



Inland Norway University department Evenstad

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Master thesis

**“Same procedure as last year” - Fidelity to
seasonal migration routes in a
temperate ungulate**

Masters in applied ecology

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Abstract

Infrastructure is expanding across the globe, and one of the consequences is habitat loss for wildlife, threatening the phenomenon of ungulate migration. Red deer in Norway live in a highly seasonal environment where partial migration is common. During spring they migrate from lower to higher altitudes to exploit newly emergent vegetation, and from higher to lower altitudes in the winter to avoid snow depth. Ungulates frequently exhibit a strong inclination to return to sites they have previously visited, a behavior known as 'site fidelity'. Even though knowledge on fidelity to home ranges and migration has increased during the last decade, there are still few studies on ungulates fidelity to migration routes. In this thesis I will investigate: (1) Red deer's fidelity to movement types across years. (2) Red deer's fidelity to seasonal migration routes over consecutive years. (3) What effect sex and age has on fidelity to migration routes. (4) How different covariates affect fidelity to migration routes. With data from 932 Global Positioning System (GPS)- marked red deer across Norway I defined movement types using the NSD method. 155 individuals were migratory and fit my requirements for data. I used the Brownian Bridge model to create 99% contours of seasonal migration routes, which was used in calculation of overlap between years. Multiple covariates were tested against overlap in four global models using linear mixed effects models. Two models for each seasonal migration, one with age and one without. The results showed that red deer had high fidelity to both movement type and migration routes. Sex alone, was not a significant variable, however, sex and age had a positive effect on the overlap. In general, female deer showed higher fidelity to migration routes compared to males. The results from the models varied between the seasonal models, however the reoccurring results for both seasons show that differences in altitude, stopovertime and distance affected the overlap. The final model from autumn migrations gave more significant variables than the final spring migration model, suggesting a more complex relationships for what affects fidelity to autumn migration.

Sammendrag

Norge utvider sin infrastruktur over hele landet, og en konsekvens av dette er tap av habitat for villlevende dyr. Dette kan true en strategi i dyrelivet, kalt migrasjon. Norsk hjort lever i ett land med store forskjeller i årstidene, noe som gjør migrasjon hos hjort svært vanlig. Om våren migrerer hjorten ofte til høyere liggende terreng for å kunne utnytte seg av plante-fenologien som følger av vårsesongen. Om høsten trekker hjorten ned til lavlandet for å blant annet unngå store snømengder. Hovdyr viser ofte en sterk evne til å vende tilbake til steder de tidligere har besøkt, en atferd kjent som stedstrokap. De siste ti-årene har forskning på temaet stedstrokap økt, men fortsatt er det flere ubesvarte spørsmål på temaet, spesielt troskap til migrasjonsruter. I denne masteroppgaven har jeg undersøkt hjortens (1) troskap mot bevegelses-strategi, (2) troskap til sesongbaserte migrasjonsruter år etter år (3) hvordan kjønn og alder påvirker troskap til rutene. (4) Hvilke kovariater/faktorer som kan påvirke troskap til migrasjonsruter. Med GPS data fra 932 hjort merket fra den sørlige delen av Norge, identifiserte jeg hvilke bevegelses-strategier og trekkruiter hjorten bruker ved hjelp av NSD-metoden. 155 individer utfylte kravene for å kvalifiseres til analysene, da de var migrerende over en sammenhengende periode på to år. Jeg brukte utvalgte trekkruiter for å beregne en brownian bridge kontur i 99%. Dette ble brukt videre ved utregning av overlapp på de sesong baserte trekkrutene mellom år. Flere kovariater ble testet mot overlappet i en (linear mixed effect) modell. To modeller for hver sesong, en inkludert alder på individer og en uten. Resultatene viser at hjort er trofast mot både sin bevegelses-strategi og mot den sesongbaserte trekkruta. Kjønn alene var ikke en signifikant variabel, men i forbindelse med alder, så hadde det en positiv effekt på overlappet. Resultatet for de sesongbaserte modellene var noe forskjellig, men noen resultater var like. Høyde over havet, tid brukt på «stopovers» og distanse på trekket var variabler som hadde en gjennomgående effekt i begge sesonger. Høst trekket hadde flere signifikante variabler noe som tyder på en mere kompleks sammenheng for hva som påvirker overlappet.

Introduction

Our planet as we know it today is rapidly changing and considering these changes it is important to study species' habitat use to conserve and manage our wildlife as best as possible. Several species are losing their habitat due to fragmentation caused by infrastructure, and habitat loss is regarded as one of the reasons we see fewer animal migrations occurring around the world (Kauffman et al., 2021). Migration is a life strategy used by several different animal species, including mammals, birds, and amphibians (Dingle & Drake, 2007) and can be defined as “the regular movement of all or part of an animal population to and from a given area” (Dorst, 2024). It is a life strategy that has been shaped by evolution, where the different species have adapted the migration to suit their needs, whether it is for mating, food or a change in climate (Shaw, 2016). Migration occurs all over the world and we find examples of these in multiple species across taxa. Some examples are migration of zebras who can travel up to 500 km (Naidoo et al., 2016) or American elk that travel in herds spanning from 6000 to 7000 individuals (Kauffman et al., 2020). While some animals travel far, others barely travel, and there are individuals or herds who migrate seasonally, whilst others only travel once in a lifetime (Dorst, 2024). A population can also be partly migratory, meaning that a part of the population stays sedentary, while the rest are migratory (Myserud et al., 2011a). One of the most studied animal migrations is the migration of large mammals, especially ungulates. However, migrating populations across the world are threatened due to increasing human footprint (Harris et al., 2020). Therefore, we still need more knowledge about animal migrations to be able to avoid negative human impact on our wildlife.

Seasonal migration is an annual animal movement between habitats, and is driven by seasonal fluctuations (Dingle, 2014a). It is quite common in highly seasonal environments, and is often the movement between winter home ranges and summer home ranges (Chapman et al., 2011). The forage maturation hypothesis is considered a key driver for seasonal migration in many populations (Myserud et al., 2012). This hypothesis is based on ungulates migrating to follow high quality forage, to optimize the quality quantity ratio (Hebblewhite et al., 2008). An example of this is the partially migratory Norwegian red deer (*Cervus elaphus*) population, where some individuals travel towards higher altitudes in summer seasons and lower altitudes in winter seasons (Albon & Langvatn, 1992). While plant phenology is considered the reason for spring migration to higher altitudes, snow depth is believed to be the main reason for migration to lower altitudes in winter (Myserud et al., 2011a). Leaving high – density areas in

winter to avoid competition, is also suggested as a theory to winter migration (Mysterud et al., 2011).

Animals with high mobility frequently exhibit a strong inclination to return to sites they have previously visited, a behavior we refer to as 'site fidelity' (Piper, 2011). This behavioral trait can enable animals to optimize food exploitation, decrease the costs associated with movement, diminish the risk of predation, and enhance fitness (Van Moorter et al., 2016). Knowledge on fidelity to migration routes is of high interest for conservation. Since technology on collecting movement data has developed immensely the last years, the data available today makes it possible to study movement on ungulates and especially the fidelity to migration routes (Tomkiewicz et al., 2010). There are several suggestions to why animals stay true to their migration routes, one being the risk associated with seeking new grounds (Møller et al., 2010). Some animals prefer returning to the same seasonal habitat, simply because their environment consists of predictable resources (Morrison et al., 2021). Other factors that impact fidelity to migration routes may be animal memory (Krochmal et al., 2021). Animals' site selection and navigation skills differ between species as well as individuals within species and can be inherited through genes and cultural impact (Wolf & Trillmich, 2007). It has been emphasized that the memory of site fidelity can be strong enough to prevent animals from adapting to environmental change (Bracis & Mueller, 2017; Wolf & Trillmich, 2007). Another hypothesis is that animals stay true to their routes as long as their seasonal habitat is favorable (Morrison et al., 2021). When habitat has lost its quality in one or another way, the animals might be more willing to change sites. This is referred to as the "win- stay, lose- switch" strategy (Kloskowski, 2021). Research shows that several partially migratory ungulates, such as moose (*Alces alces*) and Alaskan caribou (*Rangifer tarandus*), show high fidelity to their seasonal migration sites, but there are still few studies on fidelity to migration routes in most ungulate species (Joly et al., 2021; Lojander, 2013).

