Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Department of Ecology
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Linda Höglund

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Abstract

Roe deer (*Capreolus capreolus*) live in diverse environmental conditions due to their wide distribution. Because of their high variety of living conditions it is common that some individuals in a population have different summer and winter areas. These areas are generally the same over the years and the migrations between these areas occur in spring and fall. The timing and distance of these seasonal migrations was the main focus of my study. Timing of migration can be affected by various factors and by studying the impact of age, sex, seasonal phenology (determined by the Normalized Difference Vegetation Index, NDVI), winter severity, temperature, and migration distance this study investigated the relative importance of these factors in affecting timing of seasonal migration. This study showed that age and seasonal phenology were the main factors affecting the timing of seasonal migration in spring with earlier departure in early springs and by older animals. Furthermore, shorter distance between seasonal areas resulted in a greater variation in the timing of seasonal migration, both between individuals but also within the same individual for animals that were followed during several years. Age and seasonal phenology were the main factors affecting timing of seasonal migration also in the fall. However, in addition sex was also affecting the timing of migration in fall. Overall, variation in the timing of seasonal migration was greater in fall than in spring and male roe deer stayed at the summer ranges longer than females. Females, especially those who migrated >10 km, returned to winter areas earlier than short-distance migrants.

Sammanfattning

Rådjur (*Capreolus capreolus*) har på grund av sitt stora utbredningsområde, väldigt olika miljömässiga förutsättningar. Det är inte ovanligt att vissa individer utvecklat en strategi där de utnyttjar olika områden beroende på om det är sommar eller vinter. Dessa förblir ofta desamma över tid och säsongsvandringarna sker under vår respektive höst. Tidpunkten för dessa säsongsvandringar är vad jag i huvudsakligen har fokuserat på i den här studien. Tajmingen av dessa säsongsvandringar påverkas av många faktorer och genom att studera påverkan av ålder, kön, växtfenologi (bedöms med NDVI värde), vinter, temperatur och vandringsdistans undersöktes olika faktorers relativa påverkan på tajmingen av säsongsvandringarna. Denna studie visar att det på våren var ålder och växtfenologi som hade störst påverkan på tidpunkten för säsongsvandringar på Grimsö forskningsområde med tidigare säsongsvandringar under tidiga vårar och hos äldre djur. Kortare säsongsvandringar resulterade i en mer spridd tidpunkt för tajmingen av säsongsvandringarna, både mellan individer men också för de enskilda individerna som följdes under flera år. Under hösten var det också framförallt ålder och växtfenologi som påverkade tajmingen av säsongsvandringarna, men här hade även kön en stor betydelse för tajmingen av säsongsvandringarna. Generellt så hade rådjuren en större spridning av tidpunkten för säsongsvandring på hösten än på våren med framförallt bockarna som stannade längre på sommarområdet än getterna. Getterna, särskilt de som vandrade längre än 10 km, återvände till vinterområdet tidigare än kortvandrarna.

Contents

Introduction

Migration

Migration is defined as movement (Dingle et al 2007) between different habitats (Ramenofskey at al 2007). It occurs on spatial scales ranging from movements over a few hundred meters to those over thousands of kilometers (Hobson 1999). It occurs as altitude migration where movement is transpiring between one elevation to the next (Dingle et al 2007). The number of animals migrating can range from one single individual moving from one area to another, to several thousand of animal moving together (Ramenofsky et al 2007, Bolger et al 2008). Similarly, migration can occur on daily, seasonal or annual basis (Hobson 1999). Migration involve two levels, the individual and the population (Dingle et al 2007). Namely, the behavioral, physiological, and genetic level are applying to individuals, and the ecological and evolutionary level are applying to populations (Dingle et al 2007).

There are different reasons as to why migrations occur and they are split in three main categories (Ramenofsky et al 2007).

The first type of migration occurs in situations where the seasons each year change in a predictable way (Ramenofsky et al 2007). There the organisms respond to the difference in availability of food resources and the change in the physical environment (Ramenofsky et al 2007). This is called an obligate migration because the change is predictable and the organisms are reacting upon them every time (Dingle et al 2007). These migrations consist of movement between two different areas, one where breeding occurs and one that is used in winter or the non-breading season (Ramenofsky et al 2007). The migration of birds is one example (Dingle et al 2007). The second type of migration occurs more unpredictable and is driven by factors such as variation in predator numbers, human interference and severe weather conditions (Ramenofsky et al 2007). Finally, the third type of migration occurs as a result of reaction to the social interrelationships (Ramenofsky et al 2007). The social standings are something that will have an effect throughout the whole life cycle and depending on how high or low on the scale an animal is, it also will affect the availability of resources (Ramenofsky et al 2007). The second and third types of migration are called facultative migration and can occur any time during the year (Ramenofsky et al 2007). It can even result in a permanent change in the location of home range (Ramenofsky et al 2007).

Migration can be further classified depending on how predictable movement animals do between different areas and how large proportion of the population it is that migrate (Dingle et al 2007). In general, the classifications of migration are as follow: if the migrants always move from one place to another, it is called an obligate migration, but if they are reacting to some deterioration in local conditions it’s instead a facultative migration (Dingle et al 2007). If a part of the population stays and the other moves it’s referred to as partial migration (Dingle et al 2007). Examples of the latter pattern are migratory moose (*Alces americanus*, *Alces alces*) in North America, Europe and Asia where there are migratory and stationary individuals within the same population (Ball et al 2001). Which of these behaviors that is the best strategy is still uncertain and may vary between species and different systems (Lundberg 1988). But the possibility to discern what it is that drives the motion or lack thereof is an interesting aspect of partial migration (Ball et al 2001). If individuals of the same species that live in the same area exhibiting different behaviors, it is possible to compare them to examine which factors that may affect differences in that particular behavior (Ball et al 2001). Finally, the forth movement concerns difference between individuals based on their age or sex. When that happens it is called differential migration (Dingle et al 2007).

Migrations could also be split according to time and space. That is, when during the year they occur and how they are occurring. The seasonal migration concerns specific parts of those annual journeys and result with two different home ranges because of the to-and-fro migrations between them (Dingle et al 2007). A breading area and a winter area (Dingle et al 2007).

Temperate regions

In temperate climates the winter season is the main period of food shortages (Mysterud et al 2001). Food shortage affects animals of different sizes in different ways. Specifically, animals with a large body mass can use food with poorer quality (Mysterud et al 2001). Changes in availability of food and the severity of winter initiate different strategies in the deer of temperate and boreal regions (Ramanzin et al 2007). Many large herbivores migrate seasonally between home ranges which occurs in the transitions between winter and summer (Fryxell et al 1988).

The summer in temperate regions is generally the main period for reproduction-, growth and storage (Mysterud et al 2006). Newly sprung plants have better quality than older ones (Mysterud et al 2006) due to the seasonal changes in the plants chemistry (Sand et al 1996). Moreover, low temperatures in May and

June in association with high amount of precipitation allows for a season with high accumulation of crude protein, especially if the temperatures are high and the precipitation low in July and August (Sand et al 1996). This is supported by the annual variations in body growth and reproduction in moose, especially the calf weights in fall (Sand et al 1996). The quality and amount of food available in summer is therefore, indirectly, affecting survival in the winter season as well as the availability of the food during the actual winter (Mysteryd et al 2006). Moreover, if the amount of snow is high, it will decrease the chances to access the sprigs that are buried beneath it. Snow also hinders the locomotion and cold temperatures in association with the low amount of energy intake make it difficult to maintain the body temperature (Mysteryd et al 2006). Smaller animals suffer more from this than larger animals, due to the fact that they have a large surface area compared to their volume ratio (Mysteryd et al 2006).

Roe deer

Roe deer (*Capreolus capreolus*) is a medium sized ungulate (Tufto et al 1996) and is the most abundant cervid on the Eurasian continent (Tixier et al 1997). They can be found throughout almost all of Europe and parts of Asia (Sempere et al 1996) and the size of their home range is around one km^2 in south central Sweden (Cederlund 1983). Roe deer weigh 22-30 kg with only minor sexual dimorphism and the buck generally just slightly heavier than the doe (Gaillard et al 1993, Sempere et al 1996). Roe deer have a relatively small body and thereby a small rumen, this along with their rapid process of digestion require a fast intake of food (Sempere et al 1996). They prefer easily digestible food with high water content and are therefore very selective feeders. However, food supply decline during winter and the foraging become less diverse (Sempere et al 1996). During this period the animals are found in family groups (Sempere et al 1996) consisting of mostly female relatives with one or two bucks. (Kjellander et al 2004). However, increased snow depth, higher population density, low temperature and decreasing food availability results in larger groups (Sempere et al 1996). Furthermore, roe deer in the forest form smaller groups than roe deer in open fields (Sempere et al 1996).

During the summers the roe deer are more dispersed than in winter and between Mars to August the bucks hold territories (Sempere et al 1996). However, males do usually not defend territories until three to four years of age (Johansson 1996) and younger males often becomes ousted by the older ones (Sempere et al 1996). The territorial behavior is related to the rut that begins in July and ends in August (Aitken 1974). During this time some females exhibit something close to a breeding dispersal, they do excursion to a new area to mate and shortly afterwards they return to their natal home ranges (Coulon et al 2006).

The aggressive behavior from the old males is primarily directed towards other adult males and secondary towards young males without territory (Moorter et al 2008). Female roe deer are not territorial; instead they have home ranges that overlap each other (Kjellander et al 2004). However, they live solitary during summer (Kjellander et al 2004) and during the fawning period, they may show aggressiveness towards all adults in their range (Sempere et al 1996, Linnel et al 1998). In south-eastern Sweden the birth period stretches from the end of April to the beginning of July, with the mean birth date of 2 June (Jarnemo et al 2004). The females have their first fawn when they are around two years old (Sempere et al 1996). Females also tend to give birth around the same time every year, but slightly earlier the older they become (Plard et al 2013). Independent of sex, the fawns have the same body weight at birth, growth rate and survival (Pettorelli et al 2006). The offspring share their mother’s home range during the first year, but at the age of about one year they separate from their mothers and either remain, thereby continue to live close maybe even overlapping their mother’s home range, or they disperse to a new area (Coulon et al 2006). Prior to dispersal, they make excursions in the vicinity, especially in lower quality habitats (Whalström et al 1995, Van Moorter et al 2008). Natal dispersal rate in roe deer varies between 20 – 95% and factors affecting this may be number of dependent young, population density, or habitat quality (Moorter et al 2008). However, roe deer do not seem to exhibit sex biased dispersal rates (Coulon et al 2006). Closely related to dispersal is seasonal migration, where roe deer are leaving their natal home range in the spring but return again in the fall (Dingle et al 2007).

