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Individual Variation in Site Fidelity of Moose

Master's thesis in Natural Resource Management

Supervisor: Ivar Herfindal

Co-supervisor: Erling Johan Solberg, Christer M. Rolandsen, and Irja Ida Ratikainen

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Acknowledgement

First and foremost, I would like to express my sincere appreciation to my main supervisor Ivar Herfindal and co-supervisors Christer M. Rolandsen, Erling Johan Solberg, and Irja Ids Ratikainen for their guidance, unending encouragement, brilliant recommendations, and insightful feedback. They gave me the freedom to explore on my own and present my ideas. They always had time for me from the moment I began writing my research proposal to the time of final report submission despite having a hectic schedule which makes their contribution even more applause-worthy. Dear Supervisors, I will never forget the lessons I learned from you all throughout this period and I thank you all from the bottom of my heart. Without all your insightful suggestions, encouragement, and cooperation, I could not have envisioned presenting this work.

I would also like to acknowledge Norwegian Institute for Nature Research (NINA) for providing me with GPS data of moose from the moose project and to all those who are directly and indirectly involved in this project.

I must not forget to say thank you to the Faculty of Natural Science and Department of Biology, NTNU for providing me with this wonderful opportunity to carry out this research and pursuing a master's degree which was helpful to enhance my research capacity knowledge and skill. It gives me an immense and immeasurable amount of joy to have completed my research and to present my findings. Lastly, my deepest gratitude goes to my mother Mrs. Laxmi Dahal, my father Mr. Bishnu Prasad Dahal, and my brother Mr. Pujan Dahal whose love and affection have always encouraged and inspired me to perform every task well. I love you all.

Abstract

1. Site fidelity, the tendency of animals to return to the same areas within or among the years can contribute to maximizing individual fitness by improving survival and reproduction. Seasonal and temporal variation of site fidelity is known, but studies regarding individual variation are rare. Knowledge about the extent of, and variation in, site fidelity is important for effective management of the moose population. For instance, knowing females with calves using the same area year after year can aid in conserving the targeted individuals and the calving site they use.
2. Here, I investigated the individual variation in site fidelity of the moose (*Alces alces* L.) in a multi-use landscape in Trøndelag, central Norway. I looked at how within and among-year site fidelity is influenced by an individual's age, sex, reproductive status, and migratory tactics. For this, I calculated the level of site fidelity within seasons across years and among seasons within years of 82 individual GPS-marked moose from 2017 to 2021.
3. Site fidelity, measured both as the distance between seasonal ranges or range overlap, could be explained by individual characteristics, as well as season (between-year site fidelity only). The results of my study suggest that older aged moose exhibited higher site fidelity than younger ones. However, after accounting for age, there was no effect of sex. Also, migratory status (resident or long-distance migratory) did not affect the between-year site fidelity. Females with calves in two consecutive years had stronger site fidelity than females with calves in only one year, but this depended on age. This suggested older females with calves were more faithful than younger females without calves.
4. Synthesis and applications: The importance of age for site fidelity of moose suggests that the population age structure can be a crucial factor for the extent of site fidelity and thus the extent of optimal utilization of the landscape and its resources. Knowing this can help wildlife managers in the identification of important sites that certain age group use and provide guidance for future land use management. However, there is a need to evaluate how variations in environmental conditions including anthropogenic factors, affect the site fidelity of moose.

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1. Introduction

1.1 Animal Movement

Animal movement patterns is crucial to understand as it helps to access knowledge about population dynamics including population size, connectivity, and demographic processes, contributing to efficient population management and conservation strategies (Cagnacci et al., 2010). Therefore, biologists and ecologists are increasingly interested in learning about the causes and impacts of animal movement. By studying animal movement researchers have gained knowledge about animal behaviours such as habitat selection (Herfindal et al., 2009), migration (Bunnefeld et al., 2011), feeding (Pyke, 1983) , and mating (Friedrich et al., 2015). Thus, this knowledge contributes on identification and management of essential habitats by offering insights into resource usage and habitat requirements (Nathan et al., 2008). In addition, getting knowledge about the patterns of moose movement can help in the mitigation of human-wildlife conflicts for instance, wildlife managers can learn about the potential migratory routes by tracking animal over time and thus, take appropriate strategies in reducing moose vehicle collisions.

Animal movement is defined as a change in an individual's physical position over time and has a significant impact on individuals' life, and the dynamics of populations and communities (Nathan et al., 2008). For instance, animals that migrate can maximize their fitness through access to good quality forage (Albon & Langvatn, 1992), reducing predation risk (Fryxell et al., 1988), and avoiding harsh environmental conditions such as snow depth (Ball et al., 2001; Mysterud et al., 2011).

Animal movement varies over temporal and spatial scales (Nathan et al., 2008; Schneider, 2001). The scale of animal movement depends on the magnitude of change in environmental conditions and resource availability (van Moorter et al., 2013). Both small-scale and large-scale movements are important in an individual's life for instance to find nutritional forage, to find a mating partner, to reduce predation risk, for exchange of genes and individuals among populations, inbreeding avoidance, and reproductive success (Clobert et al., 2012; Milner-Gulland et al., 2011; Pyke, 1983). Animal movement differs across populations and between individuals (Bunnefeld et al., 2011). Thus, understanding these factors is important for wildlife management. In particular,

effective management of animal populations undergoing large-scale movement is required, with a particular emphasis on managing at the spatial scales. However, researchers and wildlife managers are now working to preserve and maintain biodiversity at spatial scales, concentrating on various strategic management strategies cooperating at both the global level and local level (Linnell, 2005; LINNELL et al., 2001).

Site fidelity refers to the probability of an animal coming back or reusing the particular area where they have lived before (Switzer, 1993). The particular area to which the animal is committed might be a broad breeding range (Puehringer-Sturmayr et al., 2023), calving site (Tremblay et al., 2007), a certain nesting site (Greenwood, 1980) or a mating site (Friedrich et al., 2015), and the common pattern is the usage of the seasonal range between years (Lojander, 2013; Switzer, 1993). Small seasonal ranges indicate high fidelity during the season, however the probability that an animal would return to the same seasonal ranges year after year indicates high fidelity across years (Wittmer et al., 2006).