A question frequently raised regarding the topic of fidelity to migration routes, is the influence of sex on migratory traits. A study done on wildebeests (*Connochaetes taurinus*) fidelity to migration routes in wet seasons in Northern Tanzania, shows that there was no significant difference in the sexes likelihood to switch migration route after the first year (Morrison & Bolger, 2012). However, females who successfully bred during the first year were three times more likely to switch migration patterns the following year. Another study done on big horn sheep (*Ovis canadensis*) in USA suggests that females are likely to transfer their migration routes to their offsprings through teaching (Jesmer et al., 2018).

For species migrating solitary or in small groups, the age of the individuals may impact on fidelity to migration route as well as propensity to migrate in each season. Many ungulates are prone to learning both from other individuals (Kauffman et al., 2021). It is therefore reasonable to suggest that older animals may have higher fidelity to migration routes due to more extensive exploration while seeking the perfect route and home range. In groups with both old and young migratory individuals, younger animals might acquire migration routes faster than younger ones who migrate alone, due to social learning (Kauffman et al., 2021). A study done on moose suggests that as age increased, they were less likely to migrate in areas with deep snow and roads (Singh et al., 2012). As well as the biological aspect, there are other factors that are predicted to impact fidelity, such as movement metrics. Research done on migration speed and use of stopovers during migration (stopovertime) for mule deer (*Odocoileus hemionus*) in Wyoming, USA showed that stopover time had a higher correlation with fidelity compared to speed. However, they expected speed to be more significant if the migratory route lacked high-quality forage (Sawyer & Kauffman, 2011).

Norwegian red deer is an ungulate of interest, both from an economic and ecological point of view. Its vast expansion across Norway in later years, alongside an expansion in human infrastructure, makes the knowledge concerning habitat use important (Myrsterud, 2011b). Studying fidelity to migration routes can be a key development towards planning future infrastructure and can potentially be a great step towards less fragmentation of the landscape. As well as being influential in further wildlife management. Through a variety of research projects, we have obtained more knowledge on the partially migratory red deer population, but so far, the question of fidelity to migration routes has not been extensively researched.

The main objective of this study is to examine fidelity to seasonal migration routes (among migrants) within a partially migratory red deer population in Norway and analyze what factors affects fidelity. I used data from GPS (global position system) collared red deer to study the overlap in migration routes between years and seasons, with the aim to test the following hypotheses (Table 1).

Table 1. Questions and hypotheses on fidelity to migration routes. Included in the table are the theme of the research question, the research question itself, the prediction of the outcome and literature related to the predictions.

Theme:	Question:	Predictions:	Literature:
Fidelity to migration routes	Does red deer have high fidelity to migration routes?	Migratory deer have high fidelity to migration routes	(Lojander, 2013) (Joly et al., 2021) (Wolf & Trillmich, 2007) (Dahal, 2023) (Allan Michael R., 2022)
Sex and age	Does sex and age effect fidelity?	Females have higher fidelity than males. Older individuals have a higher degree of fidelity than younger individuals.	(Bischof et al., 2012a) (Debeffe et al., 2019) (Morrison et al., 2021) (Kauffman et al., 2021)
Spring and Autumn Migration Fidelity	What variables effects the fidelity of spring and autumn migration?	Deer in areas with high population densities have higher fidelity to migration routes. Fidelity to start date and mean days of migration between years leads to higher fidelity to migration routes. Equal speed/time spent migrating between years leads to higher fidelity to migration routes. Faster migrants have higher fidelity to migration routes. Higher accuracy to distance migrated between years leads to higher fidelity to migration routes. Longer time spent at stopover sites leads to less fidelity to migration routes. Higher accuracy to altitude during migration leads to higher fidelity to migration route	(Mysterud et al., 2011) (Morrison et al., 2021) (Alerstam et al., 2006) (Jakopak et al., 2022) (Sawyer & Kauffman, 2011)
Seasonal variations in fidelity	Are there any differences in fidelity between seasons?	Higher fidelity to spring migration compared to autumn (due to spring grazing) Lower fidelity to autumn migration compared to spring (due to overlap with rutting)	(Dingle, 2014b) (Bischof et al., 2012a) (Mysterud et al., 2011)

Material and method

Study area

The GPS data from red deer in the analysis was collected in the southern parts of Norway, and includes individuals marked in the counties presented in (Table 2 and figure 1). Western Norway includes Trøndelag, Møre og Romsdal and Vestland. Eastern Norway includes Innlandet, Viken and Vestfold og Telemark, and lastly Southern Norway includes Agder. In general temperature and rainfall increases from inland to coastal areas, while snow depth increases from south to north and from coastal areas to inland areas (Mysterud et al., 2005). Around 60 % of Norway’s land area is categorized as mountains and 37.8% of the land area is covered by forest and is dominated by boreal forest (Kayes & Mallik, 2020). Only 3.5 % is considered agricultural farmland and human infrastructure covers only 1.7 % of the total land area (SSB, 2024).

County	N Female	N Male
Trøndelag	9	12
Møre og Romsdal	48	16
Vestland	33	17
Innlandet	1	0
Viken	17	3
Vestfold og Telemark	2	0
Agder	4	0

Table 2: Number of deer captured, and GPS marked per county in Norway from the dataset used in the analysis

Western Norway and Trøndelag has a temperate climate and a varied topography. The counties consist of around 30- 60% mountainous area. They stand out from the other areas in the southern and eastern parts of Norway with their large amount of precipitation and because of their steep, varied and partly unattainable terrain (Moen, 1998). Especially in Western Norway, the landscape structure has made it difficult for people to settle in higher altitudes. Most of the infrastructure is there for located in lower coastal areas.

The terrain in Eastern Norway is quite flat compared to Western Norway and has a dryer continental climate with colder winters (Ketzler et al., 2021). Of all the area, Eastern Norway has the highest amount of people living per km², which calls for more enhanced infrastructure (Viste & Birkemo, 2023).

Southern Norway is the smallest of the four land areas and has a temperate climate with mild winters. Forest makes up about 57 % of the land in this region (Moen, 1998). It has been a typical moose and roe deer area, with only patches of red deer, but in the later years the occurrence of red deer has increased (Meisingset et al., 2019)