Since roe deer are widespread in Europe, the accumulation of snow varies between different populations (Ramanzin et al 2007). In areas with large temporal variations in food abundance seasonal migrations occur (Hjeljord 2001). If the climate is mild with little snow, the roe deer will remain stationary and the seasonal home ranges will overlap (Hjeljord 2001). However, in places with severe winters like those in most parts of Scandinavia, some of the deer will show a seasonal migrating behaviour (Mysterud 1999). In mountainous areas migratory cervides generally choose high elevations in summer and a low elevation in winter (Mysterud 1999). Movements between seasonal habitats can result in heavy concentrations of animals in the winter range (Hjeljord 2001). It is important to know animal movement patterns to develop accurate management plans (Hjeljord 2001)

In this study, I examined how various meteorological factors and life history characteristics affected the timing of seasonal migration by roe deer. Specifically, I examined how timing of seasonal migration by roe deer varied in relation to sex and age, winter severity, and seasonal phenology. I was also interested in determining how far roe deer migrated and whether differences in the distance that roe deer migrated affected timing of their migrations.

Materials and methods

Study area

This study took place around Grimsö research area, in south- central Sweden (59-60° N, 15-16° E). The vegetation period - the time without frost and with a mean air temperature above 5°C - is 160 days.

The area is mainly covered by coniferous forest (72%) and due to logging it consists of more or less even aged even stands. The rotation period vary between 80-100 years and new clearings consist of birch (*Betula pubescens* and *B. pendula*), aspen (*Populous tremula*) and willow (*Salix spp*). The mature stands are mainly dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch, occurrences of aspen, willows and rowan (*Sorbus aucuparia*) are scarce, especially older trees.

The field layer is a mixture of common hair grass (*deschampia flexuosa*), which is more frequent in the clearings and dwarf shrubs such as bilberry (*Vaccinium myrtillus*) and cowberry (*Vacinium vitis-idaea*) in the forested land. In the bogs species like dwarf birch (*Betula nana*) and heather (*Calluna Vulgaris*) are more common. Bogs cover 18% of the area and different watercourses 7%. Some small parts (3%) are meadows and farmland. The landscape is flat with elevation varying from 100 m to 150 m.a.s.l.

The daily mean temperature in January is -4.4 °C and in July the mean is 16.3 °C. However, the temperatures range between -20 °C in winter to 25 °C in summer. Annual precipitation is 600-700 mm and 30% of this falls as snow. Snow is normally present from December to March, with mean snow depth of 20 – 30 cm in February.

Red fox (*Vulpes vulpes*), lynx (*Lynx lynx*), and wolves (*Canis lupus*) are common predators of roe deer and their fawns and the latter two returned to the study area in the mid 1990’s (Wikenros et al 2010).

Roe deer capture and telemetry

Roe deer were captured in box traps baited with vegetable based fodder (Viltfor/Renfor) from late November to early April. Roe deer have been caught in Grimsö research area from 1973 to present, but the data in this study was restricted to the period 1984 to 2006 because of availability of meteorological and vegetation data (see below). The animals where equipped with radio collar transmitters (151 MHz and 152 MHz; Followit Lindesberg AB, Sweden), with a standard weight of 300g. The animals were weighed, measured and an approximate age was determined by tooth wear (fawn, yearling or adult following Cederlund et al. 1991). To distinguish each animal they were marked with differently colored and numbered plastic tags in their ears.

Radio-tracking was made from a buss equipped with a Yagi antenna. However, relocation of animals from the air was done occasionally when the animal, during a longer period, was not heard within the established home range. The positions where determined by triangulation (±100 m) from easy identifiable locations such as crossroads. Depending on the year and the time of year, there was a variation of intensity in relocation of the roe deer. The basic interval was generally one to two times per week. A rough estimate of the animal’s location was given when a complete triangulation could not be made. That is, if the triangulation attempt of the roe deer was only made from one point, no specific location could be acquired, but the signal shows direction and closeness since it is within the range of the antenna, about three km. These were used to determine an estimated location of roe deer when a precise location was missing.

Three hundred and eighty seven radio-collared animals were followed during this study; 247 of these were females and 140 were males. However, 125 of these animals’ migratory strategies could not be determined because they died, were tracked only as fawns before they started to migrate by themselves, were lost due to dispersal or transmitter failure, the seasonal migration location were not known, or the number of positions were too few. However, the migratory strategy for the remaining 262 animals was determined (n = 172 females and 90 males).

Seasonal migration

I examined how timing of seasonal migration in roe deer varied in relation to age and sex, winter severity and seasonal phenology. To accomplish this some definitions and requirements needed to be fulfilled. Each animal's data was studied separately in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California), and strategy for each season was determined according the following criteria.

I defined seasonal migration as non-overlapping summer and winter ranges in combination with animals returning to their original area, this to separate migration from dispersal following Mysterud (1999). However, it was not possible to determine the animals strategies if there were < 30 positions per year. If they migrated outside Grimsö research area fewer positions were accepted due to the fact that they were seldom located in their summer ranges. Despite the main strategy, excursions could also be made and I defined these as scattered positions > 1,5 km from the center of their home range following Cederlund (1983). Moreover, the duration was within a short period, < one month. Even though some restrictions were made regarding time spent in one place and amount of positions, no distance limit were set between the seasonal migrations areas.

Roe deer were categorized as fawns, subadults, adults and old. I defined the transition from age category to the next to occur during summer, that is because I wanted all animals born the same year to be classified in the same age class and not based on whether the seasonal migration was early or late. Animals were defined as fawns during their first year and subadult when they were between one and two years old. Thereafter they were defined as adults from two to six years, and old when they were seven years or older.

The distance the animals travelled between their summer and winter ranges was estimated through ArcGIS 9.3. The central regions of both areas were estimated and the distances thereafter measured by using the measure tool. The direction of the seasonal migration from winter to summer range was classified into eight cardinal directions.

Timing of seasonal migration

I determined the timing of the seasonal migrations in four different ways depending on available data for each migratory event. See table 1 as an example.

1: The date halfway between the last time the animal was heard in one seasonal area and the first time it was heard in the other seasonal area.

2: The date halfway between the last time the animal was heard in one seasonal area and the subsequent time that it was not heard in the same area – this criterion was used for animals that moved to seasonal areas outside Grimsö research area where animals were not relocated frequently.

3: The date halfway between the last time an animal was not heard in one seasonal area and the subsequent time it was heard in the same area – this criteria is essentially the same as criteria number 2 and therefore used for animals that moved to seasonal areas outside Grimsö research area where animals were not relocated frequently. The difference being that they were searched for in an area they had not arrived to, but were expected to do shortly.

4: If the information about the dates when animals were estimated to be in the different seasonal ranges was greater than a month, I used the date it was first heard or last heard in the summer and winter areas (depending on direction of the migratory event).

Regardless of the date that migrations were initiated, migration from summer to winter ranges were always categorized spring migration and migration from winter to summer range was always called fall migration.

Table 1: *A visual of methods for determination on timing of seasonal migration*

Method of determination	Day of seasonal migration	Triangulated Winter range	Triangulated Summer range
1)	September 11	September 13 signal	September 9 signal
2)	May 11	May 9 signal May 13 no signal	
3)	September 11	September 9 no signal September 13 signal	
4)	September 13	September 13 signal	July 10 signal

Climate data and seasonal phenology

I used the cumulative snow depth during the winter, the number of days in winter with >15 cm snow depth and the number of days in winter with > 50 cm snow depth as different alternative measures of winter severity. Data on the snow depth was acquired from the Swedish Meteorological and Hydrological Institute (SMHI).

The average temperature in March and May were used as a proxy for spring temperature. Similarly, the average temperature in September and October was used as a measure of how cold or warm the fall was. The temperature itself at the date of seasonal migration was also used as a comparison. However, I corrected for seasonal changes in temperature for this estimate by using the residual value of temperature during the specific day and the expected temperature for the season (i.e. an estimate of how much warmer or colder it was that day compared to the average temperature), this is called tempCorr in my models.

I used the Normalized Difference Vegetation Index (NDVI, see below for detail) in two different ways, both of which were measurements to evaluate whether if it is greener or less green than usual during a specific time. Firstly, the NDVI gave an indication on how early or late the spring/fall was and to acquire an estimation of greenness each year for the spring and fall, I used two bimonthly values from spring and fall each. To measure this phenology in spring, I used values from the last two weeks in March and for the first two weeks in May.

Similarly, to measure this in fall I used the NDVI values for the first two weeks in September, and the NDVI for the first two weeks in October.

The other method was based on the specific time the seasonal migration event took place and called NDVIcorr in my model. This value was corrected for the seasonal changes by using the residual value of NDVI the day the seasonal migration event took place and the expected value for the season.

Data on the NDVI was acquired from the National oceanic and Atmospheric Administration satellites and thereafter processed by the GIMMS group. In this case, the data was also smoothed to process the cells estimated to be affected by snowfall and clouds (Davis 2013). The NDVI data covers 11 different places around Grimsö research area and I used the data from the years of 1984 to 2006. Each place have two stored NDVI values for each month, one from the first fifteen days and one from day 16 to the last day of the month. I added the data from the 11 different places from the same period and got two bimonthly average values for Grimsö research area each month from the different years.

NDVI

The Normalized Difference Vegetation Index (NDVI) is used to measure and monitor plant growth and vegetation cover on the land surface (USGS). It is calculated by measuring ratio of vegetation reflection in the visible and near-infrared wavelength (Pettorelli et al 2006). The visible light is mostly absorbed by the healthy vegetation while the near-infrared wavelengths are reflected, if the vegetation instead is scarce or unhealthy the relationship would be contrary (Earth observatory). The leafs have, depending on carotenoids and chlorophyll a low reflectance in the visible light, but the plant cell wall instead has a high near infrared reflectance (Wang et al 2005). Therefore, the NDVI value is related to the amount of photosynthetic activity and ranges between -1 to 1 where high values indicate a high amount of greenness. However, negative values and values near zero indicate that the area is covered by soil, water, rock, snow or clouds (USGS). Snowfall and clouds can cause rapid and false changes in the data, but this problem can also be corrected (Petttorelli et al 2005).

