 4, right columns). Stationary moose crossed public and private roads more frequently on average, while migratory crossed railroads more often on average. Average number of water crossings did not differ between the two strategies. However, migratory moose crossed more frequently in summer and early winter and stationary crossed more often in late winter and early spring. I expected different number of crossings between the two strategies during spring and fall migration, but this was not supported by the results. Fourth, propensity to cross for a given density was higher for migratory moose (Figure 5), but few differences in crossing frequency between seasons were found. There was however a trend that males had a higher probability to cross at a given density than females. Last, I did not find any significant results for realized mortality (Figure 6).

Concerning locomotion speed in moose individuals, the trend suggests a higher movement speed in migratory individuals compared to stationary (Figure 3). This is especially clear in summer and fall. The segregation appears to start in May, which is part of the spring migration. As a consequence of a higher movement speed and most likely a higher movement rate, a higher frequency of risk factor crossings is expected. However, stationary moose tend to have a higher number of road crossings compared to migratory moose (Figure 4d, f). This is most likely due to a higher density of roads within stationary home ranges (Figure 4c, e). However, it is interesting to see that in May, migratory individuals cross roads more frequently (Figure 4d, f). This is possibly a result of the increase in movement speed in May (Figure 3). During the summer migratory moose inhabit alpine areas, which have a lower density of roads. Migratory moose have a higher number of railroad crossings (Figure 4b), even though stationary have a higher density of railroads within their home ranges (Figure 4a). However, the railroad network in Nord-Trøndelag is sparsely distributed, and only a few individuals had railroads within their home range. This gave a low sample size, introducing a

lower statistical power compared to the other risk elements. During winter, both migratory and stationary moose had a relatively low movement speed, which can be explained by winter habitats being relatively homogeneous with respect to food (pine and birch) and the fact that deep snow restricts movement (Bjørneraas et al. 2011). However, the patterns of risk crossings at a given density of risk were relatively similar in winter compared to the rest of the year (Figure 5). The difference in annual pattern of speed between the two movement strategies suggests that speed also can be used to separate migratory and stationary moose. The trend of speed through the year (Figure 3) is quite similar to the trend of net displacement through the year (Figure 2). Net displacement is used for categorizing migratory and stationary moose here, but since the trends are so alike, the possibility of strengthen the categorizing by using net displacement combined with speed could be considered.

Since migratory routes seem to evolve over generations (Andersen 1991), I expected migratory moose to cross risks more often than stationary as a result of more directional movement on well-established migration routes (Neumann 2009). The number of crossings was positively related to the density of risk elements within home range (Figure 5). Given risk density within home range, migratory moose cross more frequently than stationary moose (Figure 5). At low risk densities, migratory moose have a higher frequency of crossing roads (Figure 5e-1) compared to stationary moose. However, at higher risk densities the differences in number of crossings are small. This is in accordance with Laurian et al. (2008), suggesting that moose avoid crossing roads unless necessary. The differences between the strategies decrease as risk density increase, suggest that crossings are difficult to avoid as densities of roads increase. Railroad crossings of moose differ between strategies, with migratory individuals crossing more frequent than stationary moose at a given of railroad density. However, the differences between the numbers of crossings between the two strategies are independent of railroad density. This is most likely also due to an overall low density of railroads, so avoidance of railroad crossings is possible, unlike road crossings.

Regarding human-induced risk factors such as roads and railroads, there was a difference in number of crossings given risk density. For water however, no such difference was found. Mortality related to water, such as drowning when trying to cross large rivers or falling through the ice, is among the most important causes of natural mortality in Norwegian moose (Rolandsen et al. 2010). Since water streams are larger during spring and autumn, and these periods are associated with unsafe ice, these seasons may be particular relevant for discriminating between the migratory and stationary strategy. Migratory moose had on average a higher density of water within individual home ranges (Figure 4g) compared to

stationary moose, and migratory individuals also crossed water more frequently in May (Figure 4h). This was probably because of a higher movement rate during the spring migration. Because the ice conditions may be particularly poor during this period, migratory moose are likely to be more at risk than stationary moose with respect to drowning. The lack of difference in number of crossings given water density between the strategies (Figure 5) may be a result of water being a familiar barrier, such that it not should be considered a risk of mortality at the same extent as human induced risks of mortality. Moose frequently inhabit wetlands (Hohle and Lykke 1993), and use ponds as a source of forage (Belovsky 1981). By utilizing water regularly, moose may have evolved a reduced fear of water. I did not consider different sizes of lakes and rivers, and I interpreted a line between two locations, which crossed water as a crossing. This may bias my results to some extent since different sizes of lakes or rivers exerts different risks of mortality, and an assumed crossing in my analyses can in reality be a moose walking around a lake instead of crossing the lake.