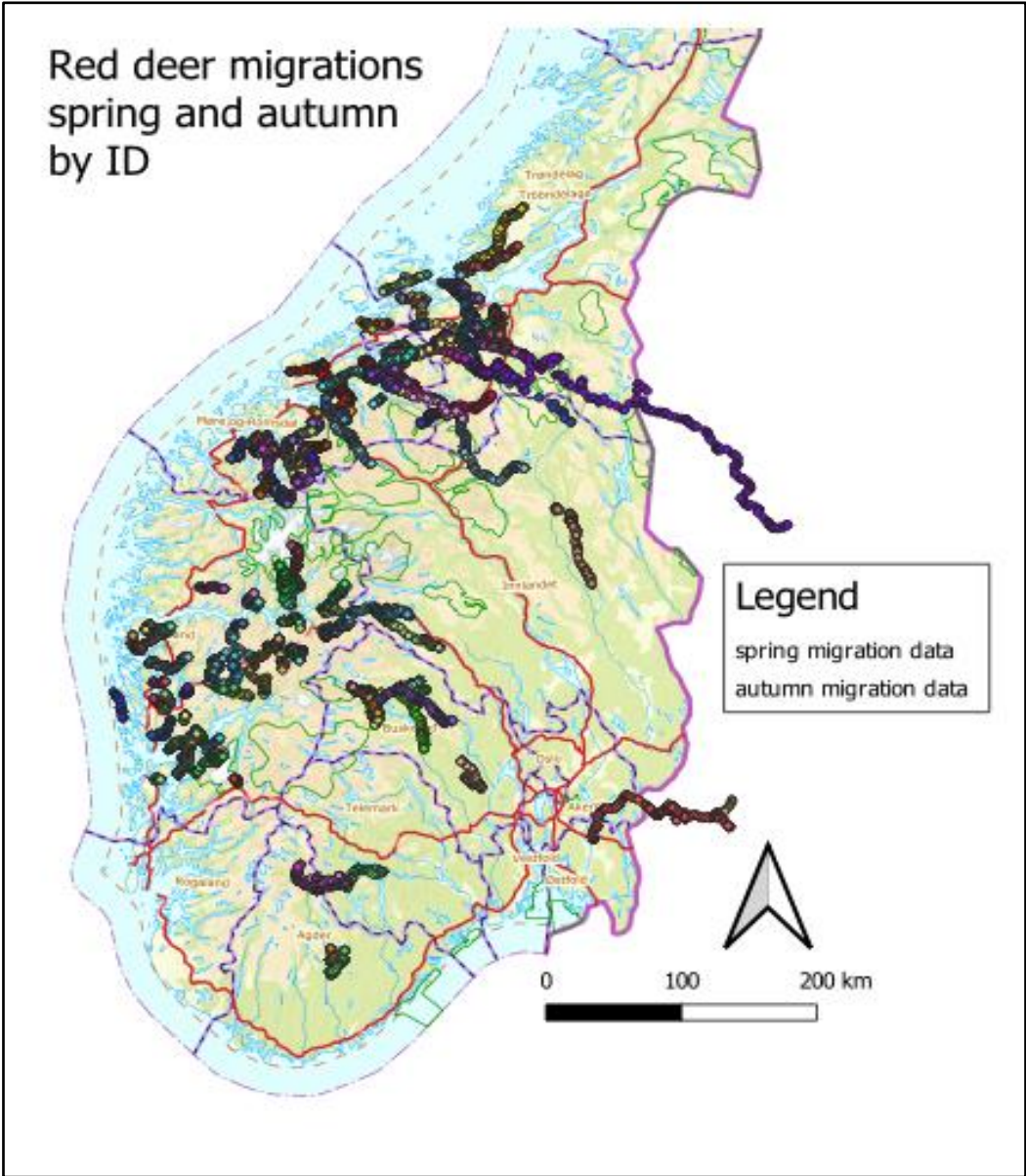


Figure 1 GPS positions from individual red deer during annual migrations in spring and autumn. Map made in QGIS.

Red deer data

The data that was used in this thesis was provided by NIBIO (Norwegian Institute of Bioeconomy Research) and has been collected throughout multiple research projects on red deer the last few decades. This data has previously been used in multiple studies on different research questions (e.g. Bischof et al., 2012, Mysterud et al., 2011a). In total I had access to position data from 635 GPS collared red deer that had been captured during winter (January - April) and monitored between the year 2002 to 2022, in 7 counties. Mean monitoring days for all red deer marked were 428 days with a standard deviation of 207 days or a median of 380 days. Capturing red deer was done by tranquilizer with a dart gun on winter feeding areas, typically places where supplementary food had been put out. Red deer that were over 1.5 years was captured and fitted with GPS collars. While deer were immobilized, researchers could collect data, such as age, for individual red deer. Methods used to capture, mark and track red deer was approved by Norwegian Animal Research Authority (Sente et al., 2014). The GPS brands that were used was Televilt/Followit, Sweden and Vectronic, Germany both designed for red deer. The GPS collars were set to log the animal's location every 1-2 hours. The duration of tracking depended on the battery life of the GPS collars, any technical difficulties with the collars, as well as any mortalities or recaptures. Data from the first 24 hours post-marking was excluded, and the leftover raw data was subsequently examined for errors, following the method outlined by Bjørneraas et al. (2010).

I utilized a model-fitting net square displacement (NSD) approach, as developed by Bunnefeldt et al. (2011) and advanced by Bischof et al. (2012) and Rivrud et al. (2016), to establish the migration pattern of each red deer and to obtain estimates of the migration timing, number of stopovers and time spent at each stopover. By using this approach, the tracked individuals were classified into one of five movement categories for each monitoring year: migratory, resident, dispersal, other or incomplete. Individuals categorized as incomplete were mostly migratory individuals where logging ended before return to winter range, usually due to the animals being shot in the summer range or during the fall migration.

Further, I selected only migratory individuals to include in the analyses. To be able to test fidelity, the migratory individuals had to meet following criteria's: 1) it had data for a long enough period both in spring and autumn with a minimum of two consecutive years; 2) it held a complete set of GPS-data and covariates for the current period.

The NSD method calculates the distances from the initial location (within the winter range) to all subsequent locations over the course of a year, then fits logistic curves to these displacement distances as they increase over time, creating what's termed the NSD movement profile (Bunnefeld et al., 2011). The calculated onset and end dates for the spring and fall migrations are identified as $x_{mid}-2scale$ (onset) and $x_{mid}+2scale$ (end). Here, x_{mid} signifies the inflection point (which corresponds to the mid-migration date) of the logistic curve fitted to each individual's GPS relocations during migration. The term 'scale' represents the duration required to traverse a quarter of the logistic curve and can thus be used as an indicator of the migration duration (refer to Bischof et al. 2012 for more details). To ensure that the whole migration route was included in what was defined as migration, the data was inspected manually by plotting GPS data into interactive maps.

With the individuals left after deselection of non-migrants ($n=135$ for spring migration, $n=97$ for autumn migration), I proceeded to calculate the overlap between consecutive individually spring and autumn migration, respectively, to be able to check the site fidelity to migration routes. I excluded individuals with less than ten GPS positions along the route to get as reliable estimates of the migration route as possible. First, I calculated the Brownian bridge movement model contour for all the migrations routes using the 'ltraj'- and 'kernelbb' functions in the r package AdehabitatHR (Calenge et al., 2009). I estimated both the 95- and 99 % individual contours for each season per year for further analyses of overlap. The overlap was calculated by using the 'kerneloverlap' function in AdehabitatHR by calculating the overlap (in %) of contour for the migration route in year two ($n+1$) in relation to the contour of the migration route in year one (n) for spring and autumn migrations, respectively.

Individual and environmental variables

In the analyses I aimed to include individual and environmental variables relevant for testing my hypotheses and predictions (see Table 1). The travel speed during the entire migration period (spring and autumn) was calculated as the sum of Euclidean distance between successive fixes, which was done by extracting the east/north coordinates and using the fixes in a formula to calculate distance. I also calculated the time used during migration. This was done by calculating the time between each position. Speed of migration was calculated by dividing the distance by time (between each position).

During seasonal migration, some individuals have stopovers along the route (Sawyer & Kauffman, 2011). This is explained as short stops during migration where the animal for

example eats, rests or in some example's mates. Stopovers were identified while conducting the NSD-method. Positions within these stops were then categorized as positions during a stopover, and time at stopover site could be quantified from the positions. Altitude [meters above sea level (MASL)] was calculated in QGIS, by using the "draped" function in an DTM 10 terrain map. I used the altitude from the first position and the last position during the migration route to calculate the difference in altitude in the summer and winter range. I also calculated the mean altitude throughout the migration route.

Lastly, I defined the age of the individual as the age in monitoring year two. Not all individuals were age classified due to different reasons, but age was defined for 76 individual deer which resulted in 155 id-years (id per year). Population density was calculated as the number of shot animals in the municipality the deer was marked, divided by the counting area in the given municipality (Mysterud et al. 2007). This gives a fairly good estimate of population density and has been used in many studies in Scandinavia on red deer and moose (E. L. Meisingset & Omholt, 2022).

After initial analyses, I ended up only using the 99% contours as the basis for estimation of the overlap between subsequent seasons as the predictor variable. The 99% contours gave more continuous migration corridors in most cases, and I considered this as the most reliable value to test the overlap between successive years (Sawyer et al., 2009). I made some minor adjustments to the final dataset by manually deselecting animals that had faults in the data. Some animals had two years of migration, but they changed either winter or summer range during that time. The animals that were manually removed were four individuals with dispersal migratory behavior and one with migratory other behavior.

Statistical analysis

I used linear mixed models to analyze what effected overlap of migration route using the lmer function in the r package lme4 (Brown, 2021). I first checked the distribution of the dependent variable, and a fitdist test showed that data fit best with gaussian distribution. I tested both id and idyear as potential random effects conducting an anova test on a clean model to see which random variable that gave the best fit and ended up including id as a random effect in the models.

Before establishing global models, I checked for correlations between possible variables. Correlations that were higher than $r > 0,5$ were then tested for each variable in a linear model

and compared with AIC. The variable with lowest AIC of the competing models were taken into the global model.

I first ran a model for analyzing the effect of season, together with age and sex on the fidelity to the migration route. Thereafter I built two models for overlap between consecutive spring and autumn season, respectively, where I included the selected environmental and individual variables. Since there was missing age data on some individuals, I built a global model without age, and one including age, which together resulted in four different global models.

The global model included the predictor variables: Sex, age (linear and quadratic term), density at municipality that red deer was marked (linear and quadratic term), difference in mean speed during migration between year $n+1$ vs year n (linear and quadratic term), mean speed during migration per ID, difference in distance of migration routes between year $n+1$ vs year n (linear and quadratic term), mean distance of migration route per ID, difference in time spent at stopover sites between year $n+1$ vs year n (linear and quadratic term), mean stopover time per ID, mean days spent migrating per ID, difference in start date of migration between year $n+1$ vs year n (linear and quadratic term), mean altitude per ID, mean altitude per ID (standard deviation), difference in mean altitude of migration routes between year $n+1$ vs year n (linear and quadratic term), difference in mean altitude (standard deviation) of migration routes between year $n+1$ vs year n (linear and quadratic term).