Because the NDVI correspond to the vegetation’s productivity, it is possible to do ecological studies from this data (Pettorelli et al 2005). Namely, the amount of greenness correlates with the quality of the available food (Pettorelli et al 2005) and herbivores are affected by plant productivity (Martinez et al 2009).

Statistical analyses

A mixed linear model (Proc Mixed, SAS Institute Inc., Cary, North Carolina) was used to examine how timing of seasonal migration varied in relation to age and sex of roe deer and in relation to winter severity, migration distance and seasonal phenology. The animal identity was used as a random factor to control for repeated observations of the same individuals. The analyses were performed separately for spring and fall (n = 86 and 79 seasonal migrations by 48 and 43 animals in spring and fall, respectively). I derived 55 a priori candidate models for each analysis where models ranged from none to all combinations of up to two of the independent variables. No interactions were included.

Measures of winter severity and seasonal phenology were generally highly correlated (r^2 = 0.18-0.84) and therefore only one measure of winter severity or seasonal phenology per model were included. Variation around the grand mean was used as a null model of no effect of either of the variables examined.

Akaike's information criterion (AIC) with small-sample adjustment (AIC_C) was used to rank models (Burnham and Anderson 2002). The model with the lowest AIC_C value was selected as the best model and models within $\Delta AIC_c < 2$ were considered to be of similar rank (Burnham and Anderson 2002).

Since NDVI data was available between the years 1984-2006 all statistical analyses are based on that period. However, roe deer tracking data was collected during a longer period and figure 1 and figure 2 on page 10 contain all off that sampled data. All of the other diagrams and figures are based on the data from my main study period of 1984-2006.

Results

Timing of seasonal migration

51 of the 262 (19%) animals made seasonal migrations during at least one season of their life (Table 2). That is, not all roe deer maintained the same behavior every year or in some cases could not be determined whether they did or not. Of the 51 animals that made seasonal migrations, 13 had a seasonal migration distance that was 10 km or longer. In this study, there were examples of individuals that made seasonal migration every year, those that started seasonal migration as two year old, animals that stopped seasonal migration, and finally those that made irregular seasonal migrations. Among the seasonal migrants, 38 were females and 13 were males which was 22% of the females for which strategies was determined and 14 % of the males for which strategies was determined. Moreover, animals migrated in all different age categories although fawns in fall were not included in my study based on the assumption that they do not make an active choice at that age and instead followed their mothers. In total, animals made 165 seasonal migrations and 134 of those were made by females and the remaining 31 by males. The average distance travelled for females was 12,3 km whereas it was 2,7 km for males. Off all the migratory animals, the average distance travelled was 10,5 km. The maximum distance travelled was 52,2 km and was made by a female during six years until she was lost due to transmitter failure. Fiftysix seasonal migrations were 10 km or longer and only two of these were made by males. Furthermore, the roe deer that was documented to do the highest number of seasonal migrations was a female that migrated every year for the 10 years she was radio tracked. The repetition of seasonal migration can be seen in figure 3.

Table 2: *Number of individuals followed in this study divided into males, females, and fawns.*
** In the table there is a female killed in traffic when migrating. This resulted in migration distances for that female being both shorter and longer than 10 km since she was followed for several years.*

	Total	**Female**	**Male**	**Fawn**
Number of individuals tracked	387	247	140	270
Number of determined strategies	262	172 (70%)	90 (64%)	120 (44%)
Number of seasonally migrating individuals	51 (19%)	38 (22%)	13 (14%)	8 (6%)
Number of seasonal migration distance > 10 km	13 (25%)	12* (32%)	1 (8%)	1 (12%)
Number of seasonal migration distance < 10 km	38 (75%)	27 (71%)	12 (92%)	7 (88%)
Number of seasonal migrations	165	134	31	Not applicable
Average seasonal migration distance	10.5 km	12.3 km	2.7 km	Not applicable
Max seasonal migration distance	52.2 km	52.2 km	15 km	Not applicable
Longest duration with seasonal migration	10 years	10 years	2 years	Not applicable

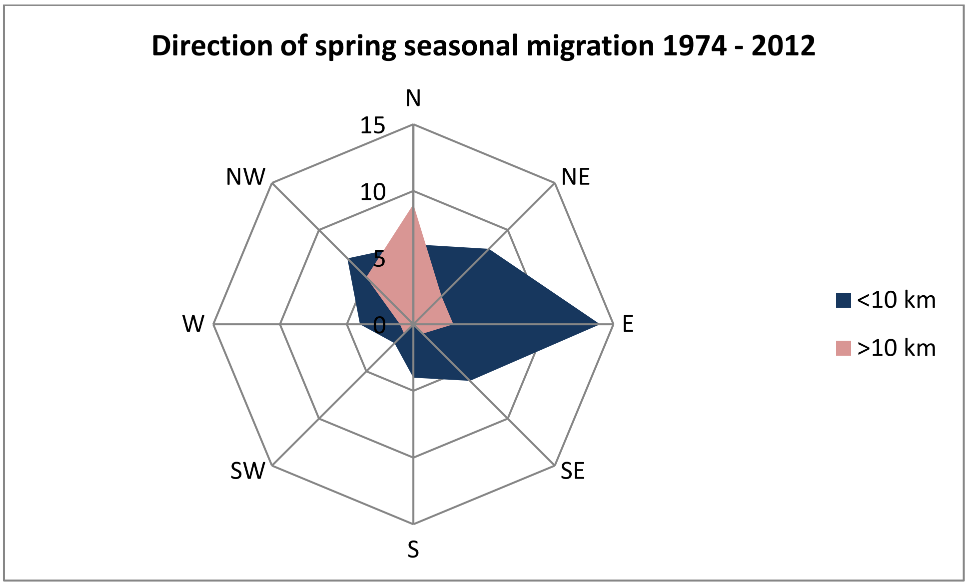

Figure 1: *Direction of seasonal migrations made in the spring where the direction of fall migrations are the reverse of those in spring. Data are split in two categories, those with seasonal migrations above 10 km and those with seasonal migrations shorter than 10 km. Data presented in this figure includes data collected both during and outside my main study period.*

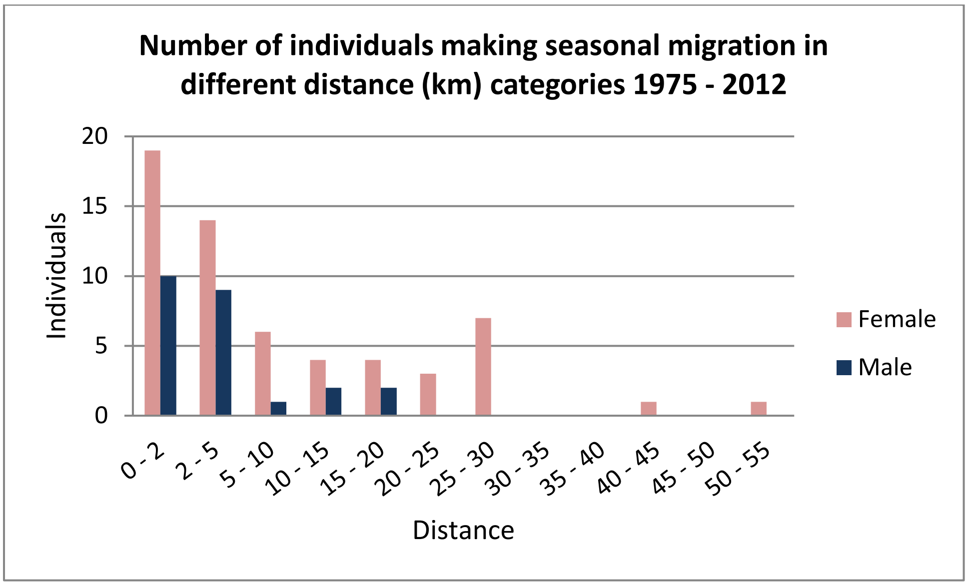

Figure 2: *Number of individuals that made seasonal migration at different migration distances. Data presented in this figure includes data collected both during and outside my main study period.*

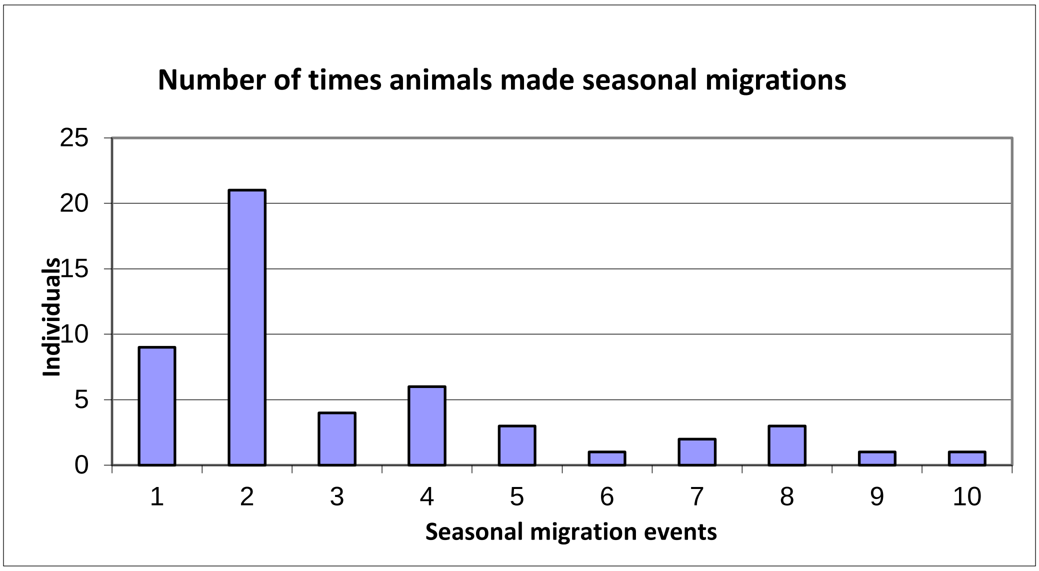

Figure 3: *Number of times that animals made a seasonal migration. These are minimum numbers of how many times animals made seasonal migrations as animals were not followed for their entire life.*

Timing of seasonal migration in spring

The model {Age + NDVIMay} described the variation in timing of seasonal migration by roe deer in spring better than the other models and accounted for 67 % of the cumulative model weight (Table 3). When the NDVI in May increased with 0.1 units, roe deer started their seasonal migration 14 ± 22 days earlier (figure 4). I found that the first seasonal migration in spring began on February 14 and the last on July 31. Furthermore, the mean migration day was on May 7 with a standard deviation of 30 days, whereas the date for different age categories was; April 25 ± 23 days for animals that were >7 year, May 2 ± 25 days for adults, May 6 ± 34 days for subadults, and June 13 ± 37 days for fawns (figure 5). Moreover, timing for males and females occurred on May 13 ± 40 days and May 6 ± 27 days, respectively (figure 6). The variance of timing in seasonal migration differed between animals that migrated 10 km or longer and those that migrated shorter than 10 km with the timing of migration spread out over a longer time period for short-distance migrants (figure 7, figure 8). The standard deviation was 20 days for long-distance migrations compared to 34 days for short distance migrants with the average timing on May 2 and May 10, respectively. In figure 9, it is seen that the difference in timing of migration in spring was more synchronized on an individual level than it was between animals.