Thus, both within-year and between-annual site fidelity are common, which may be explained by factors such as predictability in resource availability (Switzer, 1993), environment change and familiarization with previous environment (Morrison et al., 2021; Piper, 2011), previous reproductive success (Switzer, 1997; Welch et al., 2000), and food or forage availability (Garfelt-Paulsen et al., 2021). This has important fitness consequences (Forrester et al., 2015), for instance by improving survival and reproduction by understanding of where to get food and cover (Schieck & Hannon, 1989), and reducing predation risk (Gehr et al., 2020; Tremblay et al., 2007) which can lead to population persistence (Schmidt, 2004). For example, paired population (couples) of Piping plover (*Charadrius melodus*) showed higher fidelity towards its mating site compared to divorced ones (Friedrich et al., 2015), and the great crested newt (*Triturus cristatus*) showed higher site fidelity towards its breeding sites (Denoël et al., 2018). The green turtles and loggerhead turtles also returned to its previous feeding sites and wintering sites using same migratory routes (Broderick et al., 2007) and many ungulates like moose, reindeer and wild caribou showed fidelity towards its calving sites, seasonal home ranges, and migratory pathways (Garfelt-Paulsen et al., 2021; McLaren & Patterson, 2021; Ofstad, 2013; Welch et al., 2000; Wittmer et al.,

2006). However, sometimes showing high site fidelity can make an individual ignore the spatio-temporal variation in habitat qualities and preventing them from exploring new and favourable areas. For example, southern right whales (*Eubalaena australis*) used only nearest feeding grounds which cost them with higher than necessary reproductive failures (Valenzuela et al., 2009).

Animal movement is also significantly influenced by variations in the environment (Milner-Gulland et al., 2011). As a result, demonstrating site fidelity may not necessarily be caused by favouritism or the selection of the same suitable location, but rather may result from many environmental factors that cause migration into the same places at the same time in successive years (Ofstad, 2013).

1.2 Moose and it's Site Fidelity

The moose (*Alces alces* L.) is the biggest member of the deer family, and is found in boreal forests in most of Scandinavia, Finland, Baltic states, Russia and North America and they have high capacity to walk through deep snow and thrive in extremely cold climates (Lavsund et al., 2003; Timmermann & McNicol, 1988). Throughout their home ranges, moose choose different habitats at different times of the year depending on food availability (Bjørneraas et al., 2011; Nikula et al., 2004; E. G. Ofstad et al., 2019). They prefer habitats with conifers, broad-leaved trees, and deciduous shrubs (Bjørneraas et al., 2011; Timmermann & McNicol, 1988).

Moose uses a variety of mobility modes, ranging from sedentary to migratory, dispersing to nomadic, and may switch between them to adapt to regional conditions (Rolandsen et al., 2017; Singh et al., 2012). Thus, moose has been found showing site fidelity towards its seasonal home ranges i.e., summer and winter home range (Ofstad, 2013; Sweanor & Sandegren, 1988), its annual range (Lojander, 2013) and its calving site (Tremblay et al., 2007).

Moose is culturally, economically, and aesthetically valuable wildlife species, particularly in Fennoscandian countries (Norway, Sweden, Finland) and it is very good source of meat for hunters and income for landowners (Storaas et al., 2001). However, the recent growth in moose populations has made management of the moose population difficult, particularly in Fennoscandia. Main challenges include forest damage and moose vehicle collision (Lavsund et al., 2003).

Because moose harvesting is such an important source of income for landowners, moose migration may lead to conflicts of interests. During the hunting season, moose are mainly located in their summer ranges, whereas most of the damage is done in their winter ranges. Therefore, some landowners may take most of the profit from hunting, whereas others incur losses due to destroyed forest plantations (Storaas et al., 2001). In addition, the number of road accidents are higher in areas where moose population density is high during winter (Rolandsen et al., 2011). Due to these conflicts and socioeconomic consequences, management of moose at spatial scales has gained more attention (Skonhøft, 2005).

In this study I examine the extent of site fidelity within season across years, and among seasons within years, in moose in central Norway, and explore what individual factors that affect these movement characteristics. This will provide us with a better understanding of the spatial and temporal scales of moose space use and its movement in a population.

1.3 Objectives

The optimal movement of animals is known to vary among individuals according to factors affecting the benefits of specific behaviours (Nathan et al., 2008). Important factors may be age, sex, reproductive status, and migratory tactics (i.e., resident, or migratory). My project therefore has the given objective, and predictions:

- To evaluate the level of site fidelity in moose, and explore how it varies according to sex, age, reproductive status, and migratory tactics?

1.4 Predictions

P1 For age: Movement, experience, and memory are interconnected processes that help animals to learn about the locations of feed, protective cover, breeding and offspring-rearing, and predators (Fryxell et al., 2008; Merkle et al., 2022; Piper, 2011; van Beest et al., 2013). These memories, learnings and experiences can be either transferred by learning from the mother to their child as a natal philopatry (Bose et al., 2017; Colson et al., 2016) or by individuals acquiring experiences as they age. The moose are long-lived species living in a highly variable environment and would benefit a lot by learning from experiences. As they gain experience with age, they get more familiar with the

resources in their home range. Hence, I predict that moose will show higher site fidelity with increasing age.

P2 For sex: Generally, male moose occupy larger territories than female, which is understandable given that males are larger and require more food (Bjørneraas et al., 2011; Harestad & Bunnell, 1979; Herfindal et al., 2009). In addition, male movement may be less restricted than females (with calves) by deep snow, and females with calves are bound by high predation risk (for their offspring) (Bjørneraas et al., 2012). I therefore predict that males will show less site fidelity than females simply because they are less restricted by environmental conditions and predation risk in their choice of habitats.

