Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Forest Science

Synchronizing migration with birth: An exploration of migratory tactics in female moose

Synkronisering av migration och födsel: En undersökning av migrationstaktiker hos älghonor

Linnéa Näsén

Examensarbete i ämnet biologi
Department of Wildlife, Fish, and Environmental studies
Umeå
2015

Synchronizing migration with birth: An exploration of migratory tactics in female moose

Synkronisering av migration och födsel: En undersökning av migrationstaktiker hos älghonor

Linnéa Näsén

Supervisor: Navinder J. Singh, Dept. of Wildlife, Fish, and Environmental Studies

Assistant supervisor: Andrew Allen, Dept. of Wildlife, Fish, and Environmental Studies

Examiner: Kjell Leonardsson, Dept. of Wildlife, Fish, and Environmental Studies

Credits: 30 HEC
Level: A2E
Course title: Master degree thesis in Biology at the Department of Wildlife, Fish, and Environmental Studies
Course code: EX0764
Programme/education: Jägmästarprogrammet

Place of publication: Umeå
Year of publication: 2015
Cover picture: Navinder J. Singh
Title of series: Examensarbete i ämnet biologi
Number of part of series: 2015:6
Online publication: http://stud.epsilon.slu.se

Keywords: migration, calving, moose, time minimization, energy maximization

Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Forest Science
Department of Wildlife, Fish, and Environmental Studies

Abstract

Migration and giving birth are crucial decisions for animals during their life cycle, which may have lasting consequences on their population demography and fitness. Migration can entail a variety of possible effects for an individual, such as access to high quality food and reduced risk for predation. The moose (*Alces alces*) in northern Sweden is partially migratory and moose females are known to give birth to one or two calves. The synchrony between time of calving and timing of migration has not been compared before, especially in terms of energy maximizing and time minimizing perspectives, which may provide vital cues for fitness benefits of migration. I investigated effect of timing of birth and individual life history on distance, timing, stopovers and duration of 190 individually marked female moose that have been tracked for multiple years in ten different areas in northern Sweden. The effects of the life history variables (area, age, body mass, litter size) were tested by using Generalized Linear Mixed Models (GLMMs), and ANOVAs together with Turkey's HSD tests were used to explain variation in movement between females of different reproductive status. Females that gave birth during migration had the longest duration of spring migration and used the most stopovers than others. Females that gave birth before spring migration arrived later in the summer ranges than other female groups. However, those that gave birth after spring migration had the quickest spring migrations. Younger females migrated earlier in autumn than older females and females with twins migrated earlier during autumn than other female groups. Such timing adjustments between migration and reproduction demonstrate that the time minimizing versus energy maximizing behavioural trade-offs can exist within a species, where individuals make trade-offs depending upon their life history and life cycle events.

Sammanfattning

Migration och födsel av kalvar är viktiga händelser för djur under livstiden, händelser som varaktigt kan påverka populationens sammansättning och fitness. Migration kan ge en rad positiva effekter för den enskilda individen, så som tillgång till föda med högre näringsvärde och minskad risk för predation. Älgpopulationen (*Alces alces*) i norra Sverige är delvis migrerande och det är känt att älgkor föder en till två kalvar. Synkroniseringen mellan födsel av kalv och migration har aldrig jämförts tidigare, speciellt inte i termer av energimaximering och tidsminimering, vilket kan ge viktiga insikter om hur individens fitness påverkas av migration. Jag undersökte hur effekten av tidpunkt för födsel av kalv påverkar distans, timing, uppehåll och varaktighet för 190 individuellt märkta älgkor som följts under flertalet år i tio olika områden in norra Sverige. Effekterna av livshistorievariablerna (område, ålder, vikt, kullstorlek) testades genom att använda Generalized Linear Mixed Models (GLMMs), och ANOVAs tillsammans med Tukey's HSD test användes för att förklara variation i rörelse mellan älgkor av olika reproduktiv status. Kor som födde kalven under migrationen hade den längsta vårmigrationen och stannade flest gånger under migrationen. Kor som födde kalven innan vårmigrationen anlände senare till sommarområdet än de andra grupperna av kor. Däremot hade de älgkor som födde kalven efter vårmigrationen de snabbaste vårmigrationerna. Yngre älgkor migrerade tidigare under hösten än vad äldre älgkor gjorde och älgkor med två kalvar migrerade tidigare under hösten än andra grupper av älgkor. Sådana tidsjusteringar mellan migration och födsel av kalv visar att avvägningar mellan tidsminimeringsstrategin kontra energimaximeringsstrategin kan existera inom en art, där individer gör avvägningar beroende på deras livshistoria och livscykelhändelser.

Introduction

Movement is one of life’s fundamental characteristics (Nathan et al. 2008) and by moving through their environment, animals are able to use heterogeneously distributed resources (van Moorter et al. 2009) needed for reproduction and survival (Dingle 1996, Börger, Dalziel and Fryxell, 2008). Movements are suggested to enhance access to high quality food, reduce competition, bring individuals together for mating and to reduce the risk of predation (Fryxell and Sinclair 1988, Fahrig 2007, Avgar, Street and Fryxell 2013). Moving organisms are vital components in the ecosystem of which they occur, and should be taken into account in biological conservation and ecosystem management (Lundberg and Moberg 2003).

In recent years, the techniques to track animals have developed rapidly (Tomkiewicz et al. 2010, Urbano et al. 2010). GPS (Global positioning system) technologies make it possible to track individuals in remote areas, which have provided greater knowledge of animal movement (Frair et al. 2010, Gaillard et al. 2010). Knowledge of animal movement is important in population and behavioural ecology (Spencer 2012). Tracking of animals has improved our ability to answer questions as how, when and where individuals move but the question of why individuals move, still remains (Nathan et al. 2008).

Life history variables have an effect on migratory movement (Singh et al. 2012). Age effects reproduction for females, as the reproductive effort increases with age for females (Ericsson et al. 2001) and also affects the survival of individuals (Ericsson and Wallin 2001). In many organisms, body mass is a key determinant of fitness and varies between individuals in a population (Pettorelli et al. 2002). Both body mass and age are positively related to fecundity (Sand 1996). Regional differences in inter alia migratory behaviours must be involved in adaption of management strategies (Safrononv 2009). It has been seen that timing and synchrony of reproduction is dependent on climate (Loe et al. 2005) and latitudinal variation in snow depth have been related to migratory difference between populations along a latitudinal gradient (Singh et al. 2012).

Schoener (1971) introduced two concepts on the amount of time an animal should spend on feeding to maximize its reproductive output; time minimization and energy maximization. According to Schoener (1971) all animals are either time minimisers or energy maximizers if there is no conflict with other factors, and an animal using the time minimizing strategy has a fixed amount of energy and strives to obtain the fixed amount of energy during the least amount of time. The fitness of a time minimizer is greatest when the time is minimized. An animal using the energy maximization strategy has a fixed amount of time and strives to maximize the energy intake during this time period, and its fitness increases with the energy intake (Schoener 1971). In this study I refer to time minimization as a strategy to reduce the time of migration. Migratory individuals could either migrate fast and use less stopover sites during the migration path, or they could use more time to stop for foraging and would therefore maximize their energy intake during migration. Migrants may follow a phenological gradient during spring migration (Sawyer and Kauffman 2011), which is a strategy to enhance the energy intake (Bischof et al. 2012). Nevertheless, a variety of trade- offs and constraints such as predation, reproduction and patchy habitats, may prevent individuals to follow the green wave (Bischof et al. 2012), and this could mean that individuals use a time minimization strategy during migration.

There are energetic costs of movement, and individuals that migrate long distances typically takes this energy from stored fuel (Alerstam, Hedenström and Åkesson 2003). Irrespective of locomotion mode, transport of heavy fuel reserves increases the costs of transport and time-minimization has therefore been proposed as the most common migration strategy (Åkesson and Hedenström 2007). If individuals use small fuel reserves enough to cover smaller distances (i.e. split the total migration distance into smaller parts) the overall cost of migration will be minimized and individuals that travel longer distances without refuelling will have an increasing energy cost (Alerstam, Hedenström and Åkesson 2003). However, ungulates are well known to be maximizing their energy intake during growing season, (Wilmshurst et al. 1999, Fryxell, Wilmshurst and Sinclair 2004) which would therefore limit the use of stopovers during migration to maximize speeds since this is only likely if it allows maximum intake of high-quality forage (Sawyer and Kauffman 2011).

It has been observed that ungulates use stopovers in connection to a phenological gradient, i.e. tracking the green wave (Bischof et al. 2012) and if this gradient would not exist, it is likely that individuals would complete their migrations faster without stopovers or not even migrate at all (Sawyer and Kauffman 2011). Arriving early to the summer range or cutting the migration short may also benefit the migratory individual if there is a competition for shelter, mates or forage areas between individuals (Bischof et al. 2012).

Calving is one of females' life cycle events that could partially motivate or coincide with timing and duration of migration (Bischof et al. 2012). Pregnant bighorn ewes (*Ovis Canadensis)* have been seen to migrate before calving, from low-elevation areas to high-elevation areas where plant growth had yet not started. They moved from a high-quality forage to a low-quality forage, which could be a predator-avoidance strategy (Festa-Bianchet 1988). This strategy has also been seen in barren-ground caribou (*Rangifer tarandus*, Heard, Williams and Melton 1994). Birth site and offspring performance has been reported to have a close relationship in many cases (Gaillard et al. 2010) and greater maternal care should benefit offspring by maximizing growth and surviving better (Pettorelli et al. 2007).