Table 3: *Model selection for variables affecting timing of seasonal migration in spring around Grimsö research area from 1984 – 2006. The table describes the differences in AICc values between each model and the best fitting one (Δi), the number of parameters (K) and the model weight (wi). The null model illustrates that timing of seasonal migration occurs independent of the variables examined.*

Model Spring	n	K	Δ_i	w_i
Age NDVIMay	86	6	0.0	0,666
Age NDVIMar	86	6	2.4	0,201
Age NDVIcorr	86	6	4.6	0,067
Age TempMay	86	6	6.4	0,027
Age TempMar	86	6	6.5	0,026
Null model	86	2	49.3	1E-11

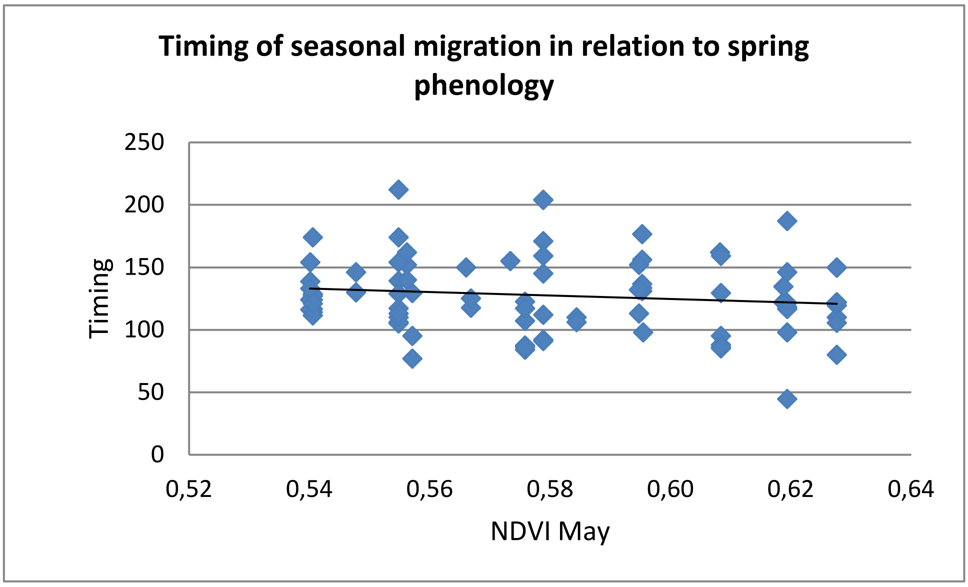

Figure 4: *The timing of seasonal migration in spring in relation to NDVI during the first two weeks in May where low NDVI values indicate a late spring. Data in the figure are not corrected for repeated measures of the same individual.*

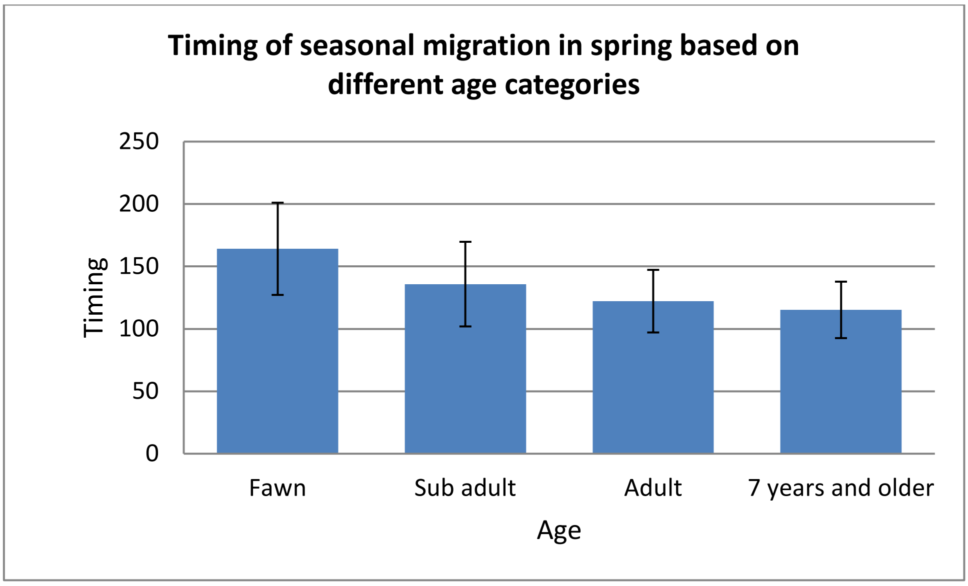

Figure 5: *Average date for timing of seasonal migration in spring for different age categories. Dates are shown as Julian dates, the error bars show the first and last date in timing of seasonal migration.*

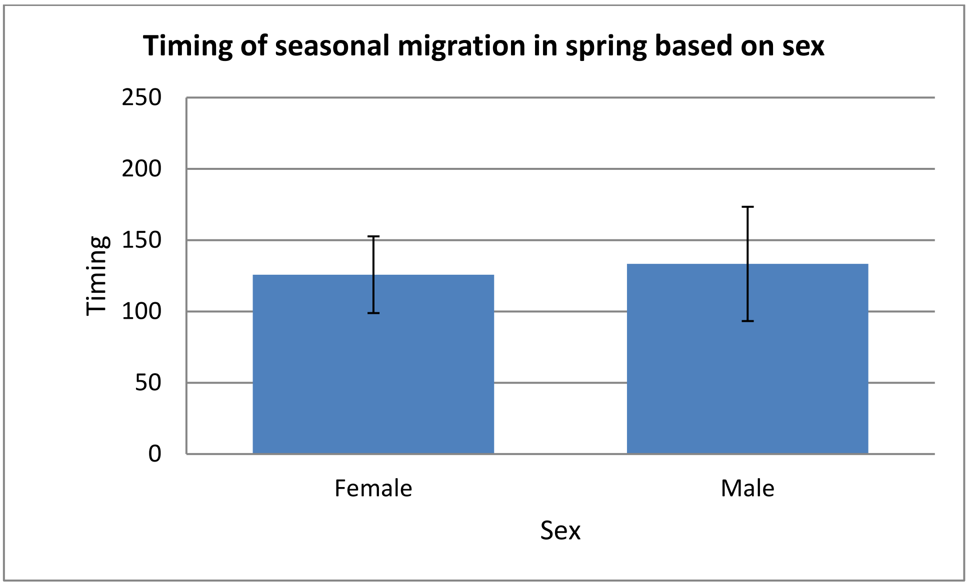

Figure 6: *Average date for timing of seasonal migration in spring made by female and male roe deer. Dates are shown as Julian dates, the error bars show the first and last date in timing of seasonal migration.*

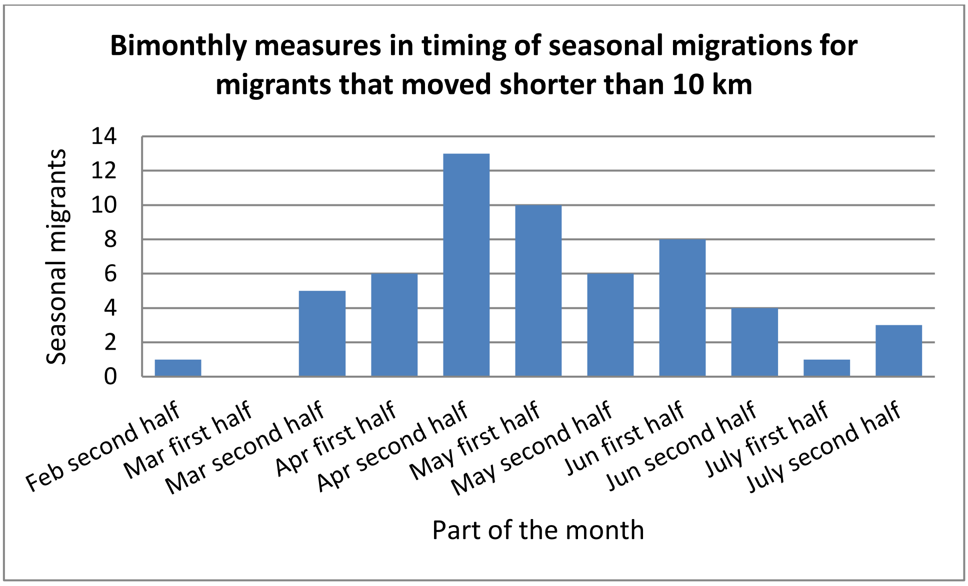

Figure 7: *Bimonthly measures in timing of seasonal migration in spring for animals that moved < 10 km.*