P3 For reproductive status (females only): Returning to the same seasonal ranges and restricting their movements to a certain calving location is common in ungulates (Bjørneraas et al., 2012; Testa et al., 2000; Welch et al., 2000). This is also found to be directly linked with the mortality risk of their calves. Female moose that lost her calf were less faithful to their calving site than females with surviving calves (Testa et al., 2000). Thus, I predicted that female moose that reproduce in two consecutive years will be more likely to return to the previous calving site than females that fails to reproduce in the first year (Switzer, 1997; Welch et al., 2000).

P4 For migratory tactic: Migratory animals move over long distances and are found to track the spatial distribution of favourable environmental conditions over larger areas (van Moorter et al., 2013). However, as the spatial distribution of optimal environmental conditions may vary between years, e.g., because of random variation in weather, migratory animals should be less faithful to a specific site than to specific conditions. Based on this, I predict that migratory individuals show lower among-year site fidelity compared to resident moose.

2. Methods and Material

2.1 Study Area

The study area, where moose was captured and marked with GPS collars, comprises the municipalities of Trondheim, Malvik, Selbu, Tydal, Stjørdal and Meråker in central Norway. Some of these moose later also migrate to, or use areas, in the neighboring municipalities Midtre-Gauldal, Holtålen and Røros, in addition to parts of Sweden. The area ranges from the coast to alpine zones and is mainly covered with forests and some farmland closer to the Trondheim fjord and in the inland valleys (Moen, 1999). The forests consists mainly of Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, and downy birch *Betula pubescens*, while farmland is used for grass production in the valleys and cereals closer to the coast. Also bogs and barren land with few or no trees, are covering part of the study area (Moen, 1999). In the study area there are also several human settlements, towns, and the city of Trondheim (c. 200,000 inhabitants), which are connected with highways, roads and railways.

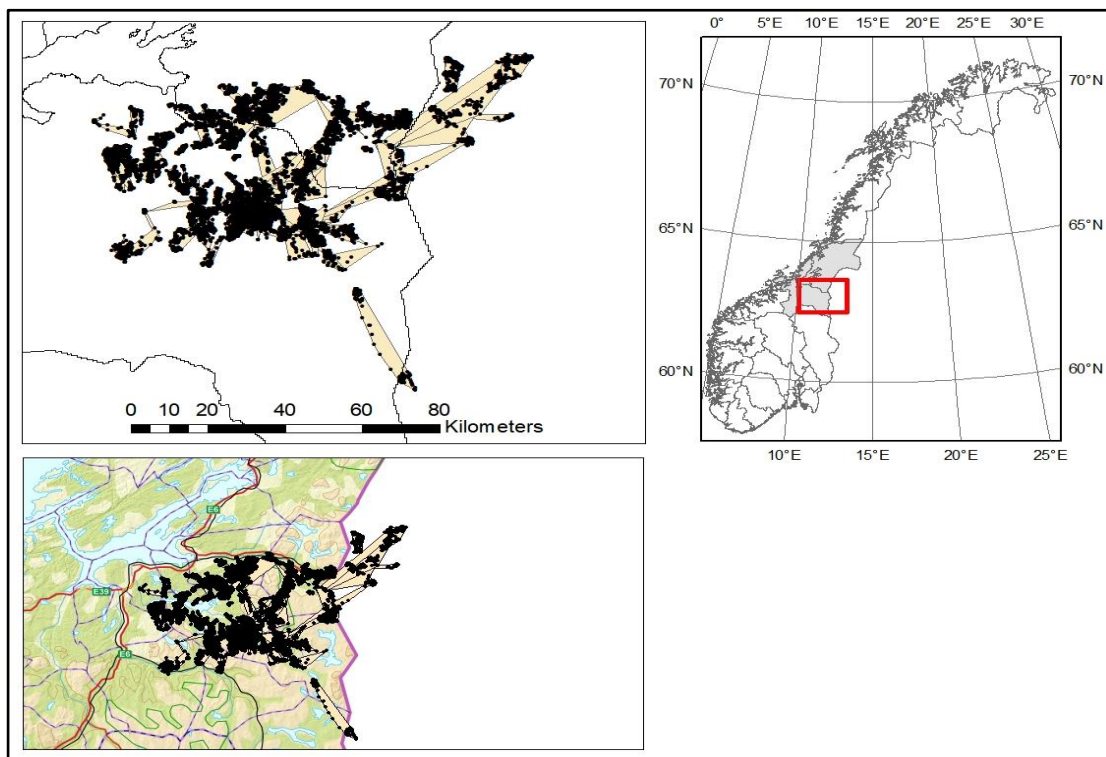


Figure 1: Map of the study area which includes part of Trøndelag County. The black solid circles denote summer and winter positions of 82 individual moose. The polygons indicate summer and winter home ranges.

2.2 Moose Data

Moose data were collected as part of a project investigating moose habitat use and movement (Rolandsen et al., unpublished data, www.dyreposisjon.no) based on the use of GPS collars. The data were collected from 82 (41 in 2017, 20 in 2018, 15 in 2020 and 6 in 2021) individual moose that was captured and marked between 2017 and 2021. GPS-collars were typically set to obtain a fix once every 13 hours. Although such an interval is somewhat low for fine-scale movement analyses, it was sufficient for describing movement patterns over long temporal scales, such as between seasons.

For all individual moose, I had information about sex, and age at first capture. For those marked in 2017 data was available from almost 5 years for individuals still alive in 2021. Some were marked as calves or yearlings ($n = 21$), which means that their age was known. Individuals that were marked as adults have unknown age, unless they are harvested or found dead later, in which age is determined based on counting the cementum annuli from incisors ($n = 14$, (Rolandsen et al., 2008; Veiberg et al., 2020). In case of unknown age, it is still possible to assess age effects by using the age relative to the first capture.