To select a final model from each of the global models, I used a backward stepwise selection procedure (Murtaugh, 2009). For each model, an analysis of variance was used to identify the parameter with the weakest relationship to the response variable (lowest F-value). This variable was removed in an updated model. The two models were then compared using a likelihood ratio test where the model with the fewest parameters was retained, if it was non-significant ($p > 0.05$). Model validation was performed using repeated k-fold cross-validation. The results from the models are presented as tables and plots.

Results

Classification of individual space use

The NSD-method (Net Squared Displacement) identified 446 individual trajectories as migratory, 305 as resident, 24 as dispersal, 109 as incomplete, and 51 as other, based on sample sizes of 935 id-years. Out of all individuals (n=635) that were fitted with a GPS collar, 265 were consistently migratory and 201 were consistently resident during the whole period of tracking. Only 30 individuals changed their movement behavior during the tracking period. In total (after individuals that categorized as incomplete were removed) 52% of all individuals were migratory, 39.4 % were resident, 2,4 % dispersal and 5,8 % other, and only 4.7 % changed their behavior between seasons.

Effects of age and sex on migration fidelity

The mean proportion overlap for both seasons were 0.56 for females and 0.47 for males. Males tend to have a lower proportion of overlap than females in terms of mean value (Table 3). The highest proportion of overlap from the dataset was a female, with a proportion of 0.96. The highest proportion of overlap for males was 0.89. Both cases were during spring migration.

Table 3. Summary of proportion overlap for males and females for autumn-, spring migration and both seasons combined, values presented are mean values, standard deviation of mean, minimum values and maximum values.

Values	Overlap Females (Autumn)	Overlap Males (Autumn)	Overlap Females (Spring)	Overlap Males (Spring)	Overlap Females (Both seasons)	Overlap Males (Both seasons)
Mean	0.57	0.53	0.56	0.49	0.56	0.47
Standard deviation	0.18	0.17	0.21	0.20	0.23	0.22
Minimum	0.04	0.00	0.00	0.00	0.00	0.00
Maximum	0.95	0.77	0.96	0.89	0.96	0.89

The model testing the effect of season, age and sex on the overlap of migration routes showed a significant positive effect of age, i.e older deer had higher overlap than younger ones (Table 4 and Figure 2). Males had a lower overlap on seasonal migration routes than females, but the

effect was marginally significant (Table 4). The seasonal effect on overlap shows no difference between spring and autumn migration (Table 4).

Table 4: Results from linear mixed effects model where overlap of the 99% Brownian bridge contour is the response variable and season, sex and age are predictor variables.

Predictor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	0.491	0.050	78.918	9.682	<0,001
Season (autumn vs spring)	-0.004	0.025	92.082	-0.158	0.874
Sex (females vs. males)	-0.070	0.037	58.082	-1.891	0.063
Age (in years)	0.010	0.005	73.991	2.106	0.038

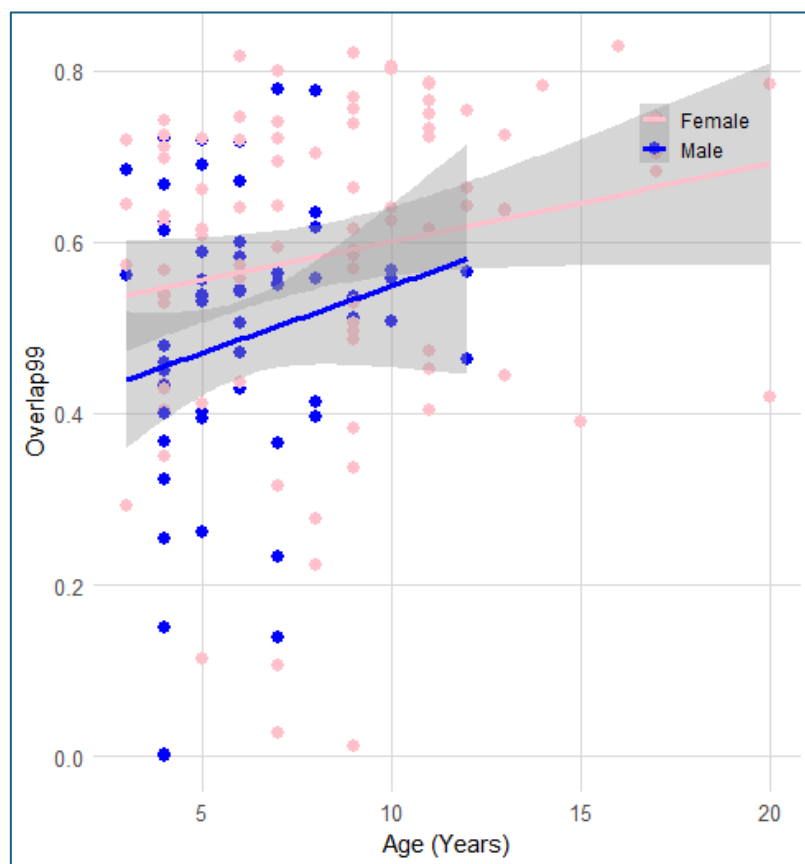


Figure 2: Linear plot of age and sex in relation to overlap in migration routes. Figure made from the results of the linear mixed effects model in table 3.

Overlap in spring migration routes

The global model on spring migrations (without age) included data from 155 observations (id per year). The results of the linear mixed-effects model (without age) are presented in (Table 5). The significant variables from the final model (without age) were difference in distance of migration routes between years, difference in distance of migration routes between years (quadratic value), difference in mean altitude of migration routes between years (quadratic value), difference in mean altitude (standard deviation) of migration routes between years, difference in mean altitude (standard deviation) of migration routes between years. (quadratic value) (Table 5).

The difference in distance of individual migration routes between year $n+1$ (second year) versus year n (first year) had a significant positive effect on the overlap. However, the quadratic term of this variable was also included in the model and was significant, indicating a non-linear negative relationship with a diminishing rate at higher difference in distance.

Difference in time spent at stopover sites between years had a significant positive effect on overlap. Thus, the increased difference in time at stopover gave an increased overlap. Difference in mean altitude of migration routes had a significant negative effect on the overlap. Increased difference in altitude between years gave a decrease in overlap. The quadratic term of this variable indicates a non-linear negative relationship with a diminishing rate at higher difference in altitude (Figure 3).

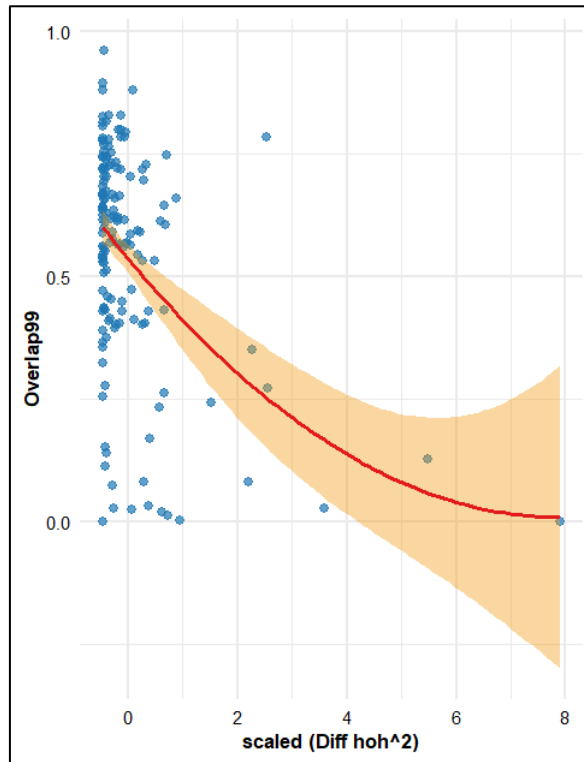


Figure 3: Quadratic plot of difference in mean altitude of migration routes between years in relation to overlap. Figure made from the results of the model presented in Table 5

The standard deviation of difference in mean altitude had also a significant relationship to overlap. Overlap had a positive increase with a higher variability, but the quadratic value is indicating a non-linear relationship with a diminishing rate.

Table 5: Results from the final model from the backward selection. The model was a linear mixed model. This model was based on 155 observations (id per year) for individuals who migrated during spring. Explanation: ID means individual identification of red deer.