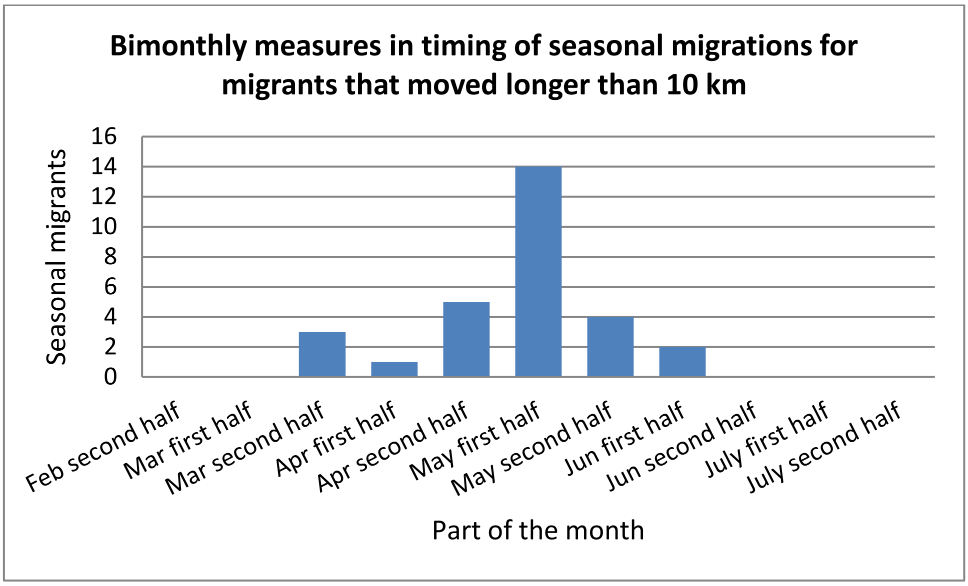

Figure 8: *Bimonthly measures in timing of seasonal migration in spring for animals that moved > 10 km.*

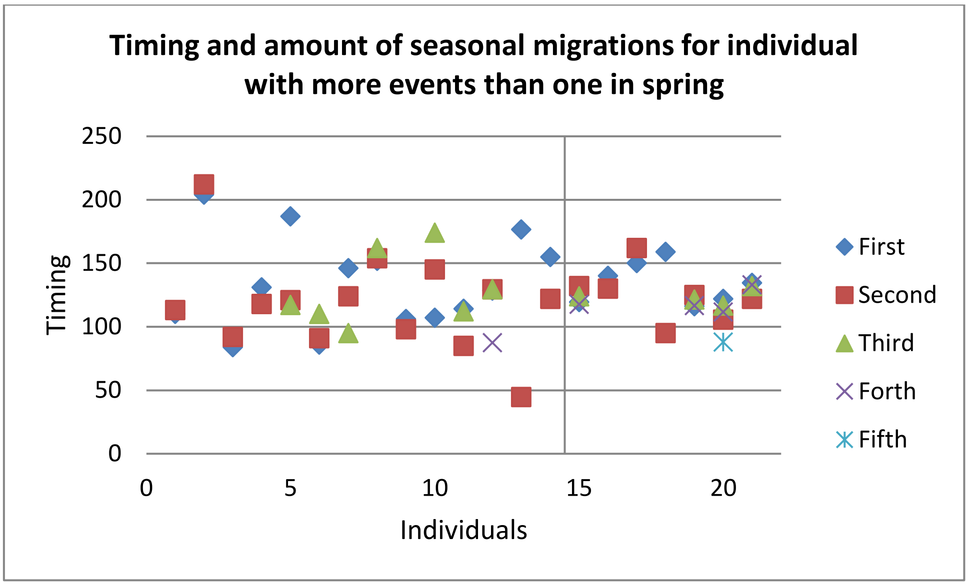

Figure 9: *Timing and number of seasonal migration for the 21 individuals with more than one year of seasonal migration in spring (values on x-axis represent the different individuals). Animals are sorted in the order of the shortest to the longest migration distance between seasonal areas. The Y axis split the seasonal migrants into individuals with <10 km (left of axis) and > 10 km (right of axis) between areas.*

Timing of seasonal migration in fall

The models {Age + NDVISept} and {Age + Sex} described the variation in timing of seasonal migration by roe deer in fall better than the other models and accounted for 72 % of the cumulative model weight (Table 3). When the NDVI in September increased with 0.1 units' roe deer surprisingly, started their seasonal migration 4 ± 12 days earlier (figure 10). In fall, the first seasonal migration started August 21 and the last on February 20. The average migration day was November 20 with a standard deviation of 41 days, whereas the date for different age categories was; November 12 ± 30 days for animals that were >7 year, November 23 ± 44 days for adults, and November 7 ± 40 days for subadults (figure 11).

Moreover, timing for males and females occurred on December 14 ± 31 days and on November 15 ± 42 days, respectively (figure 12). The difference in timing of seasonal migration differed between animals that migrated 10 km or longer and those with migrations shorter than 10 km with timing of migration spread out over a longer time period for short-distance migrants (figure 13, figure 14). The standard deviation was 28 for long distance migrations compared to 42 for short distance migrants with the average timing October 27 and December 2 respectively. In figure 15 the repeated pattern of the individual's seasonal migration events in fall is shown. Timing of migration in fall was less synchronized in fall compared to spring. Long-distance migrants were, however, more synchronized than short- distance migrants.

Table 3: *Model selection for variables affecting timing of seasonal migration in fall around Grimsö research area from 1984 – 2006. The table describes the differences in AICc values between each model and the best fitting one (Δi), the number of parameters (K) and the model weight (wi). The null model illustrates that timing of seasonal migration occurs independent of the variables examined.*

Model Fall	n	K	Δ_i	w_i
Age NDVISept	79	5	0.0	0,527
Age Sex	79	6	2.0	0,194
Sex NDVISept	79	4	2.9	0,124
Age NDVIOct	79	5	4.4	0,058
Age NDVIcorr	79	5	4.9	0,045
Null model	79	2	31.1	9E-08

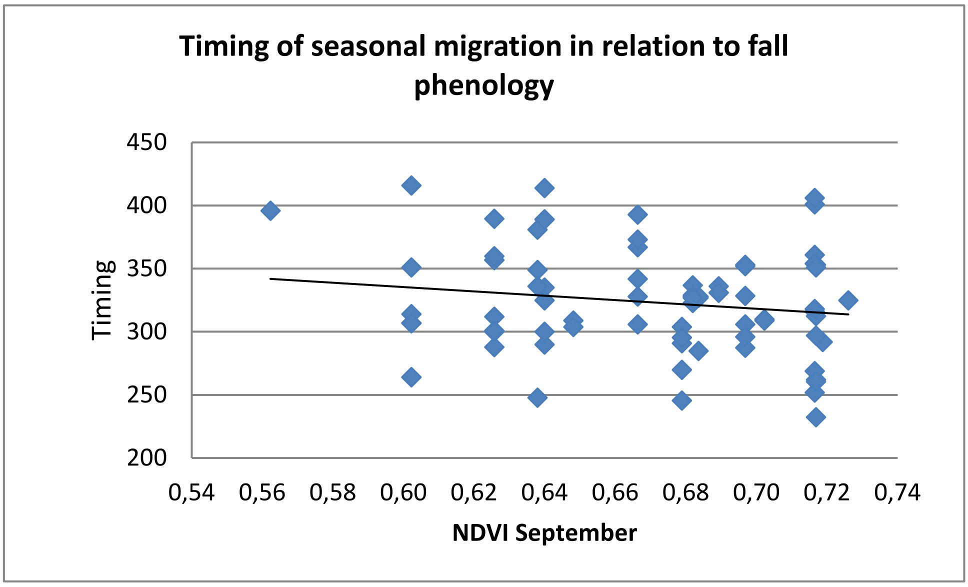

Figure 10: *The timing of seasonal migration in fall in relation to NDVI during the first two weeks in September where low NDVI values indicate an early fall. Data in the figure are not corrected for repeated measures of the same individual.*

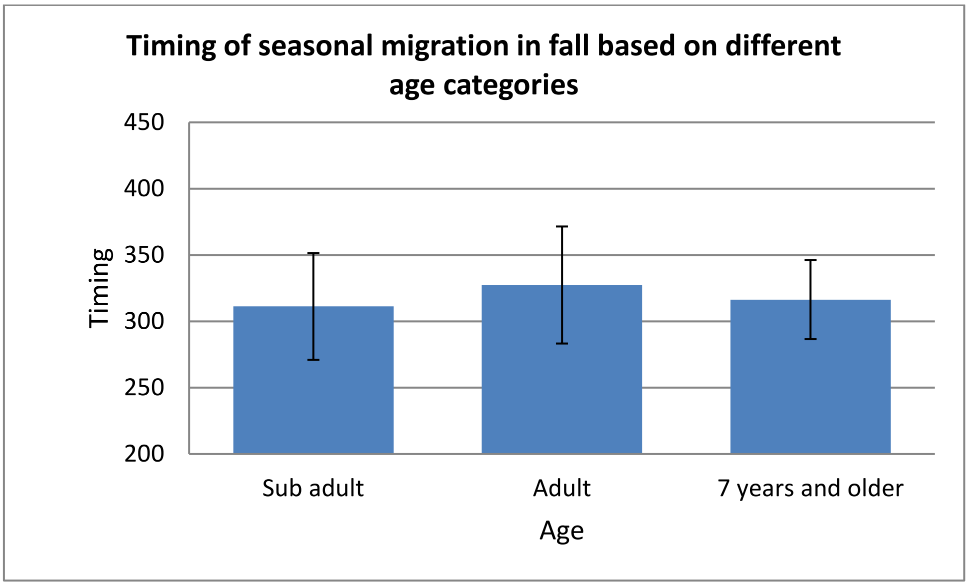

Figure 11: *Average date for timing of seasonal migration in fall for different age categories. Fawns were not included because they were not independent of their mothers. Dates are shown as Julian dates, the error bars show the first and last date in timing of seasonal migration.*