The reproductive status was estimated from observing GPS collared females. The females were approached on foot aided by the VHF-beacon, and then visually observing the number of calves seen with each female during the calving season from mid-may until late June. For a subsample, the procedure was repeated in late August and September before the start of the autumn hunting season (25 September – 31 October). In addition, we obtained information about reproductive status from hunters when the marked females and their calves were shot, or observed during hunting, or when observed and reported by field personnel or the public during winter and spring in the subsequent year. Females were considered as having no calves if number of calves was 0, while if it was > 0 they were classified as having calves on the date of observation.

Migratory tactic for adult individuals was provided by NINA. This was based on volume of intersection with the function `kerneloverlap` between seasonal utilisation distributions (Calenge, 2006). Individuals were considered as migratory if $\text{overlap} = 0$, while if it was >0 they are classified as resident.

After accessing the datasets for migratory tactics and reproductive status, it was merged with datasets including age and sex for further analysis.

2.3 Estimating Site Fidelity

I evaluated individual site fidelity among years within the same season (summer or winter), and between seasons within a year. I used locations from March to define the winter season, and July to define the summer season. Restricting to these periods ensures that the seasonal ranges are not affected by spring and autumn migration, which varies much with respect to the onset and end of migration periods among years and individuals (Rolandsen et al., 2010).

For each season I calculated seasonal home ranges by using minimum convex polygon (MCP). Next, site fidelity was calculated as 1) overlap between seasonal ranges within and among years, and 2) the Euclidean distance between winter and summer observations (centroid for each season) as seasonal site fidelity, or between observations from the same season but in two consecutive years (annual site fidelity). Fidelity measured as overlap was calculated as the proportion of the winter area that was included in the summer area (within-year fidelity) or the proportion of a seasonal range in year t that was included in the seasonal range in year $t+1$. Individuals are thought to exhibit stronger site fidelity when they have high seasonal range overlap and low Euclidean distance both within and between years, and vice versa for lower site fidelity. All estimated datasets for distance and overlaps were merged with accessed datasets of moose (age, migratory tactics, reproductive status, and season data) for statistical analysis. All analyses were done at the individual level.

2.4 Statistical Analyses

To investigate whether age, sex, migratory status, and reproductive status (females only) affected the site fidelity of moose, I fitted linear mixed effect models using the lmer function from lme4 package (Bates et al., 2015) with moose individuals as random factor to account for the fact that I had multiple estimates of site fidelity for a high proportion of the individuals. The response variable for annual site fidelity were Euclidean distance between years and overlaps once at a time. In addition, distance between summer and winter within same year and its overlap were used as response

variable for seasonal site fidelity. The estimated site fidelity measurements initially displayed skewed residual distribution. Thus, in order to normalize the residuals, I log transformed the site fidelity measurements.

To examine variation in site fidelity of moose, I applied similar modelling techniques for both annual and seasonal site fidelity. For all the models of annual and seasonal site fidelity, age, season, sex, and migratory tactics was included as fixed explanatory variables. I also included the two-way interaction between age and sex to examine if age-effects on site fidelity differed between males and females. The interaction between sex and migratory tactic was included to examine if female migratory moose had the same fidelity patterns compared to resident females, as was found in males. Finally, the interaction between age and migratory tactic was included to test whether higher experience, indicated by increasing age, affected the site fidelity more in migratory moose that has higher opportunities for spatial adjustment of their ranges, compared to resident moose.

I used only females in order to assess the effect of reproductive status on between-year site fidelity only. These models incorporated reproductive status (calves in both years or calves in only one year), age, and season as explanatory variables. I included the two-way interaction between age and reproductive status to examine if any effect of reproductive status was different between changed with age, and the interaction between season and reproductive status to see whether there were seasonal differences in how migratory status affected site fidelity.

The data included individuals with age 0, meaning that they were calves that followed the mother at least during the winter range the first year with data, and possibly also during the summer the first year. These individuals were excluded from all models because their behaviour was assumed to follow the behaviour of their mother.

In order to rank potential candidate models and choose the best model, I used information theoretic approach which helps to select best model by ranking them according to their AICc values (Akaike's information criterion to account for small sample sizes)(Burnham & Anderson, 2002). In characterizing the actual data, two models were considered to be equivalent if their Δ AICc values was less than 2. Thus, I selected the models which had lowest AICc values because it was considered as the best model to explain the variation of predictor variable on response variable. Model

ranking was done with the package ‘MuMIn’ (Bartoń, 2023). All the statistical analyses were performed in R version 4.2.0. (R Core Team, 2022) and the lme4 package version 1.1.29 (Bates et al., 2015). The values for parameter estimates of all models was calculated using Restricted Maximum Likelihood (REML) (Zuur et al., 2009). All the estimates from the models are presented as mean \pm 1 standard error of the estimates.

3. Results

The average distance between annual ranges (i.e., Euclidean distance from same observation in two different years) among all individuals was 5.57 kilometers (km) (SD=8.63). The mean distance between annual ranges for migratory moose was 2.89 km (SD=3.23), while resident had 6.58 km (SD=9.78). Likewise, females had 4.78 km (SD=8.13) and males had 7.37 km (SD=9.62) of average distance between annual ranges. In addition, female with calves had 2.98 km (SD=5.61), while female without calves had 6.83 km (SD=10.61) of average distance between annual ranges.

The mean distance between seasonal ranges (within year) among all individuals was 7.59 km (SD=9.3). The mean seasonal distance for females was 7.24 km (SD=7.5), while males was 8.33 km (SD=12.41). Migratory moose travelled 17.16 km (SD=12.33) from summer to winter ranges and resident moose travelled 3.59 km (SD=2.54) on average. However, not all factors had affected the level of site fidelity.