The moose (*Alces alces* L.) is a highly mobile large herbivore (Jensen 2004) and is distributed throughout the boreal forest zone (Pastor et al. 1988). It is present across all of Sweden (except the island of Gotland, Jensen 2004) and is the largest herbivore in the country. The population in Sweden is estimated to be around 200 000 – 300 000 individuals after hunting season (Singh et al. 2014). Mating occurs from mid October to November in the northern parts of the country and females give birth to one or two calves between the end of May to the start of June (Jensen, 2004). The Swedish moose population is partially migratory (Singh et al. 2014, Ball, Nordegren and Wallin 2001), which is a common life history strategy in highly seasonal environments (Mysterud et al. 2011, Avgar, Street and Fryxell 2013). Migratory moose move between summer and winter ranges (Jensen 2004), where the winter range typically is lowland area and the summer range can be towards high elevation areas or coast or inland (Singh et al. 2012, Figure 1), and by moving individuals should derive distinct nutritional benefits (White et al. 2014). The proportion of migratory moose increases from south to north, were a large part of the population is migratory while others use nomadic, dispersal or residential movement strategies (Singh et al. 2012).

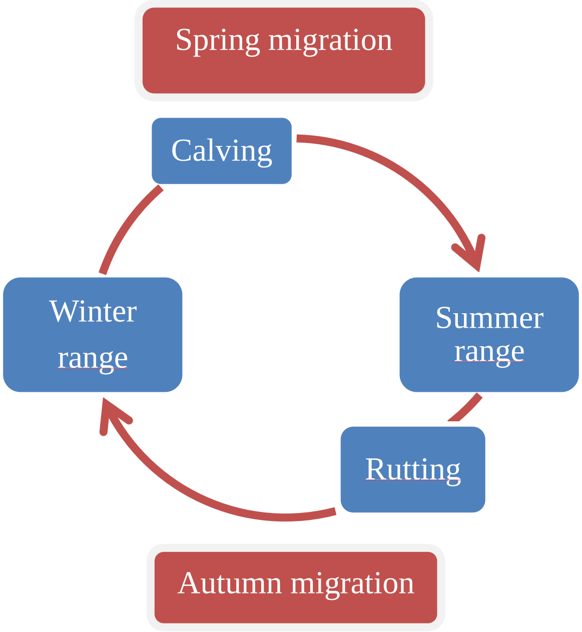

Figure 1. A typical year for a migratory moose. During spring the individuals migrates to the summer range and in autumn they migrates back to the winter ranges. Calving occurs during spring and rut during autumn.

Several studies have been made to understand movement behaviour of the Swedish moose population. Singh et al. (2012) analyzed the differences in population-level and individual movements by testing the effect of human presence in the landscape, risk and climate on movements by moose. They also tested effects of sex and age and found that males and younger individuals migrated to larger distances. The effect of snow depth, sinking depth of individuals and habitat composition were also studied by Ball et al. (2001) and Sweanor and Sandegren (1989).

Moose calves are immobile during their first days of life (Altman 1958) which makes it a critical time for survival and the chances to survive depend on the mothers selection of habitat and behaviour to reduce risk (McGraw, Terry and Moen 2014). Females with calves needs to meet the energetic demands of lactation, and movement to an area during the spring green up may allow them to meet up with the demands and thereby maximize energy intake (McGraw, Terry and Moen 2014). It has been seen that females with a calf gained less body fat during summer than did females without a calf (White et al. 2014) and this could result in a lower probability of reproduction for the next year (Testa and Adams 1998). This could imply that it is even more important for reproductive females to maximize their energy intake.

In Scandinavia, all moose females are known to give birth to one or two calves, over a two week time window in early spring (Solberg et al. 2007, Haydn 2012), but the synchrony between their time of calving and timing of migration has not been compared before, especially in terms of energy maximizing or time minimization perspective, which may provide vital cues for fitness benefits of migration. In this study I investigate the migration pattern in relation to the reproductive status of 190 moose females in northern Sweden and testes the synchrony between timing of calving and spring migration as well as the effect of reproductive status and life history on migration. Specifically I test the following predictions:

> P1) All reproductive females should give birth to calf after arrival at the summer range, i.e. after spring migration.
>
> P2) All females should, regardless of, if they are reproductive or non-reproductive, use a time minimization strategy during spring migration.
>
> P3) Females with a calf should move slower during autumn migration and those with twins should have a longer duration of migration than those with a singleton.

Materials and methods

Study area

The study area is located in the northern parts of Sweden, latitude 63 to 67, in the counties of Västerbotten and Norrbotten. The northern parts of Sweden are characterized by the Scandinavian mountains rising up to 1930m (Lantmäteriet 2014) in the west, followed by a gentle slope down towards the Baltic coast in the east (Fallsvik 2011, Hågeryd 2011). A number of large river valleys cross the landscape on their way out to the Gulf of Bothnia (Fallsvik 2011, Hågeryd 2011). Individuals were captured and equipped with GPS transmitters in ten different areas during the period 2004 to 2013. Location, name and total number of individual moose for each area are shown in Figure 2 and Table 1.

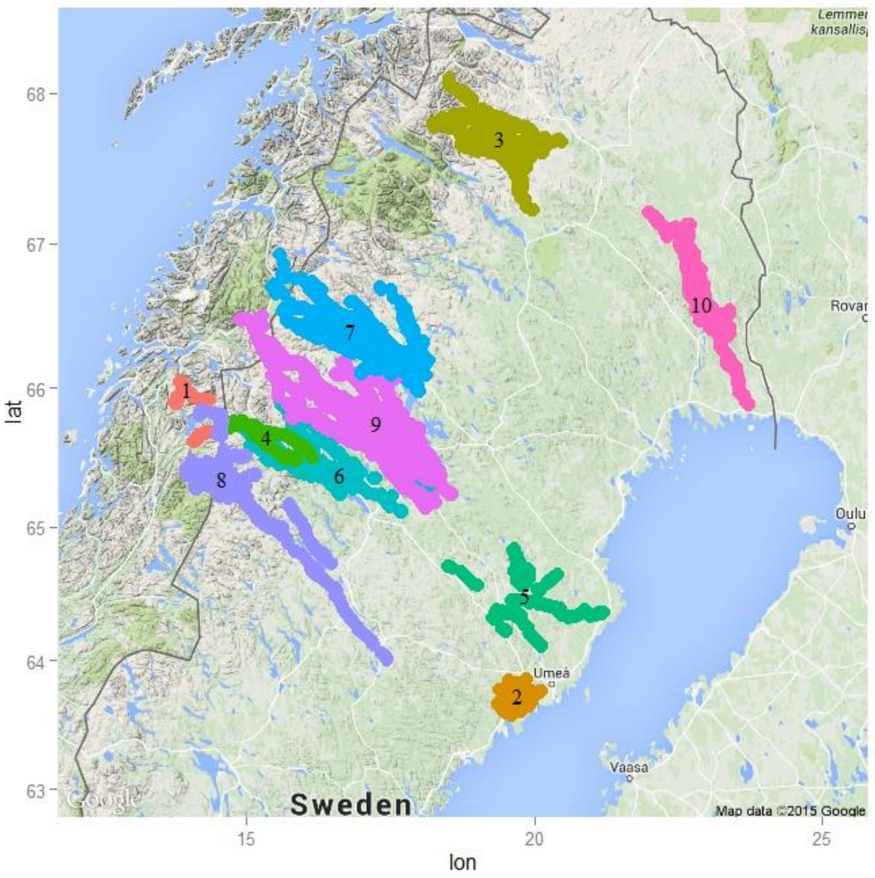

Figure 2. Areas where individuals can be found. 1=Eastern Norway, 2=Hörnefors, 3=Nikkaluokta, 4=North-West Ajauresjö, 5=Robertsfors, 6=South-East Ajauresjö, 7=South-West Norrbotten, 8=South-West Västerbotten, 9=Vindelfjällen Nature Reserve, 10=Överkalix. The colours represent the different areas and the individuals spring migration paths within the area.

Table 1. Areas with number of radio-collared individuals per area.

	Area	**Females**
1	E Norway	7
2	Hörnefors	16
3	Nikkaluokta	23
4	NW Ajauresjö	12
5	Robertsfors	19
6	SE Ajauresjö	9
7	SW Norrbotten	28
8	SW Västerbotten	25
9	Vindelfjällen NR	39
10	Överkalix	12
	Total	**190**

The average length of the growing season in the study area ranges from 100 days in the most northern parts to 160 days closer to the coast (SMHI 2014a). The yearly mean temperature for the study ranges between -3°C (mountain area) to +2°C (coastal area, SMHI 2014b). Annual precipitation is between 500-1200 mm (in some areas up to 1800 mm, SMHI 2014c) of which 35-50% falls as snow (SMHI 2014d). The average maximum snow depth in the study area during winter ranges from 70 - 130 cm (SMHI 2014e).

Moose occur in northern Sweden along with roe deer (*Capreolus capreolus*). Predators present in the study area are brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*) and occasionally wandering wolves (*Canis lupus*) (Länsstyrelsen Norrbotten 2014, Länsstyrelsen Västerbotten 2014). It is mainly the wolf and the bear that predate on moose but lynx and wolverine are known to occasionally take young, undermined or sick individuals (Jensen 2004).