Predictor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	0.553	0.019	127.21	28.285	< 0,001
Sex (Males).	-0.042	0.039	128.01	-1.097	0.274
Difference in distance of migration routes between years (year n+1 vs year n).	0.037	0.017	151.89	2.155	0.032
Difference in distance of migration routes between years (Quadratic value).	-0.041	0.018	149.21	-2.205	0.029
Difference in time spent at stopover sites between years (year n+1 vs year n).	0.027	0.011	48.27	2.396	0.020
Mean days spent migrating per ID.	-0.029	0.016	129.42	-1.780	0.077
Difference in start date of migration between years (year n+1 vs year n).	0.024	0.013	79.57	1.825	0.071
Difference in mean altitude of migration routes between years (year n+1 vs year n).	-0.029	0.015	144.71	-1.925	0.056
Difference in mean altitude of migration routes between years (Quadratic value) (year n+1 vs year n).	-0.082	0.020	122.59	-4.069	< 0,001
Difference in mean altitude (standard deviation) of migration routes between years. (year n+1 vs year n).	0.033	0.013	100.08	2.475	0.015
Difference in mean altitude (standard deviation) of migration routes between years. (Quadratic value) (year n+1 vs year n).	-0.034	0.015	142.60	-2.187	0.030

The global model on spring migrations (with age) included data from 92 observations (id per year). The results of the linear mixed-effects model (with age) are presented in (Table 6). The significant variables from the final model (without age) were sex, age of individual deer (quadratic value), differences in time spent at stopover sites, difference in time spent at stopover sights between years and difference in mean altitude of migration routes between years (quadratic value) (table 6).

Sex had a significant effect on overlap where males had a lower overlap in spring migration routes than females. The quadratic value of age had a positive effect on overlap, but with a diminishing rate. Difference in time spent at stopover sites between years had a significant positive effect on overlap. Increased difference in second year versus first year in time spent at stopover, gave an increased overlap (Figure 4).

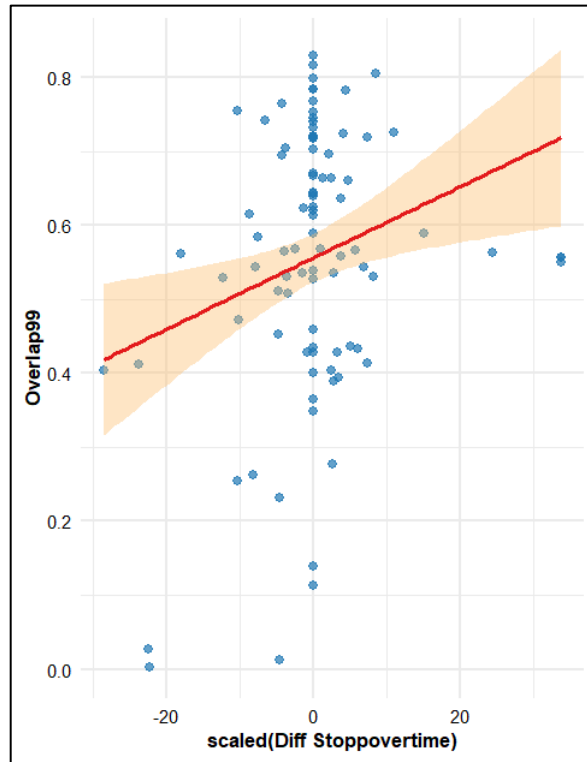


Figure 4: Linear plot of difference in time spent at stopover sites between years in relation to overlap. Figure made from the results of the model presented in Table 6.

The quadratic value of the difference in mean altitude between years had a significant effect on overlap and suggests a non-linear relationship where larger differences in altitude in second year versus first year indicating a negative effect with a diminishing rate at higher difference in altitude.

Table 6: Results from the final model from the backward selection. The model was a linear mixed model. This model was based on 92 observations (id per year) for individuals who migrated during spring and had age quantified in the data.

Predictor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	0.659	0.085	91.08	7.745	< 0,001
Sex (Males)	-0.094	0.040	74.39	-2.356	0.021
Age of individual deer	-0.028	0.018	91.28	-1.493	0.138
Age of individual deer (Quadratic value)	0.002	0.001	91.96	2.034	0.044
Difference in time spent at stopover sights between years (year n+1 vs year n).	0.059	0.013	37.20	4.568	< 0,001
Mean days spent migrating per ID.	-0.025	0.017	73.52	-1.489	0.140
Difference in mean altitude of migration routes between years (year n+1 vs year n).	0.015	0.014	74.83	1.067	0.289
Difference in mean altitude of migration routes between years (Quadratic value) (year n+1 vs year n).	-0.049	0.015	62.34	-3.266	0.001
Difference in mean altitude (standard deviation) of migration routes between years. (year n+1 vs year n).	-0.016	0.018	84.01	-0.921	0.359
Difference in mean altitude (standard deviation) of migration routes between years (Quadratic value) (year n+1 vs year n).	0.020	0.012	43.27	1.660	0.104

Overlap in autumn migration routes

The global model on autumn migrations (without age) included data from 100 observations (id per year). The results of the linear mixed-effects model (without age) are presented in (Table 7). The significant variables from the final model (without age) were difference in mean speed during migration between years (quadratic value), difference in distance of migration routes between years (quadratic value), difference in time spent at stopover site between years, Difference in time spent at stopover site between years (quadratic value), difference in start date of migration between years, Difference in mean altitude of migration routes between years (quadratic value) and difference in mean altitude (standard deviation) of migration routes between years. (quadratic value) (Table 7).

The quadratic value for difference in mean speed during migration between years was significant and suggests that the relationship a non-linear negative relationship with a diminishing rate. The same was the case for the quadratic value of difference in distance of migration routes between second year versus first year, where the relationship was negative but with diminishing rate.

Increased difference in time spent at stopover sites in second year versus first year, had a positive effect on overlap. However, the quadratic value of the variable suggests a negative

relationship that is reversed at a certain point (Figure 5). The difference in start date of migration between second year versus first year had a positive relationship with overlap. (Figure 6).

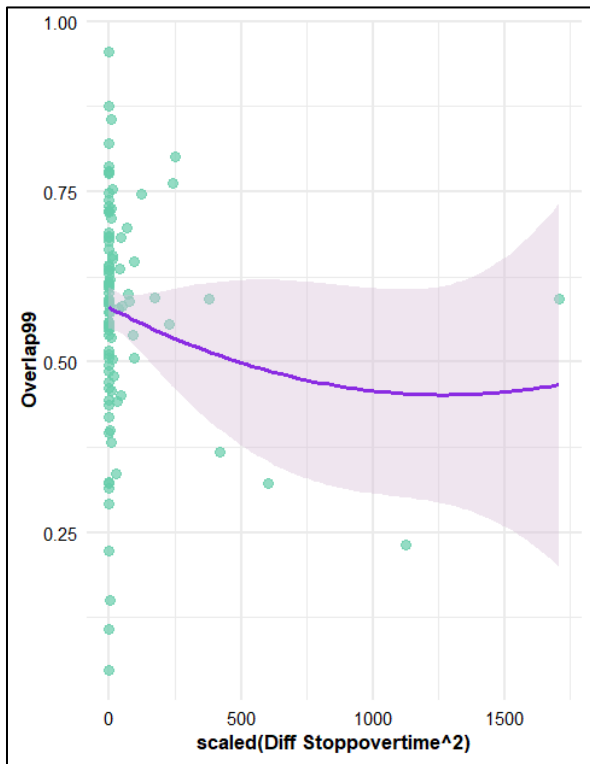


Figure 5: Quadratic plot of difference in time spent at stopover sites between year (quadratic term) in relation to overlap. Figure made from the results presented in Table 7

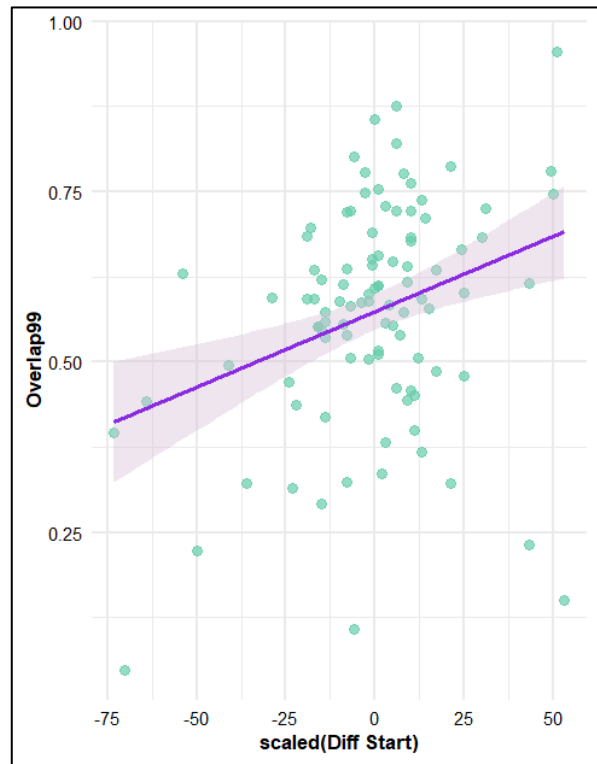


Figure 6: Linear plot of difference in start date of migration between years in relation to overlap. Figure made from the results of the model presented in Table 7

Both the quadratic value of difference in mean altitude of migration routes and difference in altitude standard deviation between second year versus first year, were significant. Difference in mean altitude of migration routes had a positive effect on overlap, while difference in altitude standard deviation showed a slight positive relationship on overlap but with a diminishing effect.