3.1 Variation in Between Year Site Fidelity

The best model for both between year distance and between year overlap included age and season as the factor that effects the annual site fidelity of moose with AICc= 157.02 and AICc= 25.49 respectively (Table 1), whereas both models including migratory tactics got low support with Δ AICc=2.16 and Δ AICc=1.68 respectively (Table 1). In addition, models including sex had low support on both the distance model (Δ AICc>2.00) and the overlap model (Δ AICc=1.79 (Table 1). The highest ranked models suggested that older aged moose of both sexes had shorter between year distance and high between year overlap (Tables 2 and 3, Figure 2). This summarizes that older moose have higher site fidelity which supports my first prediction P1 that older moose gains more experience and becomes more consistent in how and where they move. Moreover, site fidelity was higher in summer compared to winter (Tables 2 and 3, Figure 2). However, the model did not suggest differences in annual site fidelity between females and males.

Table 1: The top five models with the highest AICc rankings account for individual variation in site fidelity. Age, sex, season, and migratory tactics were included as explanatory factors. “*” between factors denotes an interaction. A is the table having AICc values of between year distance, while B has values of between year overlap models.

	Rank	Model	AICc	Δ AICc	AIC-weight
A.	1	Age +Season	157.024	0.000	0.136
	2	Age+ Season + Age * Season	157.403	0.379	0.113
	3	Age	158.168	1.144	0.077
	4	Season	158.687	1.662	0.059
	5	Age + Migratory tactics + Season	159.192	2.168	0.046
B.	1	Age + Season	25.494	0.000	0.139
	2	Season	26.044	0.550	0.106
	3	Age +Migratory tactics +Season	27.180	1.685	0.060
	4	Age +Season +Age*Season	27.267	1.773	0.057
	5	Age + season + Sex	27.286	1.791	0.057

Table 2: Parameter estimates for the best model analysing effect in between year site fidelity (Model including Euclidean distance between year as response variable).

Dependent variable			
Predictors	Estimates	Standard Error	Confidence Interval
(Intercept)	8.37	0.56	7.24 – 9.49
Age + 1 [log]	-0.57	0.25	-1.08 – -0.07
Season [Winter]	0.49	0.25	-0.01 – 0.99

Table 3: Parameter estimates for the best model analysing effect in between year site fidelity (Model including overlap between year as response variable).

Dependent variable			
Predictors	Estimates	Standard Error	Confidence Interval
(Intercept)	0.24	0.15	-0.06 – 0.55
Age + 1 [log]	0.11	0.07	-0.02 – 0.25
Season [Winter]	-0.29	0.08	-0.45 – -0.13

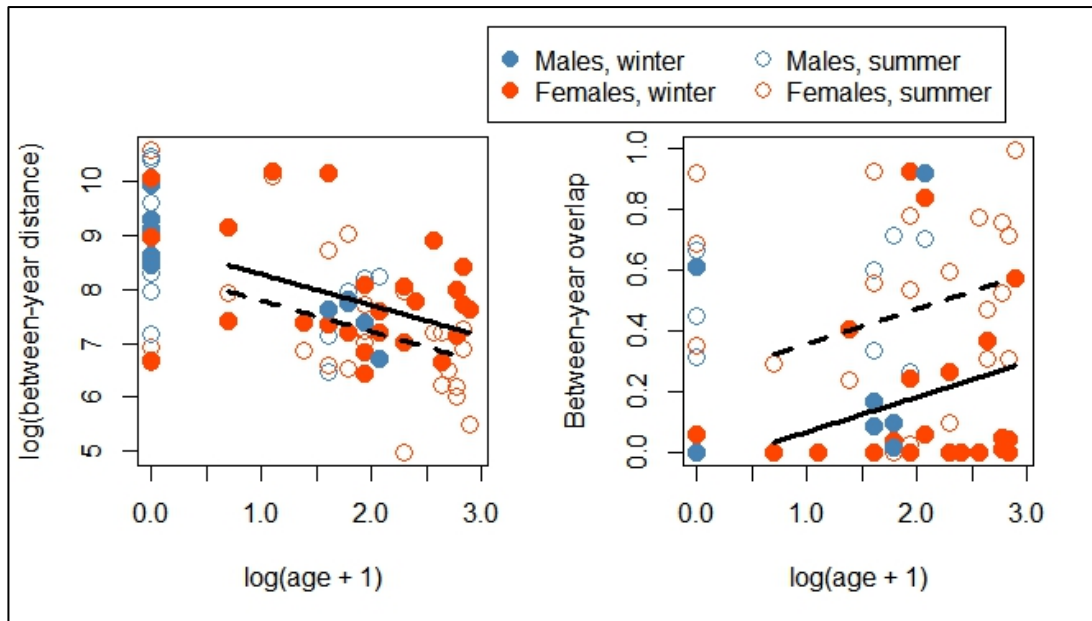


Figure 2: Variation in annual site fidelity. Solid (winter) and dashed lines (summer) indicate the age effect on both measures of annual site fidelity. Decreasing trend of both lines or the lower values on y-axis of left figure shows stronger site fidelity with increasing age. Note: The 0-year age is excluded from the model.

3.2 Variation in Within Year (Summer and Winter) Site Fidelity

The highest ranked model for within year distance from summer ranges to winter ranges included both age and migratory tactics with $AICc = 124.9$, whereas overlap model included only migratory tactics with $AICc = 41.43$ (Table 4). No other models for overlap had $\Delta AICc < 2$, while distance model including Age, migratory tactics and their interaction (Age * Migratory tactics) got weak support with $\Delta AICc = 1.729$ (Table 4). The parameter estimates from highest ranked distance model shows that resident moose had low migration distance (8.57 ± 0.24) (Table 5), which is as expected given the definition of migratory and resident moose based on their between-season movement pattern. In addition, after accounting for age, both migratory and resident moose had same level of faithfulness towards summer to winter home ranges. It is clear that, with the increase in age there is decrease in seasonal distance of both migratory and resident moose (Figure 3).

Table 4: The top five models with the highest AICc rankings account for individual variation in site fidelity. Age, sex, season, and migratory tactics were included as explanatory factors. “*” between factors denotes an interaction. A is the table having AICc values of within year distance, while B has values of within year overlap models.