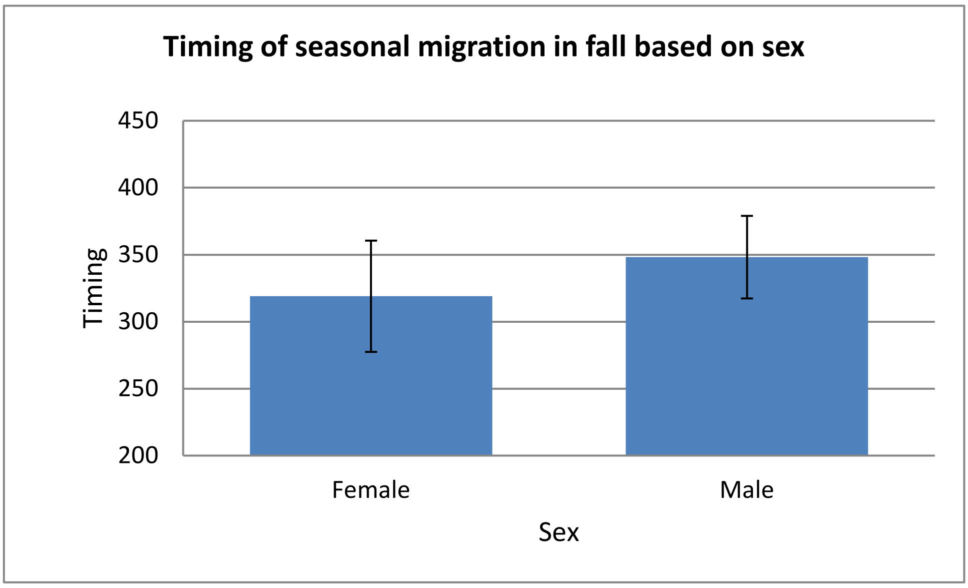

Figure 12: *Average date for timing of seasonal migration in fall made by female and male roe deer. Dates are shown as Julian dates, the error bars show the first and last date in timing of seasonal migration.*

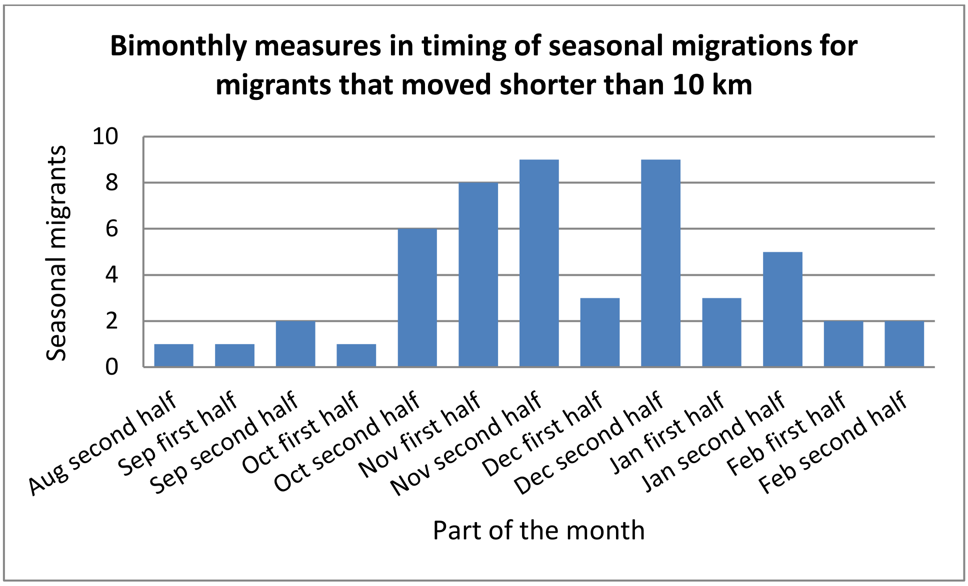

Figure 13: *Bimonthly measures in timing of seasonal migration in fall for animals that moved shorter than 10 km.*

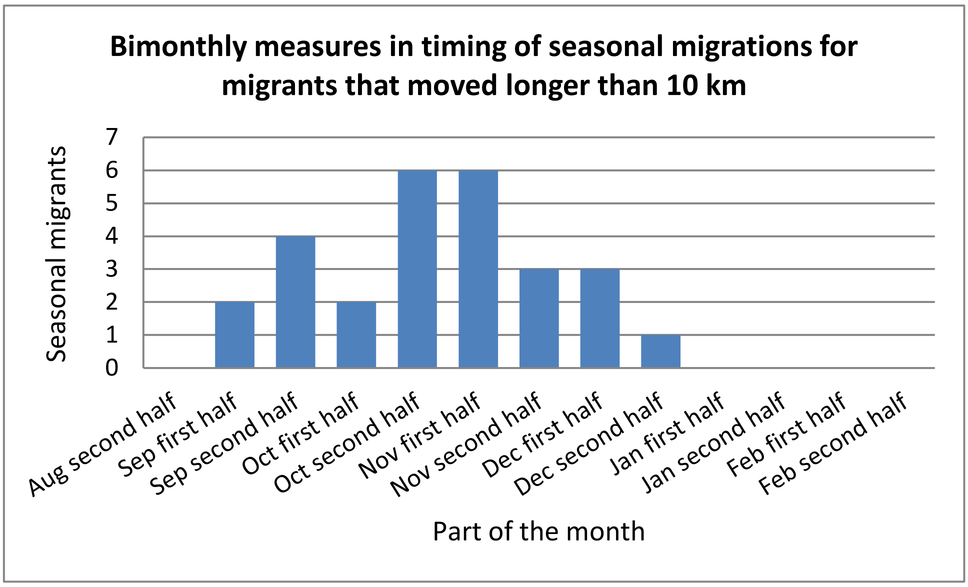

Figure 14: *Bimonthly measures in timing of seasonal migration in fall for animals that moved > 10 km.*

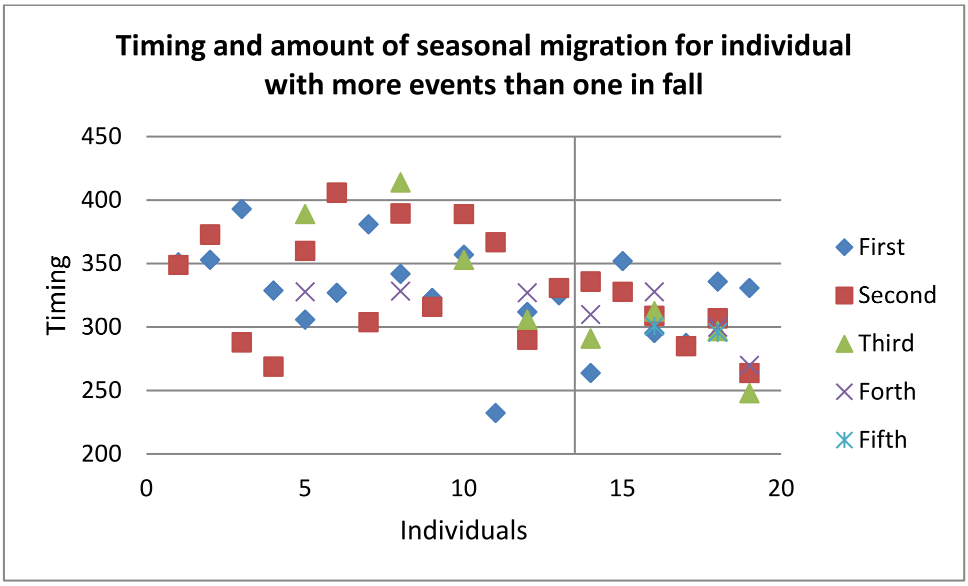

Figure 15: *Timing of seasonal migration for individuals with more than one year of seasonal migration in fall where each column is one individual. Animals are sorted in the order of the shortest to the longest migration distance between seasonal areas. The Y axis split the seasonal migrants into individuals with <10 km (left of axis) and > 10 km (right of axis) between areas.*

Discussion

This study showed that about 22% of the female and 14 % of the male roe deer in south- central Sweden performed seasonal migration which was similar to the proportion of partial migration of roe deer in other areas of Scandinavia (Mysterud 1999). This study also revealed that timing of migration was driven largely by age and seasonal phenology, but also by sex in the fall. The general direction of seasonal migration in spring was north to northwest for animals with seasonal migration > 10 km and east for animals with seasonal migration < 10 km (figure 1), the reverse is true for the fall.

Moreover, this study also showed that some of the individuals followed an obligate seasonal migration by moving between summer and winter areas every year. Other individuals tended to have a facultative response by making seasonal migration mostly at an early age, a likely effect of social interrelationships, which result in dispersal in cases when animals did not return to their natal area. Furthermore, infrequent seasonal migration was another facultative response noted in this study, where animals made seasonal migrations only a few times. Previous studies have shown that timing of seasonal migration can vary between years and also individuals (Mysterud 1999, Ramanzin 2007, Cagnacci 2011). Similarly, studies on white-tailed deer (*Odocoileus virginianus*) (Sabine et al 2002, Brinkman et al 2005) show a similar pattern with individual variation in the frequency of seasonal migration. In my study at Grimsö research area, the variation in timing of migrations was greater in fall than in spring. Finally, both male and female roe deer made seasonal migrations in my study, although this appeared to be more frequent among females than among males.

Age

It was a surprisingly small proportion (six %) of roe deer that made seasonal migration already as fawns in spring (i.e. soon to be yearlings in my data). However, of the roe deer that migrated as a fawn or as a sub adult, 79 % also migrated as adult. However, the amount of seasonal migrating fawns could be an underestimation. The result could be mirrored by the difficulty of determine if a fawn is a seasonal migrant or not. It is also difficult to discover a relocated fawn during the first seasonal migration. If the fawn remain and become stationary, the tracking continues. However, those fawns that relocate, either because of migration or seasonal migration, could be lost. This is especially true in long distance relocations because the further away from Grimsö research area, the less is the likelihood that they are to be tracked again. However, the likelihood of the roe deer to be found and be part of the study again is higher with time. This because the time of exposure is longer and someone might eventually report a sighting of a marked roe deer. However, in that case, when they are found they are no longer fawns but adult. This resulting in limited data for fawns. Therefore, the main difference in my study between seasonal migrations in fawns and seasonal migrations in adult, may not be that fawns do not make seasonal migration but that they are later in timing than older animals

In my dataset, six % of the fawns made seasonal migrations in spring. However, even though only 31 % of the animals that made a seasonal migration during their lifetime had a transmitter as fawns in spring, it was possible to determine that six % of the roe deer fawns that did not migrate as fawns, made seasonal migration later in life. This differs from the findings by Van Moorter (2008) who found that it was unlikely that older females leave the areas in which they have established. Van Moorter (2008) suggested this to be the result of adult females having fawns to care for which would make movement into unknown areas costly for both the female and her fawn. However, according to Coulon (2006) dispersal is sometimes delayed, this manly for males, but females may also delay dispersal until they are older. However, it is unclear if those females in my study had any offspring's during these migrations.