Data preparation

Data from 190 female moose tracked with GPS (Global Positioning System) collars were used in this study. Moose were sedated by dart gun injection and equipped with a GPS/GSM neck collar (Vectronic Aerospace GmbH, Berlin, Germany) during winter. During capture an estimation of the birth year of the animal was made based on tooth wear to estimate age later (Rolandsen et al. 2008). Body length measurements were made so as to get an index of body mass (kg). The wireless remote animal monitoring (WRAM) database system was used for data storage, validation and management (Dettki et al. 2013). Location data from the GPS collars were collected during time period 2004 to 2013. Some individuals have been tracked for up to five years.

Since several moose were followed during multiple years, the location data were converted into moose years of tracking. A moose year started on the 1st of March when individuals were in their winter ranges. This conversion of location data resulted in 307 female moose year. Moose years will hereafter be called moose.

Migration characteristics

The movement trajectory of an individual was categorized as migratory, resident, dispersing or nomadic using the net squared displacement (NSD) modelling approach combined with nonlinear mixed effects models (Bunnefeld et al. 2011, Singh et al 2012). A total of 233 (75.9 %) moose were categorized as migratory and moose not identified as migratory were excluded from further analyses. Movement paths (Figure 3) were split into spring and autumn migrations. The results of the NSD model were used to calculate spring and autumn migration dates (Singh, Allen and Ericsson, submitted) as well as the migration distances.

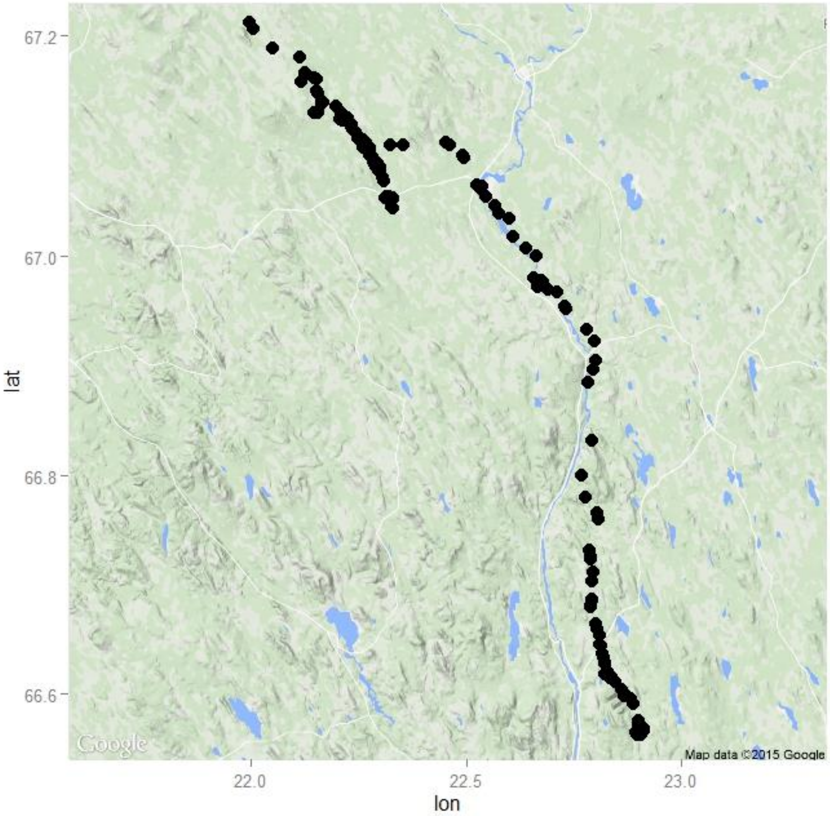

Figure 3. Example of spring migration path. Single dot represents a GPS location with a data resolution of 6 hours.

For the estimation of stopovers, GPS locations of the migratory path were used and the data was filtered to four locations per day at times closest to 00:00, 06:00, 12:00 and 18:00 hrs. Each location was classified as either start, migration or stopover, depending upon a set of given criteria. The first location of an individual´s migratory path was set as the starting location (“start”). A location was set as migration if the change in NSD was larger than 0.5 km or less than -0.5 km and as a stopover location if the change in NSD was between -0.5 km and 0.5 km. For the stopover location this allows a movement of either 500 meters forwards or backwards on the migration path (from point A to point B). When locations were classified, stopovers were estimated using certain conditions. If there were seven or more locations classified as stopover sites grouped (i.e. a stop of circa one and a half day), and if the total distance moved during this interval was between -1 and 1 kilometres it was estimated as one stopover. Total number of stopovers for spring and autumn migration were summarized for each moose year. The change in distance between locations could also be used to estimate stopovers but since migration is a directional movement (Singh et al, 2012) the change in NSD is preferred. Using change in distance between locations allows non-directional movement to be accounted in the estimation of stopovers. Another method for identifying stopovers were described by Sawyer et al. (2009), but this method identifies areas of use instead of the total number of stopovers during migration, or the duration of the stopover, which were the desired parameters in this study.

Reproductive status and litter size

Reproductive status (non-reproductive, female with single calf, female with twins, female that lost the calf) of females was noted by following cows and record the presence/absence of calves at four different time points of year; summer, before hunting, after hunting and after winter.

Reproductive status was matched with the start and end of the spring migration and the date when the calf/calves were born. Calving dates were estimated from known average calving dates for females in northern Sweden, GPS location points, and field controls. The reproductive status was established depending on, if the calving dates were within or outside spring migration for each cow. Cows that gave birth before the start of their migration were classified as ‘Before’, during their migration as ‘During’, and after spring migration as ‘After’. A fourth group of females’ known to have not reproduced were used in the analysis to compare with the other groups. For females that gave birth during migration, locations were used to see if a calf was born close to a stopover and how long did the stopover last.

Estimated movement parameters and life history parameters are displayed in Table 2.

Table 2. Description of the covariates used in the analysis to explain variation in moose movement and reproductive strategies.

Parameter	Description
Age	The age (number of years) for each individual moose.
Area	Individuals were found in 10 different areas.
Body mass	The live mass (kg) of each individual, calculated as an index based on body length and girth measurements as recorded during collaring. Note that only spring mass is used as the animals are captured in this period.
Distance	Total straight line distance between winter habitat and summer habitat travelled during migration (km).
Duration spring migration	Numbers of days for each individual to undertake spring migration.
Duration autumn migration	Numbers of days for each individual to undertake autumn migration.
Reproductive status spring	Four-level factor indicating whether females gave birth to calves 'before', 'during' or 'after' their spring migration. A comparative group consisting of non–reproducing females was also used.
Reproductive status autumn	The number of calves females was accompanied with during autumn migration.
Stopovers	Number of stops used by each individual during the migration.
Timing spring migration	Start and end of spring migration for each individual. Day of year with beginning of year at 1 of March.
Timing autumn migration	Start and end of autumn migration for each individual. Day of year with beginning of year at 1 of March.

Figure 4 displays the different data subsets obtained from the data preparation.

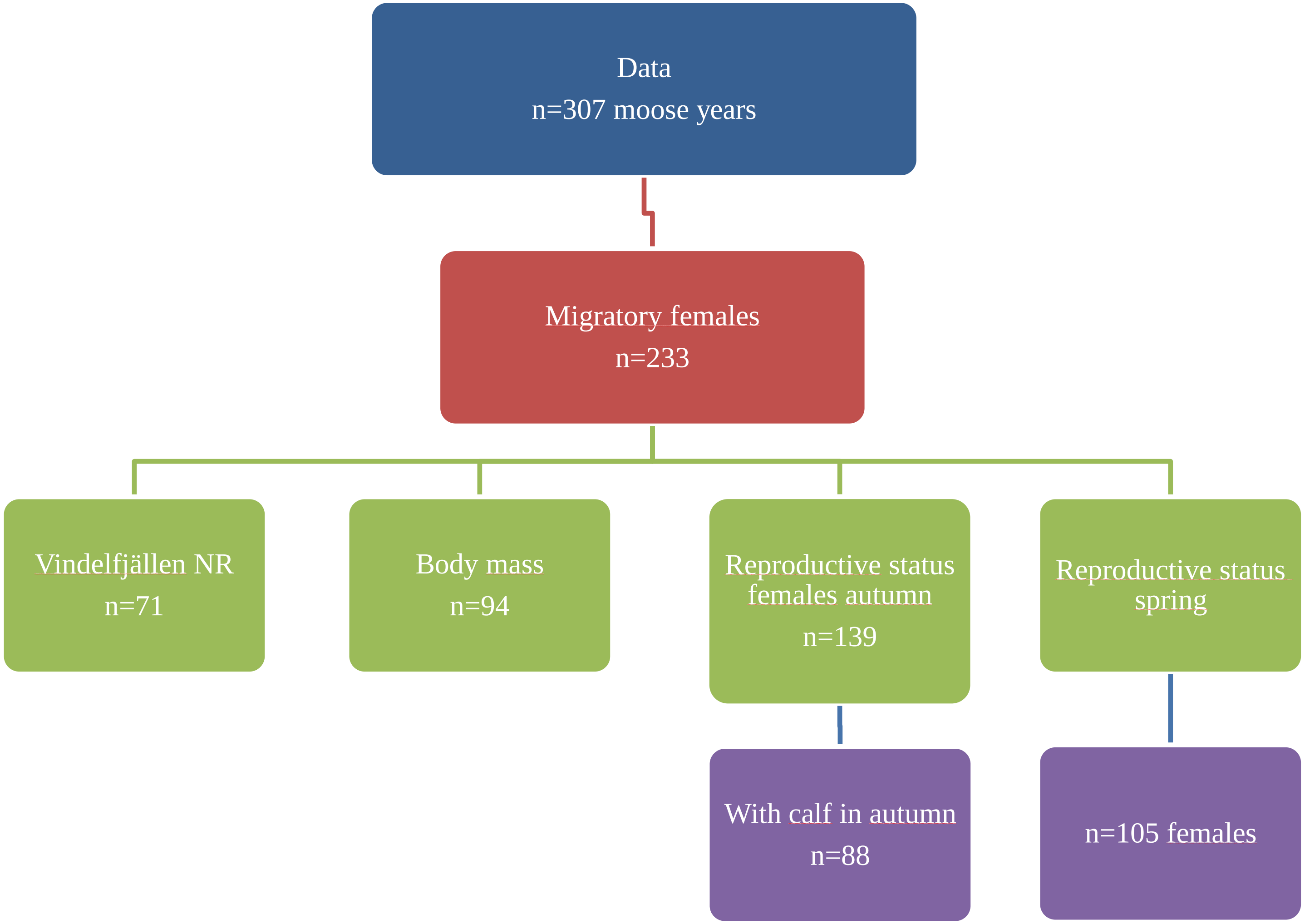

Figure 4. Data overview. Original data consists of 307 moose, of which 233 migratory female moose were extracted. Area Vindelfjällen NR holds the most of individuals, 71 females. 94 moose had data on body mass. Reproductive status of 139 females in autumn of which 88 had calf/calves present. 105 moose were included in the analysis of reproductive status in spring.