	Rank	Model	AICc	Δ AICc	AIC-weight
A.	1	Age +Migratory tactics	124.855	0.000	0.403
	2	Age+ Migratory tactics + Age * Migratory tactics	126.584	1.729	0.170
	3	Age +Migratory tactics +Sex	127.199	2.343	0.125
	4	Migratory tactics	128.294	3.439	0.072
	5	Migratory tactics + Season	128.618	3.763	0.061
B.	1	Migratory tactics	41.437	0.000	0.480
	2	Age +Migratory tactics	43.789	2.351	0.148
	3	Age +Migratory tactics +Sex	43.892	2.454	0.141
	4	Age +Migratory tactics+ Age *Migratory tactics	46.325	4.887	0.042
	5	Age +Migratory tactics +Sex	46.379	4.941	0.041

Table 5: Parameter estimates for the best model analysing effect on within year site fidelity (Model including distance between seasons within year as response variable).

Dependent variable			
Predictors	Estimates	Standard Error	Confidence Interval
(Intercept)	10.21	0.34	9.53 – 10.89
Age + 1 [log]	-0.36	0.15	-0.67 – -0.06
Migratory tactics [Resident]	-1.64	0.24	-2.13 – -1.15

Table 6: Parameter estimates for the best model analysing effect on within year site fidelity (Model including overlap between seasons within year as response variable).

Dependent variable			
Predictors	Estimates	Standard Error	Confidence Interval
(Intercept)	0.00	0.09	-0.18 – 0.18
Migratory tactics [Resident]	0.34	0.11	0.13 – 0.55

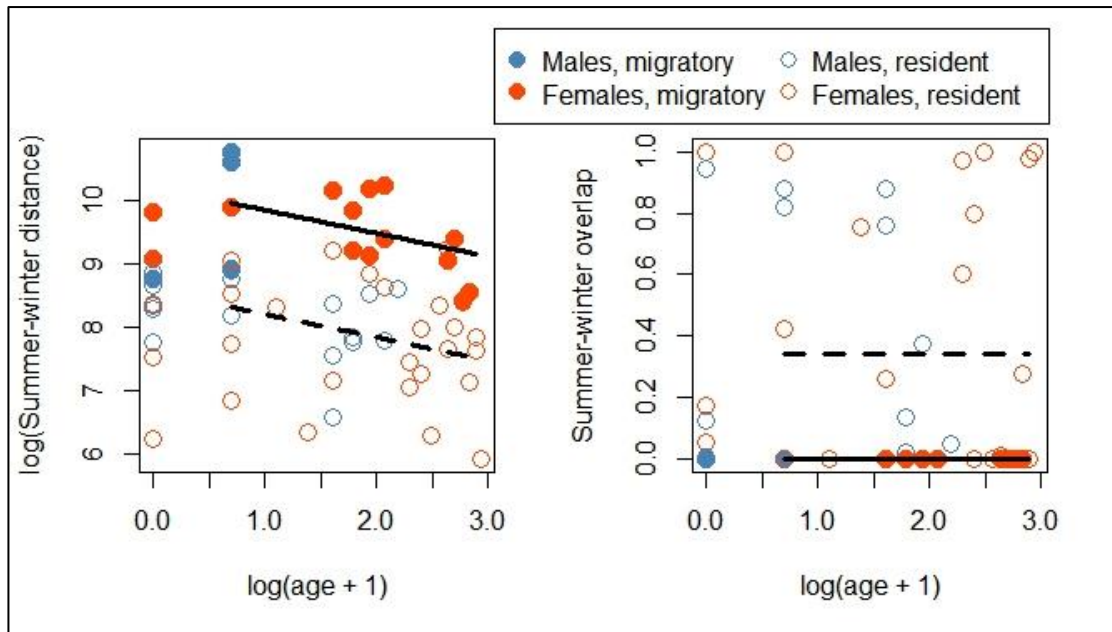


Figure 3: The relationship between within-year site fidelity and age for migratory and resident moose. Solid (migratory) and dashed (resident) lines show the predicted relationships based on models described in Tables 5 and 6. Note: The 0-year age is excluded from the model, so the solid and dashed line doesn't touch the 0 points.

3.3 Variation with Reproductive Status

The highest ranked model for the effect of reproductive status on between year site fidelity measured as distance between ranges included Age, reproductive status, and its interaction Age * Reproductive status ($AICc = 86.31$), while the highest ranked overlap model included only season with $AICc = 24.45$ (Table 7). For the distance-model, several candidate models received some support with $\Delta AICc < 2$ (Table 7), whereas for the overlap model, only the Null model (no fixed effects) received some support ($\Delta AICc = 0.81$).

The parameter estimates from highest ranked distance model suggested that older individuals had higher site fidelity (shorter distances), but only for females with calf in only one year (Table 8, Figure 4). Regarding overlap, fidelity was higher in summer than in winter, regardless of age or reproductive status (Table 9, Figure 4).

Table 7: The top five models with the highest AICc rankings account effect of reproductive status on site fidelity of moose. Age, season, and reproductive status were included as explanatory factors. “*” between factors denotes an interaction. A is the table having AICc values of between year distance, while B has values of between year overlap models.

	Rank	Model	AICc	Δ AICc	AIC-weight
A.	1	Age + Reproductive status+ Age * Reproductive status	86.311	0.000	0.182
	2	Age+ Season +Reproductive status+ Age * Reproductive status	86.579	0.268	0.159
	3	Age	86.667	0.355	0.152
	4	Age +Season	87.354	1.043	0.108
	5	Age + Reproductive status	88.026	1.714	0.077
B.	1	Season	24.457	0.000	0.331
	2	Null model	25.270	0.812	0.220
	3	Age +Season	26.585	2.127	0.114
	4	Age	27.249	2.791	0.082
	5	Season + Reproductive status	27.416	2.958	0.075

Table 8: Parameter estimates for the best model analysing effect of reproductive status in between year site fidelity (Model including Euclidean distance between year as response variable).