Table 7: Results from the final model from the backward selection. The model was a linear mixed model. This model was based of 100 observations (id per year) for individuals who migrated during autumn.

Predictor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	0.569	0.014	80.19	39.601	< 2e-16
Difference in mean speed during migration between years (year n+1 vs year n).	-0.016	0.013	90.28	-1.223	0.225
Difference in mean speed during migration between years (Quadratic value) (year n+1 vs year n).	-0.046	0.013	90.86	-3.322	0.001
Difference in distance of migration routes between years. (year n+1 vs year n).	0.001	0.020	92.13	0.064	0.949
Difference in distance of migration routes between years (Quadratic value)	-0.078	0.023	92.64	-3.394	0.001
Difference in time spent at stopover site between years (year n+1 vs year n).	0.055	0.014	99.61	3.861	< 0,001
Difference in time spent at stopover site between years (Quadratic value) (year n+1 vs year n).	-0.039	0.014	86.59	-2.762	0.007
Difference in start date of migration between years (year n+1 vs year n).	0.070	0.014	94.69	4.840	< 0,001
Difference in mean altitude of migration routes between years (year n+1 vs year n).	0.022	0.016	96.30	1.361	0.177
Difference in mean altitude of migration routes between years (Quadratic value) (year n+1 vs year n).	0.033	0.015	96.02	2.202	0.030
Difference in mean altitude (standard deviation) of migration routes between years (year n+1 vs year n).	0.008	0.014	63.51	0.566	0.573
Difference in mean altitude (standard deviation) of migration routes between years. (Quadratic value) (year n+1 vs year n).	0.046	0.016	72.46	2.885	0.005

The global model on autumn migrations (with age) included data from 61 observations (id per year). The results of the linear mixed-effects model (without age) are presented in (Table 8). The significant variables from the final model (without age) were difference in mean speed during migration between years, mean speed of migration routes per ID, difference in distance of migration routes between years (quadratic value), mean distance of migration routes per ID, difference in time spent at stopover sites between years, difference in start date of migration between years, difference in mean altitude of migration routes between years (quadratic value) and difference in mean altitude (standard deviation) of migration routes between years. (quadratic value) (Table 8)

Difference in mean speed during migration between second year versus first year, had a significant negative relationship to overlap. However, the mean speed per individual during migration had a significant positive relationship to overlap (Figure 7). The quadratic value of difference in distance of migration routes between years had a negative effect on overlap with a diminishing rate (Figure 8).

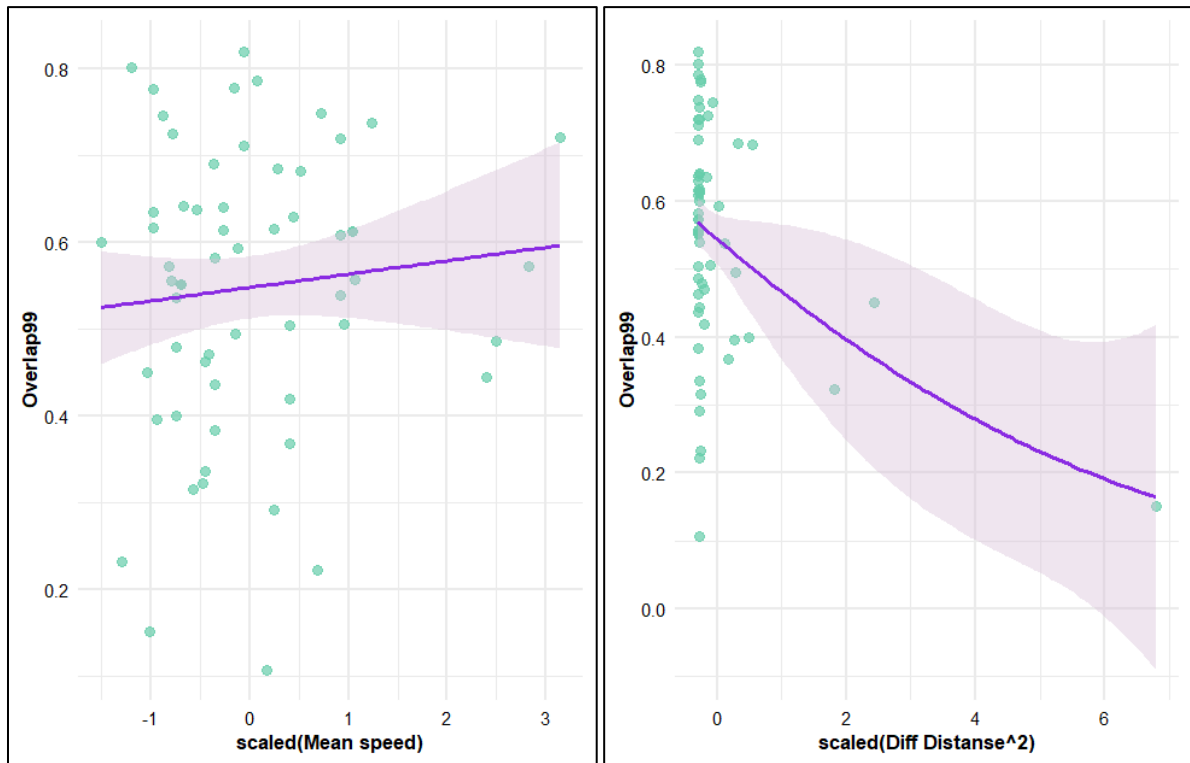


Figure 7: Linear plot that shows the effect mean speed per ID during migration between years have on overlap. Figure made from the results of the model presented in Table 8

Figure 8: Linear plot that shows the effect Difference in distance of migration routes between years (Quadratic value). Figure made from the results of the model presented in Table 8

Difference in time spent at stopover sites between years had a significant positive effect on overlap. The difference in start date of migration in second year versus first year had a positive relationship to overlap.

The difference in quadratic value of mean altitude in second year versus first year had a positive effect on overlap, but with a non-linear diminishing effect on overlap.

Table 4: Results from the final model from the backward selection. The model was a linear mixed model. This model was based of 61 observations (id per year) for individuals who migrated during spring and had age quantified in the data. ID means individual identification of red deer.

Predictor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	0.548	0.014	42.64	38.245	<0,001
Density at municipality that red deer was marked	0.029	0.015	44.74	1.884	0.066
Difference in mean speed during migration between years (year n+1 vs year n).	-0.015	0.013	58.92	-1.140	0.258
Difference in mean speed during migration between years (Quadratic value) (year n+1 vs year n).	-0.073	0.017	55.36	-4.172	<0,001
Mean speed during migration per ID	0.054	0.020	44.85	2.680	0.010
Difference in distance of migration routes between years (year n+1 vs year n).	0.015	0.015	53.31	1.008	0.317
Difference in distance of migration routes between years (Quadratic value) (year n+1 vs year n).	-0.098	0.016	51.55	-5.948	<0,001
Mean distance of migration routes per ID	-0.043	0.017	50.10	-2.449	0.017
Difference in time spent at stopover sites between years (year n+1 vs year n).	0.077	0.014	54.17	5.450	<0,001
Difference in start date of migration between years (year n+1 vs year n).	0.070	0.015	55.13	4.515	<0,001
Difference in mean altitude (of migration routes between years (year n+1 vs year n).	0.007	0.01	57.35	0.444	0.658
Difference in mean altitude of migration routes between years (Quadratic value) (year n+1 vs year n).	0.031	0.014	54.39	2.138	0.036
Difference in mean altitude (standard deviation) of migration routes between years (year n+1 vs year n).	0.009	0.015	60.81	0.595	0.553
Difference in mean altitude (standard deviation) of migration routes between years. (Quadratic value) (year n+1 vs year n).	-0.031	0.014	60.45	-2.216	0.030

Discussion

Fidelity to movement behavior

My results show that red deer have high fidelity to their movement behaviour. Most individuals stayed true to their movement behaviour and showed high fidelity to their strategy. This strongly indicate that they are an ungulate of habit, and a changing behaviour from migratory to resident and vice versa are relatively rare, which is accordant to studies on other ungulates (Morrison et al., 2021). This could be supporting evidence for a cultural and social learning between individuals (Jesmer et al., 2018; Merkle et al., 2019). My results also show that migratory red deer in general have a high fidelity to migration routes. Also suggesting that overlap was equal between spring and autumn migrations.