Data analysis

First, general movement characteristics were estimated for all migratory females. Secondly, the effect of age, area and body mass were tested on all migratory females without reproductive status and litter size taken into account, to evaluate the relation between individual life history and migratory movement. Finally, to test the specifically mentioned predictions about migration and calving for females, reproductive status and litter size were tested on the migratory movement. Models were separated for spring migration and autumn migration (Figure 5).

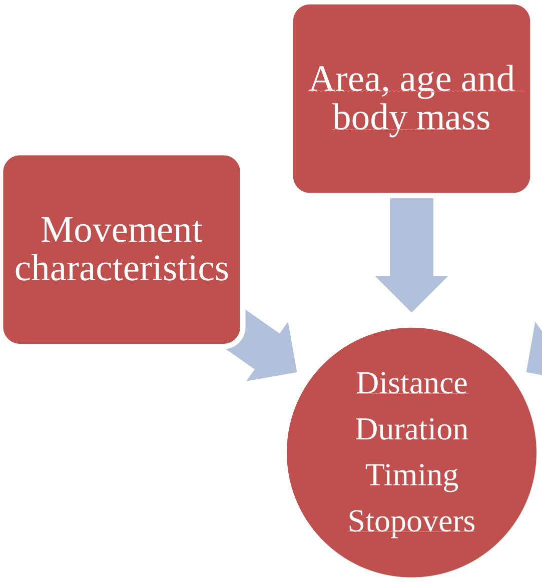

Figure 5. Overview of the data analysis. General movement characteristics were first analysed and then effect of age, area and body mass were taken into account. Reproductive status and litter size were included in the last analysis to determine variation in movement for migratory females.

Migratory characteristics

Mean (+/-S.E.) for migration distance and duration of spring and autumn migration were estimated. The mean and S.E. for start and end date of spring and autumn migration were estimated.

Effect of area, age and body mass

For estimation of relationship between movement variables and age and area, I used Generalized Linear Mixed Models (GLMMs) (Bolker et al. 2009) with a Gaussian family in the lme4 package in R (Bates, Maechler, Bolker and Walker 2014). Age and area were set as fixed effects and to account for the effect of variation from individuals with multiple years of data, animal identity was set as random effect for all GLMM models.

For analysis on the effect of body mass on movement parameters I used generalized linear models, since body mass was only recorded during capture. For comparison between areas, the model by default compared all areas with the area highest up in the alphabetical order, E Norway. Akaike´s information criterion (AIC) for model selection (Akaike 1974, Shibata 1981), in the MuMIn package in R (Barton 2014), was used to compare and select models. Based on the model selection, the coefficient of determination (R^2), were calculated for the best models. This was done in order to get an indication of how well the data fitted the statistical model and how much variation was explained by the variables included in the model.

Based on result from the models I did a separate analysis for the individuals in Vindelfjällen NR to test if distance could be explained by age or number of calves. Body mass was excluded since many of the individuals in this area had multiple years of data while observations of body mass was done once per individual.

Reproductive status and litter size

Mean and standard error for migration distance and duration of spring migration were estimated for the four different calving strategies. In addition to the average start and end date of spring migration, I also estimated the number of days the females stayed at a site after giving birth during the spring migration.

ANOVAs were used to find difference between the different female groups. Tukey´s Honest Significant Difference (Tukey 1949) test was used to test for significant difference in movement between calving strategies. 95% family-wise confidence levels were used. For females that were accompanied by calves during all of spring migration (n=9), ANOVAs and Tukey´s HSD test were used to test for the effect of one or two calves on start, duration and numbers of stopover sites during spring migration. For autumn migration, the effect of litter size was tested by GLMMs with animal identity as random effect.

All statistical analysis was carried out in R (R Core Team 2014).

Results

Migratory characteristics

Table 3 displays average values and standard error of movement variables included in the analysis for all migratory individuals. Spring migration started in May and autumn migration in November. Spring duration was shorter than autumn migration and less stopovers were used during spring migration.

Table 3. Mean (± S.E) movement characteristics for all female moose. Dates ± days for when moose start and end their spring and autumn migration.

Movement variable	Estimate
Distance (km)	69.0 ± 3.0
Duration spring (days)	20.8 ± 1.4
Duration autumn (days)	35.5 ± 2.2
Start spring migration	May 22 ± 2.2
End spring migration	June 11 ± 2.4
Start autumn migration	November 21 ± 2.2
End autumn migration	December 14 ± 3.8
Stops during spring migration	1.54 ± 0.16
Stops during autumn migration	2.75 ± 0.22

Effect of area, age and body mass

Individuals in area Vindelfjällen NR and SE Ajauresjö migrated further (p=0.009, t=2.607 and p=0.047, t=1.989) compared to area E Norway (Figure 6).

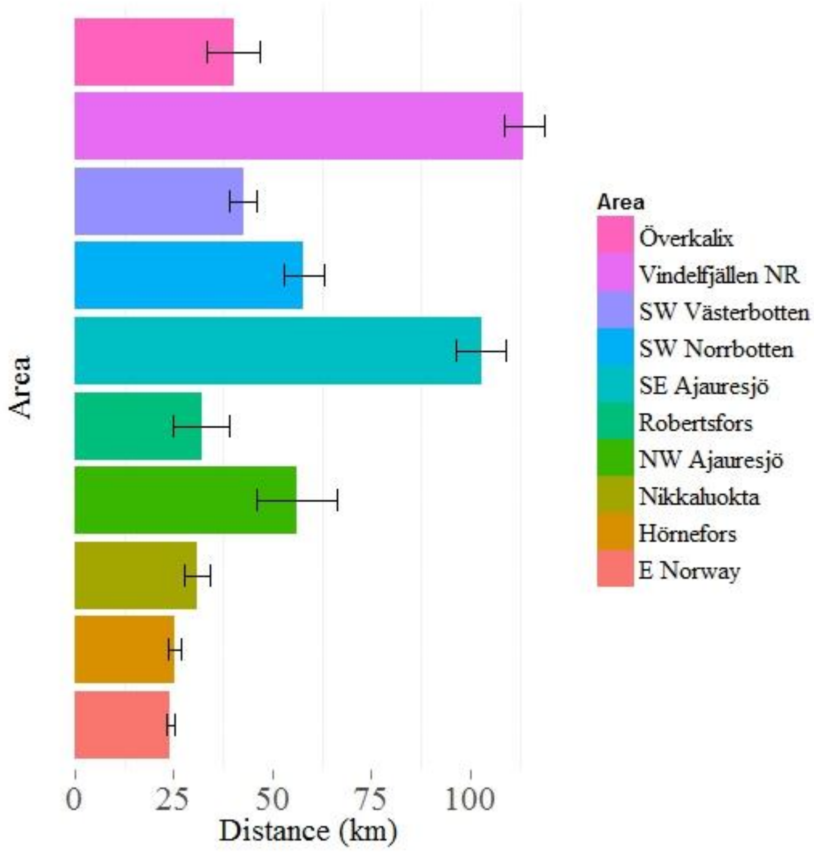

Figure 6. Mean distance and standard error for females in each area. Distances for Vindelfjällen and SE Ajauresjö are significantly longer compared to distances travelled by females in area E Norway.

The earlier significance for distance in the Vindelfjällen NR area cannot be explained for migratory females by either age (p=0.375, t=0.888) or number of calves (p=0.916, t=0.105).

Age did not affect migratory distance (p=0.419, t=-0.808).

Body mass significantly affected migratory distance of females (p=0.027, t=0.030), larger females migrated shorter distances than leaner females. The model selection indicated that the best model to explain variation in distance included age and area (weight = 1.00) for all individuals, but also body mass (weight = 0.82) for females with recorded body mass (appendix table 1). R squared values obtained were 0.52 and 0.53 respectively for the two datasets.

Area, age and body mass did not affect timing of spring migration for females with calving strategies not taken into account (p>0.05). No significant differences (p>0.05) were found for the duration during spring migration for any of the explanatory variables. In autumn, older females started their migration later than younger females (p=0.001, t=3.265). Area and age were included in the best model to explain start of autumn migration for females without calves taken into account (weight = 1.00, $R^2 = 0.21$). No significant differences ($p>0.05$) were found for the duration during autumn migration for any of the explanatory variables.