Predictors	Dependent variable		
	Estimates	Standard Error	Confidence Interval
(Intercept)	11.43	1.11	9.14 – 13.73
Age + 1 [log]	-1.68	0.48	-2.67 – -0.68
SexRepr [KuYes]	-3.56	1.39	-6.44 – -0.67
Age + 1 [log] * SexRepr [KuYes]	1.44	0.63	0.12 – 2.75

Table 9: Parameter estimates for the best model analysing effect of reproductive status in between year site fidelity (Model including overlaps between year as response variable).

Predictors	Dependent variable		
	Estimates	Standard Error	Confidence Interval
(Intercept)	0.51	0.10	0.30 – 0.72
Season [Winter]	-0.26	0.14	-0.54 – 0.02

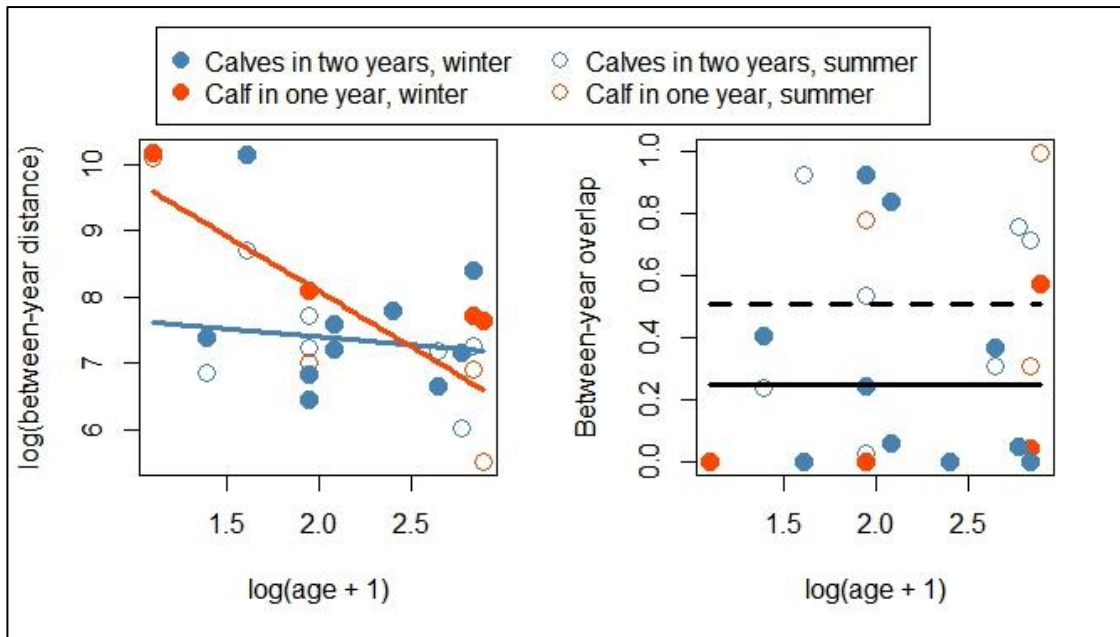


Figure 4: Impact of reproductive status on annual site fidelity of moose. Red solid line and blue solid line from left figure indicates the overall effect of reproductive status with increasing age in the site fidelity. Likewise, black solid and dashed line on the right figure indicate the impact of winter and summer season respectively in the inter year overlap.

4. Discussion

Most animals exhibit site fidelity to its previously occupied area, despite having large scale migrations and intricate patterns of dispersion (Cameron et al., 1986; Wittmer et al., 2006). Still, evaluation of variation in site fidelity at individual level are rare. Thus, I evaluated the effects of age, sex, migratory tactics, and reproductive status on different measures of site fidelity between yearly summer and winter ranges, within and among years, using an extensive data on individual GPS-marked moose in Norway. Even though the moose in my study area were partially migratory, I discovered considerable overlap between home ranges and recurrent usage of the same place over time, both of which suggested high site fidelity. By evaluating the level of variation in site fidelity accounting for different ecological factors, I found that age was the most important factor explaining site fidelity of moose. Additionally, my results showed that season and moose's reproductive state also influence how likely they are to use the same area. However, after accounting for age, sex did not have much effect on site fidelity.

I found higher between-year fidelity in moose during summer than during winter, irrespective of moose age and sex. During summer it is very important to optimize forage quality, as this is the most critical period for body growth and improved body condition before the rut (Herfindal et al., 2006). Thus, motivation for seeking the same optimal foraging conditions may be very high during summer. During winter moose are expected to select areas with good foraging opportunities but also areas where snow conditions is good. Thus, varying snow conditions may have affected the lower between-year winter fidelity. Snow conditions can be very important for what is good foraging areas between years, and snow conditions can be more variable than foraging conditions during summer.

Several studies have demonstrated that site fidelity is unrelated to an animal's age (McLaren & Patterson, 2021; Morrison et al., 2021; Tremblay et al., 2007). In contrast, my results suggest that age was an important factor of site fidelity both within and among years. Similar age-dependent site fidelity has also been reported in a bird (Northern Blad Ibis) (Puehringer-Sturmayer et al., 2023). Factors such as offspring following their mother and making their habitats near to their mother can mask the effect of age on site fidelity (Cederlund & Sand, 1992; Tremblay et al., 2007) in those

studies. Still, there could be reasons such as experience that can make aged individuals restrict their movement to a particular area.