The relatively high proportion of old animals making seasonal migration in my study differs from the findings by Wahlström and Liberg (1995) who found that it was mostly young females that made seasonal migrations. Wahlström and Liberg (1995) stated that this could be due to the fact that young females had not yet reproduced or had too few offspring's to form a new group. The reason why the older females in my study kept on making seasonal migrations is unclear. Older females in my study made these movements both before and after the lynx and wolf recolonized the study area and a higher loss of fawn due to predation may therefore not explain the difference noted between my study and Wahlström and Liberg (1995).

Age was one of the main factors explaining the variation in the timing of seasonal migrations in spring. In spring, the fawns, or soon to be yearlings, had a wide spread in the timing of their migrations and they were also late compared to older age classes which may be due to the fact that they were about to separate from their mothers and find a home range of their own. This is supported by the fact that 1) yearlings often make excursions into adjacent areas before the separation from their mother (Wahlström et al 1995) 2) seasonal migration is often considered to be connected to dispersal (Wahlström and Liberg 1995) and the majority of dispersal by roe deer occur in spring (Wahlström 1994). Irregular excursions by fawns in spring may explain the late migration by fawns in spring and the relatively high standard deviation in timing of migration by fawns in spring. Since female roe deer, according to Wahlström et al (1995) are not distributed despotically, that is high quality individuals monopolizing high quality habitats, but instead from the distribution of important recourses may indicate that female migrations are mainly determined by searching for food, while dispersal and seasonal migration by male fawns may be more or less the result of them being ousted by older males. Wahlström (1994) suggested that, except for other adult males, it is the most sexually mature male fawns that the adult males show this kind of aggression towards. However, it is important to remember that the number of fawns with a strategy of seasonal migration in spring in my data was low and consisted of only eight individuals.

Sub-adults started their migrations in spring earlier than fawns, but later than adults. Both the timing of seasonal migrations in spring and the variation in timing of these migrations were highest for fawns and lowest for animals that were seven years and older (figure 5). This means that the variation and average value in timing of seasonal migration decrease with age.

When comparing the timing of migration for the animals that were followed over several years, it can be seen that animals had a tendency to leave their winter area around the same time every year (figure 9). That is, the differences in timing of migration between individuals was greater than the differences in timing within individuals. However, the first seasonal migration made by each individual sometimes tended to be either earlier or later than other migration that individual made.

The seasonal phenology in September and age were the factors with the highest degree of explanation in timing of migration in fall, although the model support was not as strong as for the best model explaining variation in the timing of migration in spring. Regarding the variation in the timing of fall migration and its relationship with age, it did not appear to be as clear as it was in the spring (figure 5 and figure 11). The average timing of seasonal migration in fall was 20th November which was similar to that observed by Mysterud (1995). However, one difference in my study compared to that by Mysterud (1999) is that he only included animals that were two years and older. However, the variation in timing of fall migration in my study was quite large with the first seasonal migration event occurring on 19th August and the last on 20th February. On average, the subadults were the first to return to the wintering area, but the standard deviation was quite large. The standard deviation was great also for adults and animals older than seven years.

Since there was a greater difference in timing in migration among rather than within individuals, it was probably due to more irregular seasonal migration events by animals that used a facultative migration strategy. In my study, these facultative movements were in general shorter than those that were obligate migrant. Mysterud (1999) defined long distance migration as movements above 10 km. In my study, all seasonal migrations shorter than 10 km were not facultative. However, those roe deer that had seasonal migrations longer than 10 km, made them every year and did not make any excursions between the areas before the actual seasonal migration event. However, the data from the time after 2006 consists of two severe winters, and during that time, animals that previously had not shown any sign of seasonal migration suddenly, late in the season, moved distances > 10 km to a different winter area. If this was due to the snow or some other reason is impossible to tell, but it shows that facultative seasonal migration also can occur over long distances. However, facultative migration appears to be largely connected to short- distance migrations. This have been found also by Caggnaci et al (2011) who used GPS collars which are not limited in how well excursions can be detected as relocation of animals equipped with GPS collars occur independent of previous location.

In my study, the data from the obligate seasonal migrants show a different pattern than the short distance migrants. For long distance migrants, old and adult animals returned at similar dates in fall while subadults did not return until almost two month later on average. Similarly, the difference in timing of migration between animals migrating > 10 km and animals migrating <10 km was also noticeable. The difference in timing of migration between long- and short- distant migrants was not only due to the sex difference because females were still, when males were not included highly non-synchronous in timing of migration in fall and showed greater spread in their timing of migration than females that migrated > 10 km.

In the fall, the timing of migration varied between seasons for the individuals that were followed over several years. However, the long-distance seasonal migrants were more synchronized on an individual level than was the variation among individuals. The timing of the fall migration did not differ much between the years for animals that were followed over several years and the same individual usually returned to the winter area around the same time. If an individual is an obligate seasonal migrant, it might not respond as strongly to seasonal cues as the facultative (mostly short distance) individuals because it takes less energy to relocate a short distance than a long one.

Sex

The distance migrated and extent of seasonal migrations, differed between sexes as well as the timing of migration. Ramanzin et al (2007) observed that both male and female roe deer made seasonal migrations in an altitudinal gradient in Norway. In my study, I noticed both male as well as female with repeated seasonal migrations, however the females had more long-distance migrants. Males in my study did not tend to make seasonal migration in the same extent as females did with 14 % of the males and 22% of the females making seasonal migrations. Males also moved shorter than females with mostly all seasonal migrations by males being limited to within the Grimsö research area whereas females traveled further and outside the research area at Grimsö. However, when I compared with the data from 2006 to 2011 (i.e. 5 years following the main study period of my study), male seasonal migration was slightly different than during the period I studied. When comparing seasonal migrations between 1984-2006 and 2006-2012 there were males that migrated greater distances in 2006-2012 than during my study. However, even though male seasonal migration seemed to have changed, it was still shorter in distance between seasonal home ranges and duration in years when compared to the females. This may be due to the strong link to summer ranges by males, that is, males did not abandon the area where they had established their territory.

Females usually get their first fawn as two years old (Sempere et al 1996), which in my data set were around the time of spring migration as sub adults just before becoming adults. Since the fawning period stretches from May to June (Jarnemo et al 2004), I suggest that depending on when her fawn was born, it could have had an effect on timing of female migration in spring, depending on factors such as timing of birth and fawn survival.

The variation in the timing of spring migration for females in my study was greater for short distance migrants than for long distance migrants. This may have been the result of the fact that females that made longer seasonal migration travelled before the fawns were born or not at all and that females with short seasonal migration distance could relocate despite the fact that they had fawns. That is, females that had fawns were more inclined to travel shorter distances than those without fawns. If females start the migration too early the conditions at the summer ranges might not be favorable for the female and her fawn and the cost of travelling back to the winter areas too high. I suggest that the females may time their migration to their summer areas to optimize the food conditions for her and her fawn similar to Pettorelli et al (2006) showing that the NDVI value around the onset of the vegetation period was a good predictor of body weight of fawns the following winter. Since roe deer are selective feeders, females should select the area where the food conditions are optimal for providing her fawn the best start. The importance of this period was also supported by Sand et al (1996) regarding spring conditions and plant chemistry and thereby improved weights in moose calves in winter. Since female roe deer do not establish territory (Kjellander et al 2004), they should select home ranges according to optimal feeding conditions and not in relation to the distribution of other female.

The variation in timing of migration by male roe deer in spring was quite high when compared with female roe deer. However, by splitting males into different age categories, I found that the variation in timing of migration by adult males and adult females were quite similar (± 26 days and ±27 day, respectively). Due to small sample size for the oldest male category, it was not possible to compare timing of migration between sexes for that age category. That was true also for males that migrated over 10 km as this were rare among the males.

Males are not limited by young and have even been shown to start dispersal as late as when they turn three years old (Moorter et al 2008). However, males are territorial in summer and Johansson (1996) found that establishment of territories started in late March to early April which in turn indicate that they generally stay in the area where they are successful in establishing a territory. However, Johansson (1996) also found that territorial males responded less aggressively towards known neighbors than to strangers which, in contrast, suggest that males may have problems to establish a territory in a new area during summer. A seasonally migrating male may therefore remain stationary until he can take an area of his own. The area he eventually establishes in, if he stops with the seasonal migrations, should therefore be where he had his summer territory. This since males in winter, according to Wahlström and Liberg (1995), are easier accepted than females in a social group of unrelated roe deer. If he succeeds to establish a territory in his natal area he should not migrate at all, this because he thereby already has a territory. However if he attempts to establish a territory in his natal area, but is not successful, he would have delayed onset of migration, thereby arriving at the summer area later and maybe find that it is already occupied by someone else.

During the winter period males are easier accepted by an unrelated matriarchal group than females are (Wahlström and Liberg 1995) and males could therefore more easily enter a new group; while the females might have more problems at finding a group that accept them in winter (Wahlström and Liberg 1995). This difference in social relationships should indicate a difference in behavior between the sexes.

Males were later in returning to their winter areas than were females. However, compared to spring migrations (figure 6, figure 12) it was not much difference between the sexes in when they left the summer ranges.

The onset of migration in fall was one month earlier for long distance migrants than it was for short distance migrates. Despite the facultative seasonal migrations that seemed to have an effect on the short distance migrants, it could also have been that sex had an effect on the timing of return in fall and its relation to long versus short distance migrants. Specifically, males who made short distance migrations returned later to the wintering areas than females that made short distance migrations in fall and both sexes had large variation in the onset of fall migration. Since both were short distance categories it seems likely that the sex difference affected the roe deer in that males in general stayed in the summer area longer than the females did.