131 of the 233 moose used stopover sites in the spring. One female used as many as 20 stopovers during its spring migration. There was no significant effect of age, area or body mass on number of stopovers used by females ($p>0.05$). 161 of the 233 moose used stopover sites in the autumn. One female used as many as 14 stopovers during its autumn migration. Similar to the spring migration there was no significant effect of age or area on numbers of stopovers used for females ($p>0.05$).

Effects of reproduction and litter size

Of all the females that were checked for calves, 80 out of 105 gave birth to one or two calves. Nine births occurred before, 15 during and 56 after migration. Mean and standard error for movement variables for each of the calving strategies and for females without calves are displayed in appendix table 2. Calves were born between June 1 and June 5 for all calving strategies (Table 4).

Table 4. Average birth date and standard error (days) for different calving strategies in relation to spring migration.

Reproductive status	Birth date	±S.E.
Before	June 1	1.3
During	June 5	2.5
After	June 4	1.3

There was no significant difference in migratory distance between groups ($p>0.05$). Birth of a calf had more impact on timing, duration and stopovers of migration. Females that gave birth before their migration started their migration later than all other groups. Females that gave birth after migration started their migration earlier than non-reproductive females and arrived earlier at the summer ranges than all other groups. Females that were accompanied by a calf during all or part of the migration (birth before or during) arrived later on the summer range than females without a calf. Calves born during migration entailed a longer duration and increased the number of stopovers compared to all other groups. (Figure 7). For significance and 95% confidence levels see appendix table 3.

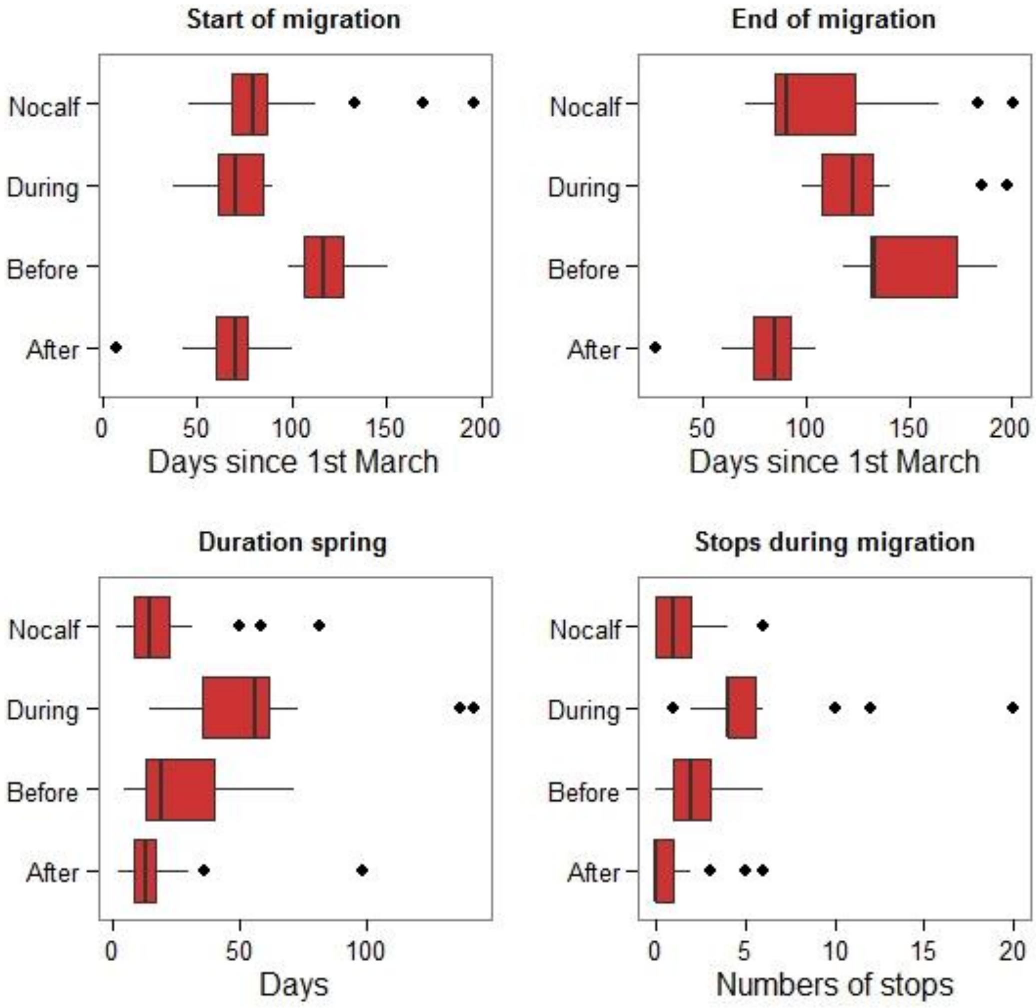

Figure 7. Box plot of start, end, duration of migration and stopovers of females with different calving strategies. The box represents the range where half of the sample values are located with the median as the vertical line. Upper and lower quartile of the data is represented by the whiskers that ends with largest and smallest observation. Dots represents outliers.

Females that gave birth during migration used a stopover in connection to birth. The stopover lasted for 8 (S.E. ± 1.48) days.

Number of calves (one or two) during migration did not affect the duration or start of migration (p>0.05, appendix table 4). Females with two calves during spring migration used 3.3 ± 2.52 stopover sites during migration while females with one calf used 2.0±2.28 stopovers. However no significant effect were found (p>0.05, appendix table 4).

Females with two calves started their fall migration earlier than females with a singleton (p=0.001, t=-3.279). Area, age and number of calves were included in the best model selected to explain start of autumn migration for females accompanied by a singleton or two calves during autumn migration (weight=0.97, R^2=0.27). No significant differences (p>0.05) were found for autumn duration for any of the explanatory variables.

Number of calves in autumn did not affect number of stopovers sites used during migration (p=0.775, t=0.285). Females with no calf used 2.59 ±0.46 stopovers, females with one calf 2.29±0.29 and females with two calves 2.77±0.79.

Discussion

The key finding from my study was the synchrony of timing and duration of spring migration in relation to calving, and its implications on the time minimization- versus energy maximization tactics of moose females. The migratory distance varied according to area of study, where in two areas, females migrated longer distances than in other. In addition leaner females migrated to longer distances than larger females. Age affected the timing (start) of migration in autumn migration with younger individuals starting their migration earlier than older individuals. Most females gave birth after migration, but many also, before and during migration. Depending on how migration was synchronized with calving, females used time minimizing and energy maximizing strategies variably, as observed by the differences in the timing and duration of migration. Litter size affected the timing of autumn migration, where females with twins started earlier than those with a singleton.

Migratory characteristics

It is well know that some animal species is seasonally migratory. It has been seen that timing of migration has varied in relation to snow depth, spring green up and between different areas (White et al. 2010). In red deer, population density had an effect on the migration distance, as the distance decreased with and increasing density of the population as well was the autumn timing delayed at higher densities (Mysterud et al. 2011). Timing of spring migration has been seen to vary depending on the altitude of the summer ranges and for autumn migration a certain snow depth has been seen to act like a limit for latest start of migration (Mysterud 1999). Duration in spring and autumn migration for migratory mule deer did not differ (Sawyer and Kauffman 2011) as it did in this study. Mule deer did also use more stopovers during spring migration than during autumn migration (Sawyer and Kauffman 2011). Singh et al. (2012) found that migratory movement characteristics varied with latitude at the population level, and with age and sex on the individual level.

Effect of area, age, and body mass

Area-specific variation have been found regarding the distance of migration and this result is likely due to the topographic gradient observed in the landscape, where migrants may follow the increase and decrease of landscape relief and connected vegetation patterns. Females in Vindelfjällen follow a long topographic gradient, which runs from coast towards the mountain with increasing elevation. As animals tend to track certain changes in the landscape, e.g. vegetation phenology, one would expect the migrants to follow that gradient as far as the energetic demands are met with the availability of high quality food for the longest amount of time. Also known as the forage maturation hypothesis or the energy maximizing tactic (Bergman et al. 2001, Hebblewhite and Merril 2009). This has been shown in earlier studies e.g. Bischoff et al. (2012), van Moorter et al. (2013).

The fact that leaner females migrated longer distances than larger females could be due to the competition they face from older females. Competition can affect animal performance and behaviour (Gaillard et al. 2010), and therefore to meet the energetic demands, leaner females maximize energy by migrating to longer distances in search of summer habitats with high forage quality. Travelling longer distances however would require more energy (Alerstam, Hedenström and Åkesson, 2003) and therefore leaner females might trade-off migration cost and future energy intake. Age did not affect the migratory distance in this study. Younger animals have been seen to migrate to larger distances and the propensity to migrate should decline with age (Singh et al. 2012). The best model to explain variation in distance contained area, age and body mass. The coefficient of determination for this model was 0.53 which mean that more than half of the variation found for distance was explained by area, age and body mass. More than just one variable determines the migratory distance and there are probably one or more other variables not tested in this study that affects the distance as well.