Males tended to have a higher movement speed (Figure 3), and may therefore also experience a higher encountering of risk factors. Given risk density, males tend to cross more frequently compared to females (Figure 5), indicating a less risk-adverse behavior in males. The difference in speed between males and females also increase in May and June (Figure 3), which could be related to females calving during this period, leading to lower mobility compared to males (Rolandsen et al. 2010). Summer also coincides with the most important period for body growth in moose (Sæther et al. 1996), In addition, there was a large difference in movement speed between males and females in September and October, coinciding with time of mating (Leblond et al. 2010).

I did not find any significant differences in realized mortality between stationary and migratory female moose. There are two possible explanations for this. The mortality rates are based on a small sample size in this context. In addition, the individuals are followed over a relatively short time period compared to the expected lifespan of a female moose. The natural mortality rates of Scandinavian moose are low, mainly due to low densities of predators in most of the geographical range of moose (Swenson et al. 2005, Wabakken et al. 2010). Moreover, males were not included in my mortality analysis since hunting was not included as a mortality factor. Males experience a high hunting pressure (Solberg et al. 2006) and because of a high mortality due to hunting, males were excluded. Consequently, few mortality factors are left for the individuals included in the mortality analyses. Combined with the short sampling period, I probably had too low statistical power to detect small differences in mortality rate between migratory and stationary moose. However, given the higher crossing

frequency of risk elements of males than females, males seem to be less risk adverse, and the trends of realized mortality could be different if males were included.

My results suggest a difference in risk encountering and crossing of risk elements between migratory and stationary moose. Stationary moose tended to encounter risk elements more often while migratory moose crossed more frequently given the density of risk elements. In addition, migratory moose tended to experience an increased cost of locomotion as a consequence of a higher movement speed than stationary moose. Since the movement rates of moose varies between individuals (Bunnefeld et al. 2011), and the cost of moving in snow is likely to affect the movement behavior of moose (Lundmark and Ball 2008), the cost of locomotion also varies between individuals. Given the costs of migration, more studies on benefits should be conducted. By this, a broader view of net gain from migration can be investigated. Understanding the movement behavior with its costs and benefits may improve our knowledge on partial migration. Such understanding can improve the conservation of moose, creating a sustainable harvesting plan considering the migration behavior of moose.

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References:

- Andersen, R. 1991. Habitat deterioration and the migratory behavior of moose (*Alces-alces* L) in Norway. *Journal of Applied Ecology* **28**:102-108.
- Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology* **7**:39-47.
- Belovsky, G. E. 1981. Optimal activity times and habitat choice of moose. *Oecologia* **48**:22-30.
- Bjørneraas, K., B. Van Moorter, C. M. Rolandsen, and I. Herfindal. 2010. Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. *Journal of Wildlife Management* **74**:1361-1366.
- Bjørneraas, K., E. J. Solberg, I. Herfindal, B. Van Moorter, C. M. Rolandsen, J.-P. Tremblay, C. Skarpe, B.-E. Sæther, R. Eriksen, and R. Astrup. 2011. Moose (*Alces alces*) habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology* **17**:44-54.
- Bowlin, M. S., I. A. Bisson, J. Shamoun-Baranes, J. D. Reichard, N. Sapir, P. P. Marra, T. H. Kunz, D. S. Wilcove, A. Hedenstrom, C. G. Guglielmo, S. Akesson, M. Ramenofsky, and M. Wikelski. 2010. Grand Challenges in Migration Biology. *Integrative and Comparative Biology* **50**:261-279.
- Brower, L. P. and S. B. Malcolm. 1991. Animal migrations – endangered phenomena. *American Zoologist* **31**:265-276.
- Bunnefeld, N., L. Borger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* **80**:466-476.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.
- Clobert, J. 2001. *Dispersal*. Oxford University Press, Oxford.
- Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the new world. *American Naturalist* **126**:451-474.
- Dingle, H. 1996. *Migration: the biology of life on the move*. Oxford University Press, New York.
- Dingle, H. and V. A. Drake. 2007. What Is Migration? *BioScience* **57**:113-121.
- Ferguson, S. H. and P. C. Elkie. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology* **262**:125-134.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant. *American Naturalist* **131**:781-798.
- Fryxell, J. M. and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution* **3**:237-241.
- Gunson, K. E., G. Mountrakis, and L. J. Quackenbush. 2011. Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. *Journal of Environmental Management* **92**:1074-1082.