Timing of migration by males in fall, was opposite in my study compared to Mysterud (1999), where the males returned to the winter area before the females. Mysterud’s (1999) finding was also opposite to (Cagnacci et al 2011) who found that male resided longer in their summer ranges and return later to the winter area than females. In the study of Ramanzin et al (2007) no difference in winter area arrival date was observed and in Wahlström and Liberg (1995) no males were observed to do seasonal migration. There is thus large variation among studies in timing and whether male roe deer make seasonal migrations. This was also the pattern found by Cagnacci et al (2011) where they found differences in the timing and proportion of male roe deer that made seasonal migrations when comparing among study areas. However, regarding the timing of seasonal migration by males, the result from the different sites in Cagnacci et al (2011), showed similar result as my study with fewer seasonal migrations in males and a later return date than females to their winter areas. In flat areas where severe winter is unpredictable, the occurrence of seasonal migration seems to be rare in both sexes (Cagnacci et al 2011).

Females that made seasonal migrations returned to their summer area before the males, but the variation in the timing of migration for females that made short distance migrations was greater than the variation for the long distance migrants. Since males, in contrast to females, have a strong fidelity towards summer ranges (Cagnacci et al 2011) it might not be that surprising that the males returned later to the winter area than the females did. The fact that the short distance migrants were more irregular in the timing of migrations might be explained by the negative seasonal effect that follows with fall and the reduction in plant quality. However, Cagnacci et al (2011) stated that their large inter-individual variation in timing of migration depended on the low synchronicity in the onset of fall between different study sites. It thus appears as if the climatic factors that affect roe deer are more varied in some areas and more stable in other areas. In the south central part of Sweden were my study took place, the winter conditions are not easily predicted and the animals therefore appeared to act on current stimuli since the cost of departure was not severe as has been suggested by Cagnacci et al (2011) whereas the cost of delay in the onset of migration might be too high regarding winter and social interrelationships, for the long distance migrants and they may therefore respond by moving before conditions make them too exposed, especially females with fawns.

Winter severity

Winter severity had limited impact on timing of seasonal migration in my study. This was true both for winter severity expressed as snow accumulation for the whole winter and number of days with snow above 15 cm and 50 cm. However, according to a study of white-tailed deer by Sabine et al (2002) some migrations were triggered by the disappearance of snow early in winter and when the snow came back during the same season some of the migrants had already reacted on the disappearance and migrated to their summer area. Even though I had animals migrating to their summer area already in the middle of February, the model did not explain the effect of winter severity particularly well. However, I could not detect whether these migrations were due to a sudden and temporary melting of the snow because I used winter severity for the whole winter.

Contradictory to my study, Ramanzin et al (2007) found that the snow depth seemed to have an effect on the arrival time of roe deer at winter sites. However, most roe deer left summer area before the first snow had fallen and taking long time to return to winter area in contrast to their quick arrival at the summer area. The declining temperatures in fall did, as in my study, not appear to have any effect on timing of migration. In September, the snow has yet to come and the productivity of plants is still high. However, Sabine et al (2002) who compared obligate and facultative white-tailed deer found that facultative migratory animals travelled shorter distance than obligate animals and that it developed in response to delaying departure from the area. Moreover, if the white-tailed deer were surprised by winter storms, they risked being trapped on their summer range or face a greater cost in time and energy by migrating, which would increase by the migration distance. It is thus possible that the risk of delaying the onset of migration for long-distance migrants in my study was higher than it was for short-distance migrants. The reason that females returned earlier to their wintering areas than males may be because if females were surprised by snow that would affect not only their survival but also that of their fawns. However, by starting the seasonal migration early, the probability of animals returning before the snow arrived and thereby had less need for information of winter conditions when they started moving.

Seasonal phenology

Seasonal phenology affected timing of migration in both fall and spring. Together with age, spring phenology explained timing of migration better than sex, migration distance, and the climate variables. My analyses showed a week indication that a late fall made the animals leave the summer areas earlier. This since there was a negative correlation to progress of fall (figure 10), which implies that the vegetation phenology in itself may not be what guides the animals in fall. This since the animal should not return to the winter area earlier if the fall was late. It could also mean that the seasonal changes in fall was not concentrated enough in the Grimsö research area for a simultaneous response. However, the best model in fall contained age and seasonal phenology in September. During September, snow has not fallen and the only factor affecting the NDVI value was the amount of greenness – i.e. the quality and availability of food for forages. Since the fall some years is a prolonged process it seems that the facultative migrants might not react at the same time, and not as the individual had done previous years. They can change area early as well as late in the season. The obligate migrants, on the other hand, appeared to react more like the long distance migrants in that they timed their seasonal migrations similarly among years. That is, they had less variation in the timing of seasonal migration than those with shorter distances. For the long distance migrants it seemed like the seasonal phenology was not important in affecting timing of migration since their timing of migration did not appear to correlate to the seasonal phenology. Instead it seemed that timing of migration for long-distance migrants was affected more by time of the year, namely the date. However, those animals that seemed to be affected by the amount of green vegetation appeared to be affected in the opposite way than predicted in that animals should stay longer in their summer ranges in a late fall, especially males as they are more “faithful” to their summer ranges, but that was not the case in my study.

Migration distance

During 1984 – 2006, the average migration distance for the roe deer in the Grimsö area was 10,5 km, which was close to the distance migrated by roe deer in Østfold, Norway, but longer than the distance migrated by roe deer at high density areas in Ekenäs and Bogesund, Sweden (Mysterud et al 1999).

Migration distances by roe deer at the Grimsö research area were, however, likely longer also than the distances moved by roe deer in Østfold as that study did not include animals that migrated shorter distance than two km and thus biased migration distance high compared to my study where I included migration distances shorter than two km. For my study, figure 2 describes the difference distance and how many roe deer it was in each category. If excluding animals that migrated shorter than two km in my study, it gave an average distance of 15,7 km which is greater than in Østfold. Wahlström et al (1995) suggest that dispersal by roe deer is density dependent at intermediate densities and that roe deer are pre-saturation dispersers. Therefore, if seasonal migration starts as natal dispersal, the two behaviors may be affected in the same way. However, animals that continue with their seasonal migration during their life time would respond to changes in the density of their different seasonal home ranges. Migration distances may therefore change over the years with factors such as roe deer density which is a factor that has changed dramatically over the last 30 years at the Grimsö research area which may have affected migration distances during this time period. This because home range size and territory may change because of density or the higher density might make it harder to find a suitable new home range or territory for migrants. Moreover, the individuals that migrated less than 10 km had a larger variation in the timing of seasonal migration than individuals that made longer migrations. Only one male migrated a distance above 10 km whereas 40 % of female migration events were further than 10 km. My results are similar to those by Mysterud (1995) who did not find any male migration longer than 10 km, while 30 % of the females made such migration. Ramanzin et al (2007), in contrast, did not find any difference between sexes in the distances that they migrated. However, male seasonal migration was with shorter distance between the areas than female seasonal migration.

Why do some animals travel far? Wahlström et al (1995) made a study of dispersal distances and suggested two distinctly different dispersal strategies for roe deer. One category that disperse long distances and one category that disperse distances shorter than 10 km. If seasonal migration and dispersal are closely related it is possible that the theory by Wahlström et al (1995) could explain differences in migration distances for different individuals, since the amount of suitable habitats, competition and abundance of food, may not be enough to explain differences in migration distance by roe deer.

The migration distance did at first not appear to have any effect on timing of migration when migrations were separated into long and short distance migration. However, for long distance migrants, the timing was not as widely distributed as for short distance migrants. This may have been due to facultative migration. If the weather conditions were favorable, and in some cases, the distances easily overcome, seasonal migration may have occurred independent of migration distance. I noticed that for some animals that migrated short distances, a couple of hundred meters up to a few kilometers, had a tendency to make an excursion to the other area before they made the actual migration. For animals that migrated longer distances, this behavior was not noted. This may be due to the fact that longer distance takes more energy and if the conditions get worse they may have to return. The migration distance thereby had an effect on the timing of migration for long distance migrants when compared to short distance animals in regards to distribution. It could indicate that long distance migrants were less affected by temporary conditions than short distance migrants. However, the further away from Grimsö research area the roe deer migrated, the less the likelihood of the animal to be found. This would bias migration distances towards short distance migrations, since more animals would be found near the main study area compared to animals that moved longer distances, although air tracking by plane decreased this bias to some extent.

A reason for the high amount of animals with a migration distance between zero and two km was likely due to the feeding traps used at the Grimsö research area. During some part of the winter roe deer did not move far from these traps (L. Jäderberg, pers. comm..) and because of that being classified as seasonal migrants in my dataset since they were not there during the rest of the year. The feeding stations and traps may therefore have had greater effect for short-distances migrants and thereby resulting in facultative migration for that category. That is, the animals may not have been obliged to travel to the feeding stations if they still had food in their summer area. Moreover, if they indeed traveled to their winter area they might have been taking trips back to their summer areas. Such return trips were documented by Cagnacci et al (2011) who deemed them quite common for facultative migrants. However, animals with summer areas further away also traveled to these traps to find food (L. Jäderberg, pers. comm).

The variation in timing of seasonal migration in fall was high, especially for short-distance migrants. Long distance migrants appeared to return to their summer areas earlier than short- distance migrants that returned both early and late. Short-distance migrants also had larger variation on an individual level than those with longer distances. However, the return date to the winter area for the same individual during multiple years was larger variation in fall, regardless of migration distance, than it was in summer. There was no tendency that the longer the seasonal migrating distance was, the earlier the animal returned. As mentioned earlier, it is possible that the late timing of return to winter area in males was not due to the sex difference, but distance.

Short–distance migrants had a larger variation in timing of return to the summer areas than long-distance migrants. The fact that Mysterud (1999) found that male returned to the winter area before female and in my study males returned after the females suggests that the late return by the males was a result of both distance as well as sex. Females that made short distance migrations had less variation in the timing of migration than both the males and the long distance migrants. Unfortunately, I had no data of long distance migrating males in fall during this period and a comparison with them was therefore not possible. Data from later years consist of two seasonal migrating males with distances > 10 km. They had an average timing in fall of November 5 ± 23 days, but both had just turned sub adults and the sample size is very small. Despite that, they were much closer to the timing of long distance migrating females although they were still later than the females.

The return dates in fall seemed to be less varied for animals that migrated outside Grimsö research area. The data for the return to winter areas in fall was less detailed than the data of leaving the winter area in spring and if animals were not expected to return, that is if they were believed to have dispersed, they might not have been checked regularly and the actual arrival data therefore not have been found.

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