The life history variables did not have any effect on the start of spring migration, and this is probably more linked to snow depth, plant phenology (Monteith et al. 2011) and timing of migration in relation to calving for reproductive females (see below). Older individuals have been observed to delay their start of autumn migration compared to younger individuals which is in contradiction with the result found by Singh et al. (2012). This could mean that older females are taking risks by delaying their autumn migration, i.e. risks of encountering harsh weather which could lead to a possible loss of foraging opportunities that comes with deep snow (Monteith et al. 2011). However, if theses risk-taking females arrive at the winter range successfully, they may benefit by staying longer at the summer habitat with the higher-quality forage (Albon and Langvatn 1992, Mysterud et al. 2001) which could be an attempt to support reproduction by maximizing the nutritional gain (Stearns 1992). The delay of the autumn migration could also be because of better knowledge of the true risks and experience of forage distribution and experience of weather patterns in autumn (Monteith et al. 2011). Area and age were included in the best model to explain variation in start of autumn migration. However, the R squared was fairly small (0.21) which implies that this variation probably is due to some other variable not taken into account in this study.

Spring migration duration is connected to reproductive status of females and timing of calving in relation to migration. Duration during autumn migration could not be explained by any of the life history variables, and is probably more in relation to snow depth (Monteith et al. 2010).

Number of stopovers in spring and autumn migration was independent of age, sex, area, and number of calves. Using stopovers in spring migration can be a way to synchronize with plant phenology and by that maximize energy rate instead of maximizing the speed of migration (Sawyer and Kauffman 2011). Number of stopovers in autumn is probably connected to the forage quality along the migration path, weather and if individuals have mated or not.

Effect of calving and litter size

Females used different migratory strategies in relation to calving. A larger part of all reproductive females gave birth after migration, while others gave birth during or before spring migration. P1) is thus rejected. Distance did not significantly differ between females of different categories and is probably more related to available high quality forage habitat, local climate and competition among females. Based on the variation in the other movement variables for the different calving strategies, female moose alternated between time minimizing and energy maximizing strategies during spring migration dependent on upon their reproductive status (Figure 8). A majority of the females aimed to get to the summer range before calving, which is probably the fastest and the most energy efficient way possible (time minimizing strategy). This is likely because the energetic demands increase rapidly after the birth of an offspring and if a female is already in the energy rich areas, both mother and offspring may then benefit greatly and use the energy maximizing strategy of habitat selection during the summer. These females also used the least number of stopovers further ascertains the time minimization strategy. These females migrated faster than even the non-reproductive females, which are not driven by reproductive demands and hence undertake the best possible strategy (either energy maximizing or time minimizing) that suits them at a given time in space (Singh and Ericsson 2014).

Females that gave birth during migration are probably forced to extend the duration of migration because of the immobility of the calf during its first days in life. In addition they are also expected to trade-off movement and feeding, against safety of the offspring from predators. This may add further costs of movement to the mothers and slow them down (Singh and Ericsson 2014). These females may also need to use more stopovers sites in relation to feeding, movement and safety. Females that give birth during migration may therefore adopt both strategies simultaneous (Lendrum et al. 2014), i.e. initially adopt a time minimizing strategy and after the calf is born, switch to an energy maximizing one.

Some females delayed their spring migration to give birth. These females started later than other female groups and arrived the last at the summer ranges. These females, by staying longer at the winter home range, may allow the calf to increase its mobility before starting migration, but on the other hand they may miss the timing of peak productivity at sites along the migration paths and may therefore spend longer time searching for high quality habitats during migration, while being vigilant to increase their calf survival. Moreover, these females may also be able to avoid competition with other females for high quality habitats by being segregated from other in space and time. This result does not support P2) and the prediction is thus rejected.

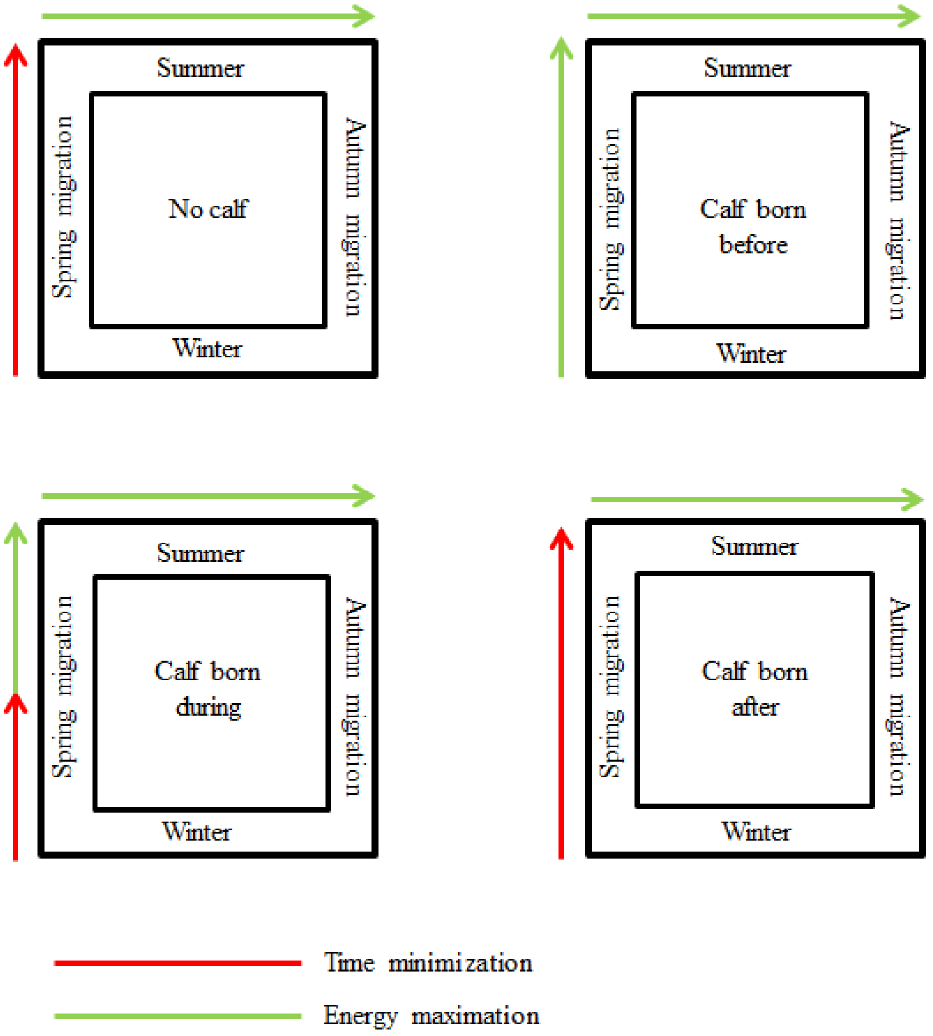

Figure 8. Figure displaying time/energy strategies during spring migration by the calving strategies. Outer box represent one moose year. Red arrow means time minimization strategy and green energy maximization.

Females that gave birth during migration used a stopover in connection and stayed for ~ 8 days. McGraw et al. (2014) found that females stayed ~7 days at the birth site. This could be, firstly because of the immobility of the calf, and secondly, it could be a strategy to avoid predators. Staying in a small area makes the risk to be encountered by a predator smaller (Bowyer et al. 1999), nevertheless staying in a small area to long increases the risk of being found by a predator (McGraw et al. 2014).

There was no effect of having one or two calves at heel during spring migration, which might be due to the fact that the amount of time needed for one or two offspring to be sufficiently mobile to follow the mother, being similar. Females with two calves on the other hand started their autumn migration earlier than females with a singleton. This could be seen as a trade-off between maximizing energy intake (by staying at the habitat with the higher quality forage) and ensuring survival of the calves. No significant variation in duration and number of stopovers was found for numbers of calves. As calves start to be less dependent of females in autumn (Jensen 2004), i.e. the females do not lactating anymore, females might not need to stay just as close to the calf as in the first time period of the calf´s life and the duration and number of stopovers is thus less dependent on the calf. P3) is rejected since there was no difference in duration during autumn migration between non-reproductive or reproductive females, as well as the duration did not differ between females with a singleton or females with twins.

An important implication of these different movement strategies in relation to birth is their fitness consequences. The main question that arises from these results is – is one female group better in survival and reproduction than the other. In other words, what might be the fitness benefits of a multiple strategy within the same species. One possible reason can be the local adaptation towards the seasonality and the environments, the individuals inhabit. Perhaps by being flexible, females are able to increase their survival in the landscape which show large seasonality and variability in terms of food, climate, predation risk and human disturbance. These aspects have not been dealt with in this study, are crucial for a better understanding of the ecosystem dynamics and population persistence.

Classification of migratory paths and estimations of movement variables was estimated by the NSD model approach, which has been criticised. One of the issues with the model is related to the starting location of the data/animal, if the starting location occurs during the migratory phase of the animal this could make the estimations incorrectly (Singh, Allen, and Ericsson, submitted). The method used to estimate stopovers have never been published and given criteria set is made on observations.

Conclusion

Variation in spring migration movement for female moose is dependent on reproductive status and the relation between calving and migration. Most females aim to give birth after spring migration, at the summer range, but some females give birth during or even before migration. The variation in calving strategies implicates that females use time minimization and energy maximization strategies in different sense and that this could affect both the female and the calf in terms of future survival and reproduction, which in a larger context could affect the population as a whole.

Synchronization of migration and calving of moose has never been compared before and this study is a first step in trying to understand what impact this could have on the individual. As timing of calving in relation to migration determines some of the movement variation in spring migratory movement, this should be included in all future studies regarding migration of ungulates. It is also important in terms of populations dynamics and understanding survival and reproduction of moose.