- Hansen, B. B., R. Aanes, and B. E. Saether. 2010. Partial seasonal migration in high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **88**:1202-1209.
- Hebblewhite, M. and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* **152**:377-387.
- Hebblewhite, M. and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* **90**:3445-3454.
- Histol, T. and O. Hjeljord. 1993. Winter feeding strategies of migrating and nonmigrating moose. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **71**:1421-1428.
- Hohle, P. and J. Lykke. 1993. *Elg og elgjakt i Norge*. Gyldendal, Oslo.
- Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009. Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti. *American Naturalist* **173**:431-445.
- Laurian, C., C. Dussault, J. P. Ouellet, R. Courtois, M. Poulin, and L. Breton. 2008. Behavior of moose relative to a road network. *Journal of Wildlife Management* **72**:1550-1557.
- Leblond, M., C. Dussault, and J. P. Ouellet. 2010. What drives fine-scale movements of large herbivores? A case study using moose. *Ecography* **33**:1102-1112.
- Litvaitis, J. A. and J. P. Tash. 2008. An approach toward understanding wildlife-vehicle collisions. *Environmental Management* **42**:688-697.
- Lundmark, C. and J. P. Ball. 2008. Living in snowy environments: Quantifying the influence of snow on moose behavior. *Arctic Antarctic and Alpine Research* **40**:111-118.
- Miller, F. L. and A. Gunn. 1986. Observations of barren-ground caribou traveling on thin ice during autumn migration. *Arctic* **39**:85-88.
- Misund, O. A., H. Vilhjalmsen, S. H. I. Jakupsstovu, I. Rottingen, S. Belikov, O. Asthorsson, J. Blindheim, J. Jonsson, A. Krysov, S. A. Malmberg, and S. Sveinbjornsson. 1998. Distribution, migration and abundance of Norwegian spring spawning herring in relation to the temperature and zooplankton biomass in the Norwegian Sea as recorded by coordinated surveys in spring and summer 1996. *Sarsia* **83**:117-127.
- Moen, A., A. Lillethun, and A. Odland. 1999. *Vegetation. Norges geografiske oppmåling, Hønefoss*.
- Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *Journal of Zoology* **247**:479-486.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* **70**:915-923.
- Månsson, J. 2009. Environmental variation and moose *Alces alces* density as determinants of spatio-temporal heterogeneity in browsing. *Ecography* **32**:601-612.
- Månsson, J., C. Kalen, P. Kjellander, H. Andren, and H. Smith. 2007. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. *Scandinavian Journal of Forest Research* **22**:407-414.
- Neumann, W. 2009. Moose *Alces alces* behaviour related to human activity. Doctoral Thesis. Swedish University of Agricultural Sciences, Umeå.

- R Development Core Team 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robinson, B. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia* **164**:265-275.
- Rolandsen, C. M. 2010. Elgundersøkelsene i Nord-Trøndelag, Bindal og Rissa 2005-2010: sluttrapport. Norsk institutt for naturforskning, Trondheim.
- Rolandsen, C. M., E. J. Solberg, K. Bjørneraas, M. Heim, B. Van Moorter, I. Herfindal, M. Garel, P. H. Pedersen, B.-E. Sæther, O. N. Lykkja, and Ø. Os. 2010. Elgundersøkelsene I Nord-Trøndelag, Bindal og Rissa 2005-2010 Sluttrapport. NINA Rapport **588**.
- Seiler, A. 2005. Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology* **42**:371-382.
- Solberg, E. J., V. Grotan, C. M. Rolandsen, H. Broseth, and S. Brainerd. 2005. Change-in-sex ratio as an estimator of population size for Norwegian moose *Alces alces*. *Wildlife Biology* **11**:163-172.
- Solberg, E. J., V. Veiberg, O. Strand, R. Andersen, R. Langvatn, M. Heim, C. M. Rolandsen, F. Holmstrøm, and M. I. Solem. 2008. Hjortevilt 2007 - Årsrapport fra Overvåkingsprogrammet for hjortevilt. Norsk Institutt for Naturforskning.
- Solberg, E. J., C. M. Rolandsen, I. Herfindal, and M. Heim. 2009. Hjortevilt og trafikk i Norge: an analyse av hjorteviltrelaterte trafikkulykker i perioden 1970-2007. Norsk Institutt for Naturforskning, Trondheim.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Swenson, J. E., J. M. Arnemo, E. Bellemain, S. Brunberg, B. Dahle, O.-M. Drageset, H. Hustad, J. Katajisto, J. Kindberg, E. Nerheim, K. H. Solberg, P. Segerström, O.-G. Støen, A. Söderberg, and A. Zedrosser. 2005. Rovvilt of Samfunn (RoSa) - Det skandinaviske bjørneprosjektet. Oversikt over gjennomførte aktiviteter; Sluttrapport til Norges forskningsråd. NINA Rapport:24.
- Sæther, B. E., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. *Ecology* **77**:1493-1500.
- Thirgood, S., A. Mosser, S. Tham, G. Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. Fryxell, A. R. E. Sinclair, and M. Borner. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation* **7**:113-120.
- van Langevelde, F. and C. F. Jaarsma. 2004. Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology* **19**:895-907.
- Wabakken, P., Å. Aronson, T. H. Strømseth, H. Sand, E. Martmann, L. Svensson, Ø. Flagstad, E. Hedmark, O. Liberg, and I. Kojola. 2010. Ulv I skandinavia. Statusrapport for vinteren 2009-2010. Høgskolen i Hedmark. Oppdragsrapport.
- White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation* **135**:502-510.