Sex and age

The fidelity to migration routes differed between the sexes. Although sex, alone, was not a significant variable for overlap, sex combined with age had a positive effect, however, it should be noted that neither sex nor age was retained in the final autumn model. The overlap increased with age for both sexes, with females having a higher overlap at all ages. These results support that older animals have higher fidelity and that they get more experienced with increasing age (Morrison et al., 2021). Females tend to stay with close relatives (small herds of females and calves) for a longer period in their first years, compared to males who tend to wander off from their mother at the age of 1.5 years old, due to their biology (Meisingset, 2008). My results may also support that migration routes could be culturally transmitted between generations (Jesmer et al., 2018). It could therefore be natural to think that males take a longer time to find their route, then females who stay with their mother and can adopt the route (Langvatn & Loison, 1999).

Influences on fidelity to seasonal migration routes

The spring analysis showed that difference in stopover time had a statistically significant positive effect on overlap. This could be the results of increased fidelity to a specific stopover site (Sawyer & Kauffman, 2011). In contrast, if the individual spends less time in a stopover site, they may be more likely to explore other alternatives causing a decrease in overlap to previous years. It's also worth mentioning that increased time spent at stopovers will generate more GPS- points within the route, thus affecting the Brownian Bridge contour with more

overlapping GPS- points. As well as difference in stopover time, difference in mean altitude was also statistically significant, but with a negative effect on the overlap. This could be the result of abiotic factors, such as snow depth, preventing red deer from foraging at higher altitudes (Mysterud et al., 2011). Snow depth can vary a lot from year to year and can be especially unpredictable in spring season. The spring analysis without age showed somewhat different results to the one with age, this may be caused by a larger sample size. The results that were recurring from the analysis with age, was difference in stopover time and difference in mean altitude. However, compared to the spring analysis without age, difference in distance (quadratic) was statistically significant and had a positive effect on the overlap, but with a diminishing rate. A longer distance travelled in year two, compared to year one, could generate more GPS – points within the route, affecting the Brownian bridge contour. However, only up to a certain point where the positive effect will start decreasing. The diminishing rate could be due to individuals straying off the route, resulting in lower overlap and longer distance travelled. Sex was also statistically significant, indicating that males had a lower overlap percentage than females. Supporting the theory and my hypothesis that sex is an important factor to fidelity to migration routes. This could be the result of females relying more on predictable high-quality forage due to raising offsprings, thereby following the same route (Bischof et al., 2012b).

The autumn analysis with age had many statistically significant variables in the final model, suggesting that autumn migration may be more complex in terms of what affect the overlap. Both mean speed, difference in stopover time, difference in start and difference in mean altitudes had a positive effect on the overlap. A positive relationship between mean speed and overlap could be natural as higher speed may lead to less time for detours, which could result in a higher overlap. Difference in timing of migration also lead to a higher overlap, possibly explained by a later start resulting in higher speed (in year two), and thereby a higher overlap. However, the relationship between start time and speed has not been tested in this analysis. In contrast to the results for spring migration models, indicating a negative coherence between difference in mean altitude and overlap, the autumn analysis suggests a more complex relationship where difference in altitude will affect the overlap positively, but with a diminishing rate. Also, this could be perceived as a natural result considering that increased differences in any forms is an indication that individuals chose a different- or have small adjustments to their route. Increased mean distance and decreased overlap may be the result of a longer route caused by temptation to choose other alternative routes along the way, as well as the individuals' chances for facing obstacles on the route. Difference in standard deviation of

mean altitude leading to lower overlap suggests that when there is a higher variation in altitudes, red deer might not be travelling through the same areas.

Conclusions and management implications

The results provided in this analysis support the hypothesis of animal memory and could be useful in planning future expansion in infrastructure. The fact that individual red deer stay true to their migratory behavior is also of great significance to wildlife management. It encourages cooperation between landowners, municipalities and counties to manage red deer on a larger scale and requires meticulous planning. To keep and facilitate the phenomenon of migration in northern ungulates, information about how individuals behave during migration could be of uttermost importance.

References

- Albon, S. D., & Langvatn, R. (1992). Plant Phenology and the Benefits of Migration in a Temperate Ungulate. *Oikos*, *65*(3), 502–513. <https://doi.org/10.2307/3545568>
- Alerstam, T., Hake, M., & Kjellén, N. (2006). Temporal and spatial patterns of repeated migratory journeys by ospreys. *Animal Behaviour*, *71*(3), 555–566. <https://doi.org/10.1016/j.anbehav.2005.05.016>
- Allan Michael R., L. and A. (2022, september 1). *Calving site selection and fidelity in a restored elk (Cervus elaphus) herd in Bancroft, Ontario, Canada*. <https://library-archives.canada.ca/eng/services/services-libraries/theses/Pages/item.aspx?idNumber=1019508457>
- Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., & Mysterud, A. (2012a). A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? *The American Naturalist*, *180*(4), 407–424. <https://doi.org/10.1086/667590>
- Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., & Mysterud, A. (2012b). A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? *The American Naturalist*, *180*(4), 407–424. <https://doi.org/10.1086/667590>
- Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1855), 20170449. <https://doi.org/10.1098/rspb.2017.0449>
- Brown, V. A. (2021). An Introduction to Linear Mixed-Effects Modeling in R. *Advances in Methods and Practices in Psychological Science*, *4*(1), 2515245920960351. <https://doi.org/10.1177/2515245920960351>

- Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., & Ericsson, G. (2011). A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. *Journal of Animal Ecology*, *80*(2), 466–476. <https://doi.org/10.1111/j.1365-2656.2010.01776.x>
- Calenge, C., Dray, S., & Royer-Carenzi, M. (2009). The concept of animals' trajectories from a data analysis perspective. *Ecological Informatics*, *4*(1), 34–41. <https://doi.org/10.1016/j.ecoinf.2008.10.002>
- Chapman, B. B., Brönmark, C., Nilsson, J.-Å., & Hansson, L.-A. (2011). The ecology and evolution of partial migration. *Oikos*, *120*(12), 1764–1775. <https://doi.org/10.1111/j.1600-0706.2011.20131.x>
- Dahal, P. (2023). “*Individual Variation in Site Fidelity of Moose*” [Master thesis, NTNU]. <https://ntnuopen.ntnu.no/ntnu-xmlui/handle/11250/3079494>
- Debeffe, L., Rivrud, I. M., Meisingset, E. L., & Mysterud, A. (2019). Sex-specific differences in spring and autumn migration in a northern large herbivore. *Scientific Reports*, *9*(1), 6137. <https://doi.org/10.1038/s41598-019-42639-3>
- Dingle, H. (2014a). *Migration: The Biology of Life on the Move*. Oxford University Press.
- Dingle, H. (2014b). Seasonal migration patterns. I H. Dingle (Red.), *Migration: The Biology of Life on the Move* (s. 0). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199640386.003.0009>
- Dingle, H., & Drake, V. A. (2007). What Is Migration? *BioScience*, *57*(2), 113–121. <https://doi.org/10.1641/B570206>
- Dorst, J. P. (2024). *Migration | Definition, Animals, & Facts | Britannica*. <https://www.britannica.com/science/migration-animal>