Acknowledgement

I would like to express my gratitude to my supervisor Navinder J. Singh for the useful comments, remarks and engagement through the learning process of this master thesis. Furthermore I would like to thank my assistant supervisor Andrew Allen for valuable comments and support during the progress of this thesis. Without their assistance and dedicated involvement in every step throughout the process, this paper would have never been accomplished.

References

Akaike, H. 1974. A New Look at Statistical Model Identification, IEEE. Transactions on Automatic Control 19: 716-723.

Albon, S.D, and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos. 65: 502-513.

Alerstam,T., Hedenström, A. and Åkesson, S. 2003. Long-distance migration: evolution and determinants. Oikos. 103: 247-260.

Altman, M. 1958. Social integrations of the moose calf. Animal behavior. 6: 155-159.

Avgar, T., Street, G., and Fryxell, J.M. 2013. On the adaptive benefits of mammal migration. Canadian Journal of Zoology. 91: 1-10.

Ball, J.P. Nordengren, C. and Wallin, K. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology. 7(1): 39-47.

Barton, K. 2014. MuMIn: Multi-model inference. R package version 1.10.5. http://CRAN.R-project.org/package=MuMIn

Bates, D. Maechler M. Bolker, B. and Walker, S. 2014. _lme4: Linear mixed-effects models using Eigen and S4_. R package version 1.1-7, <URL: http://CRAN.R-project.org/package=lme4>.

Bergman, C.M., Fryxell, J.M., Gates, C.C. and Fortin, D. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? Journal of Animal Ecology. 70: 289-300.

Bischof, R., Loe, L.E., Meisingset, E.L., Zimmerman, B., van Moorter, B. and Mysterud, A. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? The American Naturalist. 180(4):407-424.

Bolker, B.M, M Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, H. Stevens, and J.S. White 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24(3): 127-135.

Bowyer, R.T., Van Ballenberghe, V., Kie, J.G. and Maier, J.A.K. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. Journal of Mammology. 80: 1070-1083.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. and Ericsson, G. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology. 80:466-476.

Börger, L. Dalziel, B.D. and Fryxell, J.M. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters. 11: 637-650.

Dettki, H., Ericsson, G., Giles, T. and Norrsken-Ericsson, M. 2013. Wireless Remote Animal Monitoring (WRAM) – A new international database e-infrastructure for telemetry sensor data from fish and wildlife. p. 247-256. In: Proceedings Etc 2012: Convention for Telemetry, Test Instrumentation and Telecontrol (Eds. The European Society of Telemetry). Books on Demand, pp. 292, ISBN: 978-3-7322-5646-4.

Dingle, H. (1996). *Migration: The Biology of Life on the Move.* [Electronically] New York: Oxford University Press. Available: Ebrary. [2014-12-09]

Dingle, H. and Drake, V.A. 2007. What is migration?. Bioscience. 57(2): 113-121.

Ericsson, G. and Wallin, K. 2001. Age-specific moose (Alces alces) mortality in a predator-free environment: Evidence for senescence in females. Ecoscience. 8(2): 157-163.

Ericsson, G., Wallin, K., Ball, J.P. and Broberg, M. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology. 82(6): 1613-1620.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology. 21:1003-1015.

Fallsvik, J. 2011. Översiktlig klimat- och sårbarhetsanalys – Naturolyckor. Rapport SGI Diarienummer: 2-1005-0372. Linköping.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia. 75:580-586.

Frair, JL., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, NJ. and Pedrotti, L. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1550):2187-2200.

Fryxell, J.M. and Sinclair, A.R.E.1988. Causes and consequences of migration by large herbivores. TREE. 3(9): 237-241.

Fryxell, J.M., Wilmshurst, J.F. and Sinclair, A.R.E. 2004. Predictive models of movement by Serengeti grazers. Ecology. 85(9):2429-2435.

Gaillard, J-M. Hebblewhite, M. Loison, A. Fuller, M. Powell, R. Basille, M. and van Moorter, B. 2010. Habitat-performance relationships: finding the metric at a given spatial scale. Philosophical Transactions of The Royal Society B. 365:2255-2265.

Haydn, A. 2012. *Calving site selection by moose* (Alces alces) *along a latitudinal gradient in Sweden.* University of Natural Resources and Applied Life Sciences. Master Thesis. www.alg-forskning.se/media/haydn_moosecalvingmasterthesis.pdf

Heard, D.C., Williams, T.M., and Melton, D.A. 1994. The relationship between food intake and predation risk in migratory caribou and wolf populations. Rangifer. 2:37-44.

Hebblewhite, M. and Merrill, E.H. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology. 90(12): 3445-3454.

Hågeryd, A-C. 2011. Översiktlig klimat- och sårbarhetsanalys – Naturolyckor. Rapport SGI Diarienummer: 2-1006-0454. Linköping.

Jensen, B. 2004. Nordens däggdjur. 2ed. - Stockholm: Prisma.

Lendrum, P.E., Andersson, Jr., C.R., Monteith, K.L., Jenks, J.A. and Bowyer, T. 2014. Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. Mammalian Biology. 79: 369-375.

Loe, L.E., Bonenfant, C., Mysterud, A., Gaillard, J-M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N. and Stenseth, N.C. 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting an calving in Norway and France. Journal of Animal Ecology. 74: 579-588.

Lundberg, J. and Moberg, F. 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. Ecosystems. 6: 87-98.

Länsstyrelsen Norrbotten (2014). *De stora rovdjuren i Norrbotten.* http://www.lansstyrelsen.se/norrbotten/Sv/djur-och-natur/rovdjur/stora-rovdjur-i-norrbotten/Pages/default.aspx [2014-09-18].

Länsstyrelsen Västerbotten (2014). *Stora rovdjur i Västerbotten.* http://www.lansstyrelsen.se/vasterbotten/Sv/djur-och-natur/rovdjur/Stora-rovdjur-i-Vasterbotten/Pages/default.aspx [2014-09-18].

McGraw, A.M., Terry, J. and Moen, R. 2014. Pre-parturition movement patterns and birth site characteristics of moose in northeast Minnesota. Alces. 50: 93-103.

Monteith, K.L., Bleich, V.C., Stephenson, T.R., Pierce, B.M., Conner, M.M., Klaver, R.W. and Bowyer, R.T. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere. 2(4): 1-34

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., Langvatn, R., Yoccoz, N.G. and Stenseth, N.C. 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.

Mysterud, A. Loe, L.E. Zimmerman, B. Bischof, R. Veiberg, V. and Meisingset, E. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for densiy dependence? Oikos. 120: 1817-1825.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P.E. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences. 105(49):19052-19059.

Pastor, J. Naiman, R.J. Dewey, B. and McIness, P. 1988. Moose, microbes, and the boreal forest. BioScience. 38(11):770-777

Pettorelli, N., Gaillard, J-M., Van Laere, G., Duncan, P., Kjellander, P., Liberg, O., Delorme, D. and Maillard, D. 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. Proceedings of The Royal Society London B. 269:747-753.

Pettorelli, N., Pelletie, F., von Hardenberg, A., Festa-Bianchet, M. and Côté, S.D.2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology. 88(2): 381-390.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rolandsen, C.M., Solberg, E.C., Heim, M., Holmstrøm, F., Solem, M.I. and Sæther, B-E. 2008. Accuracy and repeatability of moose (*Alces alces*) age as estimated from dental cement layers. European Journal of Wildlife Research. 54:6-14.

Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. Oecologia. 106: 212-220.

Sawyer, H. Kauffman, M.J. Nielson, R.M. and Horne, JS.2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications. 19(8): 2016-2025.

Sawyer, H. and Kauffman, M.J. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology. 80: 1078-1087.

Schoener, T.W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics. 2:369-404.

Shibata, R. 1981. An Optimal Selection of Regression Variables. -Biometrika 68: 45-54.

Singh, N.J. Börger, L. Dettki, H. Bunnefeld, N. and Ericsson, G. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecological Applications. 22(7): 2007-2020.

Singh, N.J., Allen, A. and Ericsson, G.E., *submitted*. Quantifying migration using Net Squared Displacement approach: clarifications and caveats.

Singh, N.J. and Leonardsson, K. 2014. Partial migration and transient coexistence of migrants and residents in animal populations. PLOS ONE. Volume 9. Issue 4. E94750

Singh, N.J., Danell, K., Edenius, L. and Ericsson, G. 2014. Tackling the motivation to monitor: success and sustainability of a participatory monitoring programme. Ecology and Society. 19(4): 7.

SMHI, 2014a (2014-04-23). *Vegetationsperiod.* http://www.smhi.se/kunskapsbanken/klimat/vegetationsperiod-1.6270. [2014-09-15].

SMHI, 2014b. (2014-04-23). *Normal årsmedeltemperatur.* http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-arsmedeltemperatur-1.3973 [2014-09-18].

SMHI, 2014c. (2014-04-23). *Normal uppmätt årsnederbörd, medelvärde 1961-1990.* http://www.smhi.se/klimatdata/meteorologi/nederbord/normal-uppmatt-arsnederbord-medelvarde-1961-1990-1.4160 [2014-09-18].

SMHI, 2014d. (2014-04-23). *Normal andel snö av årsnederbörden, medelvärde 1961-1990.* http://www.smhi.se/klimatdata/meteorologi/nederbord/normal-andel-sno-av-arsnederborden-medelvarde-1961-1990-1.4172 [2014-09-18].

SMHI, 2014e. (2014-04-23). *Normalt största snödjup under vintern, medelvärde.* http://www.smhi.se/klimatdata/meteorologi/sno/normalt-storsta-snodjup-under-vintern-medelvarde-1.7931 [2014-09-18].

Solberg, E.J., Heim, M., Grøtan, V., Sæther, B-E. and Garel, M. 2007. Annual variation in maternal age and calving date generate cohort effects in moose (*Alces alces*) body mass. Oecologia. 154: 259-271.

Spencer, W.D.2012. Home ranges and the value of spatial information. Journal of Mammalogy. 93(4): 926-947.

Stearns, S.C. 1992. *The evolution of life histories.* Oxford University Press, Oxford, New York, USA.

Sweanor, P.Y. and Sandegren, F. 1989. Winter-range philopatry of seasonally migratory moose. Journal of Applied Ecology. 26(1): 25-33.

Testa, J.W. and Adams, G.P. 1998. Body condition and adjustments to reproductive effort in female moose. Journal of Mammology. 79: 1345-1354.

Tomkiewicz, S.M. Fuller, M.R. Kie, J.G. and Bates, K.K. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1550):2163-2176.

Tukey, J. 1949. Comparing Individual Means in the Analysis of Variance. Biometrics. 5(2): 99-114.

Urbano, F., Cagnacci, F., Calenge, C., Dettki, H., Cameron, A., & Neteler, M. 2010. Wildlife tracking data management: a new vision. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1550):2177–2185.

van Moorter, B. Visscher, D. Benhamou, S. Börger, L. Boyce, M.S.and Gaillard, J.M. 2009. Memory keeps you at home: a mechanistic model for home range emergence. Oikos. 118: 641-652.

van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C.M., Solberg, E.J. and Sæther, B-E. 2013. Understanding scales of movement: animals ride waves and ripples of environmental change. Journal of Animal Ecology. 82: 770-780.

White, P.J. Proffitt, K.M., Mech, L.D., Evans. S.B., Cunnigham, J.A. and Hamlin, K.L. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. Journal of Mammalogy. 91(4): 827-837.

White, K.S., Barten, N.L., Crouse, S. and Crouse, J. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology. 95(1): 225 – 237.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. and Henschel, C.P. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology. 77:1223-1232.

Åkesson, S. and Hedenström, A. 2007. How migrants get there: Migratory performance and orientation. BioScience. 57(2):123-133.

Appendix I

Appendix table 1. Model selection for each response variable that showed significant variation and subsets.

Data subset		Model	AIC	Weights
All Females				
Distance				
	1	Distance ~ Area + Age	2067.59	1.00
	2	Distance ~ Area	2133.94	0.00
	3	Distance ~ Age	2160.29	0.00
Start autumn migration				
	1	Start autumn ~ Area + Age	2172.44	1.00
	2	Start autumn ~ Age	2193.00	0.00
	3	Start autumn ~ Area	2253.79	0.00
Body mass Females				
Distance				
	1	Distance ~ Area + Age + Weight	870.31	0.82
	2	Distance ~ Area + Age	873.62	0.16
	3	Distance ~ Area + Weight	877.91	0.02
	4	Distance ~ Area	883.79	0.00
	5	Distance ~ Age + Weight	918.57	0.00
	6	Distance ~ Age	925.99	0.00
	7	Distance ~ Weight	926.45	0.00
Females with calf in autumn				
Start autumn migration				
	1	Start autumn ~ Area + Age + Calves	805.91	0.97
	2	Start autumn ~ Area + Age	813.65	0.02
	3	Start autumn ~ Age + Calves	815.97	0.01
	4	Start autumn ~ Age	818.26	0.00
	5	Start autumn ~ Area + Calves	842.62	0.00
	6	Start autumn ~ Area	849.24	0.00
	7	Start autumn ~ Calves	851.42	0.00

Appendix table 2. Average and standard error for the distance, duration, stopovers , start, and end dates for each of the calving categories.

	Before	During	After	No calf
n	9	15	56	25
Distance (km)	71.3 ± 18.9	93.6 ± 12.8	63.4 ± 5.7	67.4 ± 9.2
Duration spring migration (days)	27.0 ± 7.2	58.4 ± 9.4	15.1 ± 1.8	19.4 ± 3.7
Start spring migration	June 28 ± 6.0	May 9 ± 4.6	May 8 ± 2.0	May 27 ± 6.7
End spring migration	July 26 ± 9.5	July 7 ± 7.6	May 22 ± 1.9	June 16 ± 6.9
Number of stopovers spring migration	2.44 ± 0.77	5.87 ± 1.24	0.86 ± 0.17	1.40 ± 0.36

Appendix table 3. Result from the Tukey multiple comparisons of means test based on ANOVA tests for the calving strategies. Difference is between parameters, lower and upper values for 95% confidence limits, degrees of freedom for the different groups (Strategy) and for observations (Residuals), and standard error for the residuals. P-values in bold with star means significant difference between groups.

	Diff	Lower	Upper	p-value	Degrees of freedom		Residual SE
Distance					Strategy	Residuals	
Before-After	7.88	-34.82	50.58	0.963	3	101	45.52
During-After	30.18	-4.39	64.75	0.109			
Nocalf-After	3.99	-24.16	32.59	0.983			
During-Before	22.30	-27.84	72.43	0.652			
Nocalf-Before	-3.89	-50.11	42.33	0.996			
Nocalf-During	-26.19	-65.02	12.65	0.298			
Duration spring migration							
Before-After	11.90	-6.97	30.78	0.357	3	101	20.12
During-After	43.30	28.02	58.58	**0.000***			
Nocalf-After	4.34	-8.30	16.98	0.806			
During-Before	31.40	9.24	53.56	**0.002***			
Nocalf-Before	-7.56	-27.99	12.87	0.769			
Nocalf-During	-38.96	-56.13	-21.79	**0.000***			
Start spring migration							
Before-After	50.99	30.78	71.20	**0.000***	3	100	21.52
During-After	0.88	-15.50	17.25	0.999			
Nocalf-After	18.83	5.27	32.39	**0.003***			
During-Before	-50.11	-73.81	-26.41	**0.000***			
Nocalf-Before	-32.16	-54.02	-10.31	**0.001***			
Nocalf-During	17.95	-0.41	36.31	0.058			

End spring migration							
Before-After	64.54	42.01	87.07	**0.000***	3	101	24.02
During-After	45.74	27.50	63.97	**0.000***			
Nocalf-After	24.78	9.69	39.87	**0.000***			
During-Before	-18.80	-42.25	7.65	0.253			
Nocalf-Before	-39.76	-64.15	-15.37	**0.000***			
Nocalf-During	-20.96	-41.45	-0.47	**0.043***			
Stopovers during spring migration							
Before-After	1.59	-0.57	3.75	0.226	3	101	2.30
During-After	5.01	3.26	6.76	**0.000***			
Nocalf-After	0.54	-0.90	1.99	0.761			
During-Before	3.42	0.89	5.96	**0.003***			
Nocalf-Before	-1.04	-3.38	1.29	0.649			
Nocalf-During	-4.47	-6.43	-2.50	**0.000***			

Appendix table 4. Result from the Tukey multiple comparisons of means test based on ANOVA tests for females accompanied by one or two calves during spring migration. Difference is between parameters, lower and upper values for 95% confidence limits, degrees of freedom for the number of calves (Calves) and for observations (Residuals), and standard error for the residuals.

Two calves - one calf

					Degrees of freedom		
	Difference	Lower	Upper	p-value	Calves	Residuals	Residual S.E.
Duration	11.5	-25.96	48.96	0.491	1	7	22.40
Start	-15.17	-44.61	14.27	0.263	1	7	17.61
Stopover sites	1.33	-2.60	5.26	0.449	1	7	2.35

SENASTE UTGIVNA NUMMER

2014:9 Nyckeltal för älg och fodertillgång på tall Pinus sylvestris och rönn Sorbus aucuparia.
Författare: Mikael Åkerblom Andersson

2014:10 Rissepareringens effekter på viltets nyttjandegrad av GROT.
Författare: David Rehmberg

2014:11 Fysiska strukturer i Umeälvens gamla älvfåra och dess inverkan på laxsmoltens utvandringsframgång.
Författare: Viktoria Tegenfeldt

2014:12 SNP-based conservation genetics of the southern Swedish brown bear (Ursus arctos) population.
Författare: Joanna Fahlén

2014:13 Comparison of tree cavity abundance and characteristics in managed and unmanaged Swedish boreal forest.
Författare: Sophie Michon

2014:14 Habitat modeling for rustic bunting (Emberiza rustica) territories in boreal Sweden
Författare: Emil Larsson

2014:15 The Secret Role of Elephants - Mediators of habitat scale and within-habitat scale predation risk
Författare: Urza Flezar

2014:16 Movement ecology of Golden eagles (Aquila crysaetos) and risks associated with wind farm development
Författare: Rebecka Hedfors

2015:1 GIS-based modelling to predict potential habitats for black stork (Ciconia nigra) in Sweden
Författare: Malin Sörhammar

2015:2 The repulsive shrub – Impact of an invasive shrub on habitat selection by African large herbivores
Författare: David Rozen-Rechels

2015:3 Suitability analysis of a reintroduction of the great bustard (Otis tarda) to Sweden
Författare: Karl Fritzson

2015:4 AHA in northern Sweden – A case study
Conservation values of deciduous trees based on saproxylic insects
Författare: Marja Fors

2015:5 Local stakeholders' willingness to conduct actions enhancing a local population of Grey Partridge on Gotland – an exploratory interview study
Författare: Petra Walander

Hela förteckningen på utgivna nummer hittar du på www.slu.se/viltfiskmiljo