- Harris, S. M., Descamps, S., Sneddon, L. U., Bertrand, P., Chastel, O., & Patrick, S. C. (2020). Personality predicts foraging site fidelity and trip repeatability in a marine predator. *The Journal of Animal Ecology*, *89*(1), 68–79. <https://doi.org/10.1111/1365-2656.13106>
- Hebblewhite, M., Merrill, E., & McDermid, G. (2008). A Multi-Scale Test of the Forage Maturation Hypothesis in a Partially Migratory Ungulate Population. *Ecological Monographs*, *78*(2), 141–166. <https://doi.org/10.1890/06-1708.1>
- Jakopak, R. P., Sawyer, H., LaSharr, T. N., Randall, J., Dwinnell, S. P. H., Fralick, G. L., & Monteith, K. L. (2022). Diel timing of migration is not plastic in a migratory ungulate. *Animal Behaviour*, *192*, 51–62. <https://doi.org/10.1016/j.anbehav.2022.07.008>
- Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., Monteith, K. L., & Kauffman, Matthew. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, *361*(6406), 1023–1025. <https://doi.org/10.1126/science.aat0985>
- Joly, K., Gurarie, E., Hansen, D. A., & Cameron, M. D. (2021). Seasonal patterns of spatial fidelity and temporal consistency in the distribution and movements of a migratory ungulate. *Ecology and Evolution*, *11*(12), 8183–8200. <https://doi.org/10.1002/ece3.7650>
- Kauffman, M. J., Aikens, E. O., Esmacili, S., Kaczensky, P., Middleton, A., Monteith, K. L., Morrison, T. A., Mueller, T., Sawyer, H., & Goheen, J. R. (2021). Causes, Consequences, and Conservation of Ungulate Migration. *Annual Review of Ecology, Evolution, and Systematics*, *52*(Volume 52, 2021), 453–478. <https://doi.org/10.1146/annurev-ecolsys-012021-011516>
- Kauffman, M. J., Copeland, H., Cole, E., Cuzzocreo, M., Dewey, S., Fattebert, J., Gagnon, J., Gelzer, E., Graves, T. A., Hersey, K., Kaiser, R., Meacham, J., Merkle, J., Middleton,

- A., Nunez, T., Oates, B., Olson, D., Olson, L., Hall Sawyer, ... Thonhoff, M. (2020). *Ungulate Migrations of the Western United States, Volume 1* [Dataset]. U.S. Geological Survey. <https://doi.org/10.5066/P9O2YM6I>
- Kayes, I., & Mallik, A. (2020). Boreal Forests: Distributions, Biodiversity, and Management. I W. Leal Filho, A. M. Azul, L. Brandli, A. Lange Salvia, & T. Wall (Red.), *Life on Land* (s. 1–12). Springer International Publishing. https://doi.org/10.1007/978-3-319-71065-5_17-1
- Ketzler, G., Römer, W., & Beylich, A. A. (2021). The Climate of Norway. I A. A. Beylich (Red.), *Landscapes and Landforms of Norway* (s. 7–29). Springer International Publishing. https://doi.org/10.1007/978-3-030-52563-7_2
- Kloskowski, J. (2021). Win-stay/lose-switch, prospecting-based settlement strategy may not be adaptive under rapid environmental change. *Scientific Reports*, *11*(1), 570. <https://doi.org/10.1038/s41598-020-79942-3>
- Krochmal, A. R., Roth, T. C., & Simmons, N. T. (2021). My way is the highway: The role of plasticity in learning complex migration routes. *Animal Behaviour*, *174*, 161–167. <https://doi.org/10.1016/j.anbehav.2021.02.005>
- Langvatn, R., & Loison, A. (1999). Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildlife Biology*, *5*(4), 213–223. <https://doi.org/10.2981/wlb.1999.026>
- Lojander, P. (2013, april 15). *Site fidelity of a migratory species towards its annual range* [Second cycle, A2E]. SLU, Dept. of Wildlife, Fish and Environmental Studies. <https://stud.epsilon.slu.se/5422/>
- Meisingset, E. (2008). *Alt om Hjort*. Tun Forlag.
- Meisingset, E. L., & Omholt, S. W. (2022). *Bestandsestimering av hjort ved bruk av jegerrapporterte data*.

- Merkle, J., Sawyer, H., Monteith, K., Dwinell, S., Fralick, G., & Kauffman, M. (2019). Spatial memory shapes migration and its benefits: Evidence from a large herbivore. *Ecology Letters*, 22. <https://doi.org/10.1111/ele.13362>
- Moen, A. (1998). *Vegetasjon*. Norges geografiske oppmåling. <https://www.nb.no/items/6cb6ce7881b7e83fd165251271ecec03?page=5>
- Morrison, T. A., & Bolger, D. T. (2012). Wet season range fidelity in a tropical migratory ungulate. *Journal of Animal Ecology*, 81(3), 543–552. <https://doi.org/10.1111/j.1365-2656.2011.01941.x>
- Morrison, T. A., Merkle, J. A., Hopcraft, J. G. C., Aikens, E. O., Beck, J. L., Boone, R. B., Courtemanch, A. B., Dwinell, S. P., Fairbanks, W. S., Griffith, B., Middleton, A. D., Monteith, K. L., Oates, B., Riotte-Lambert, L., Sawyer, H., Smith, K. T., Stabach, J. A., Taylor, K. L., & Kauffman, M. J. (2021). Drivers of site fidelity in ungulates. *Journal of Animal Ecology*, 90(4), 955–966. <https://doi.org/10.1111/1365-2656.13425>
- Murtaugh, P. A. (2009). Performance of several variable-selection methods applied to real ecological data. *Ecology Letters*, 12(10), 1061–1068. <https://doi.org/10.1111/j.1461-0248.2009.01361.x>
- Mysterud, A. (2011). Selective harvesting of large mammals: How often does it result in directional selection? *Journal of Applied Ecology*, 48(4), 827–834. <https://doi.org/10.1111/j.1365-2664.2011.02006.x>
- Mysterud, A., Bischof, R., Loe, L. E., Odden, J., & Linnell, J. D. C. (2012). Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates. *Ecosphere*, 3(10), art92. <https://doi.org/10.1890/ES12-00177.1>
- Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., & Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes – a role for

- density dependence? *Oikos*, *120*(12), 1817–1825. <https://doi.org/10.1111/j.1600-0706.2011.19439.x>
- Mysterud, A., Meisingset, E., Langvatn, R., Yoccoz, N. G., Stenseth, N. Chr., & Benton, T. (2005). Climate-Dependent Allocation of Resources to Secondary Sexual Traits in Red Deer. *Oikos*, *111*(2), 245–252.
- Møller, A. P., Fiedler, W., & Berthold, P. (2010). *Effects of Climate Change on Birds*. OUP Oxford.
- Naidoo, R., Chase, M. J., Beytell, P., Preez, P. D., Landen, K., Stuart-Hill, G., & Taylor, R. (2016). A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. *Oryx*, *50*(1), 138–146. <https://doi.org/10.1017/S0030605314000222>
- Piper, W. H. (2011). Making habitat selection more “familiar”: A review. *Behavioral Ecology and Sociobiology*, *65*(7), 1329–1351. <https://doi.org/10.1007/s00265-011-1195-1>
- Sawyer, H., & Kauffman, M. J. (2011). Stopover ecology of a migratory ungulate. *Journal of Animal Ecology*, *80*(5), 1078–1087. <https://doi.org/10.1111/j.1365-2656.2011.01845.x>
- Sawyer, H., Kauffman, M. J., Nielson, R. M., & Horne, J. S. (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, *19*(8), 2016–2025. <https://doi.org/10.1890/08-2034.1>
- Sente, C., Meisingset, E. L., Evans, A. L., Wedul, S. J., Zimmermann, B., & Arnemo, J. M. (2014). Reversible Immobilization of Free-ranging Red Deer (*Cervus elaphus*) with Xylazine-Tiletamine-Zolazepam and Atipamezole. *Journal of Wildlife Diseases*, *50*(2), 359–363. <https://doi.org/10.7589/2012-10-267>
- Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, *30*(6), 991–1007. <https://doi.org/10.1007/s10682-016-9860-5>

- Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, 22(7), 2007–2020. <https://doi.org/10.1890/12-0245.1>
- SSB. (u.å.). *Arealbruk og arealressurser*. SSB. Hentet 31. oktober 2024, fra <https://www.ssb.no/natur-og-miljo/areal/statistikk/arealbruk-og-arealressurser>
- Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & 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. <https://doi.org/10.1098/rstb.2010.0090>
- Van Moorter, B., Rolandsen, C. M., Basille, M., & Gaillard, J.-M. (2016). Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology*, 85(1), 21–31. <https://doi.org/10.1111/1365-2656.12394>
- Viste, R. H., & Birkemo, G. Al. (2023, desember 12). *Geografisk fordeling av sivile ressurser for forsvaret av Norge*. Norsk. <https://www.ffi.no/publikasjoner/arkiv/geografisk-fordeling-av-sivile-ressurser-for-forsvaret-av-norge>
- Wolf, J. B. W., & Trillmich, F. (2007). Beyond habitat requirements: Individual fine-scale site fidelity in a colony of the Galapagos sea lion (*Zalophus wollebaeki*) creates conditions for social structuring. *Oecologia*, 152(3), 553–567. <https://doi.org/10.1007/s00442-007-0665-7>