According to research on site fidelity, if the habitat quality varies between different areas, animals are more motivated to change location in the hope that their increased fitness would offset the expenses of their migration (Switzer, 1993). This might benefit animals to gain knowledge and experience about water resources, food availability, habitat condition, predator avoidance strategies and cost of changing territories. Accordingly, only older animals have experienced different kinds of life events such as previous reproductive success (Switzer, 1997; Welch et al., 2000) and space use pattern such as migration vs residency that can affect feeding conditions or predation risk (Rolandsen et al., 2017; Wittmer et al., 2006). Thus, understanding and experiencing life events could make moose more consistent in how and where they move which can be one reason for higher site fidelity in older moose. The higher fidelity of aged moose can also be related to costs of migrations, e.g. caused by snow depth (Singh et al., 2012). Additionally, young individuals may have to trade-off between using known resources and discovering new ones which could lead to poorer site fidelity. Another reason for lower site fidelity in young individuals might be high competition between older and younger age groups in terms of resources and habitat utilization in new areas. For instance, in American bison (*Bison bison*), younger ones were dominated by older cows (Rutberg, 1983), and younger white tailed deer were dominated by older (Townsend & Bailey, 1981). Accordingly, my results suggest that younger moose might have to choose habitat of poorer quality due to the dominating behaviour of older and more experienced individuals. Younger moose may therefore have to move around using larger areas which might lead to lower site fidelity in young ones.

In general, male moose migrate larger regions and covers bigger space of home range as they are not bounded by predation risk of their off spring (Bjørneraas et al., 2012; Herfindal et al., 2009). Thus, I expected female moose to have higher site fidelity than male because male only focuses on optimal foraging and do not have to care about offspring, while females must ensure protective cover to safeguard their young ones (Bjørneraas et al., 2012). However, contradictory to my prediction, I found no significant differences between males and females about being faithfulness to the previous site after accounting for individual age (Figure 2 and 3). Instead, both males

and females showed similar site fidelity. This result was inconsistent to findings of (E. Ofstad, 2013), which found that males and females had different levels of site fidelity and that this difference was likely due to the male's greater propensity for opportunism in choosing habitats in response to variations in the distribution of resources over time. Given the fact that animal movement and site fidelity is driven by availability of resources and its distribution (Garfelt-Paulsen et al., 2021; van Moorter et al., 2013), my findings suggest that older males are likely travel to the same area despite having more opportunities. This may be because older male moose have gained experience and are more aware of how resources are distributed after seeking out opportunities when they were younger.

Additionally, male have greater nutritional requirements because of their bigger body size and thus have larger home ranges (Harestad & Bunnell, 1979; Herfindal et al., 2009) and as a result, male might have knowledge about the forage quality in larger areas. Thus, it seems that the area that male moose previously used consists of high-quality forage which allowed them to reuse the area year after year.

Furthermore, one probable reason for age effect to be dominant over sex could be my sample data consisting of a greater sample size of higher aged females than males. It is possible that the highly skewed range of ages in the data for male moose can be used to explain why older males have very little influence on site fidelity relative to female moose.

Given that movements of female moose and their choice of habitat selection is affected by the mobility and need for protection of their calves (Testa et al., 2000), I expected females with calves in two year exhibits higher site fidelity. In support of my prediction P3, I found females with two calves in two years exhibits higher fidelity than female without calves, however, this effect depended on age and was not present for old individuals. My finding was a bit similar to one of the study where females who had lost their calves moved much more distance than female who successfully protected their calves from predation (Testa et al., 2000). Similarly, in female red winged Blackbirds (*Agelaius phoeniceus*) past nesting success had an impact on their decision to return to past nesting sites or not (Beletsky & Orians, 1991). One of the reasons why reproductive status could affect site fidelity, according to (Switzer, 1997), is that animals are able to access the quality of habitats based on prior reproductive experience.

Contrary to this, (Tremblay et al., 2007) didn't find past reproductive success affecting site fidelity, however they reported that distance travelled by the individual in that study was similar to the values of females who lost their calves as in (Testa et al., 2000). In order to enhance fitness and survival, females might alter their behaviour on how they use their area in response to the availability of food and utilize majority of their time foraging (Aronsson et al., 2016; Lidgard et al., 2020). In accordance with this, my results suggests that females without calves seems to be more opportunistic and move like males.

Whether moose are migratory or resident has a major impact on how much of area they use (Bunnefeld et al., 2011). I predicted migratory moose to have lower site fidelity because they are more opportunistic as they undertake seasonal movements between different ranges and can detect the spatial distribution and also can decide which place to stay (van Moorter et al., 2013). However, I didn't find any difference in site fidelity among years exhibited by migratory and resident after accounting for age (Figure 3). For large herbivorous individual, the driving force of migration are variation in density, environmental condition, predation risk and resource availability (Ball et al., 2001; Fryxell & Sinclair, 1988; Hebblewhite & Merrill, 2007; Mysterud et al., 2011; van Moorter et al., 2021). Still, the result of my study suggests that even if there is change in environmental conditions, migratory moose do not vary their ranges among year more than resident moose. It is not uncommon that individuals switch between being migratory and non-migratory among different years according to environment conditions and population density (Cagnacci et al., 2016; Hansen et al., 2010; Singh et al., 2012). For instance, (Rolandsen et al., 2017) found a switching rate of 9 % for the moose in Trøndelag. We did not have detailed information about such individual variation in migratory tactics for our individuals, and lack of migratory tactics effects on site fidelity after accounting for age might be due to, moose that were migratory on previous year became resident on next year or vice versa. Although, individuals are classified according to specific migratory tactics, there might be variation within each group in terms of specific routes used, the time of movement and so on (Bunnefeld et al., 2011; Rolandsen et al., 2017) that might affect site fidelity.

Because both migration and dispersal disturb the pattern of site fidelity (Bunnefeld et al., 2011), another probable reason for lacking the impact of migratory tactic could be

removal of the periods that is assumed to include the majority of dispersal events during the analysis. Additionally, there may be other factors that affect site fidelity but were not taken into account during study, such as social behaviour and environmental variables like snow depth (Morrison et al., 2021). However, environmental variation in time and space, including anthropogenic disturbance, affect large-scale movement such as migratory tactics should be a focus for future research.

5. Management Implications

High moose population density have resulted in lot of moose-vehicle collisions in Norway which also makes wildlife managers and researchers focusing more on the spatial aspect of moose management (Lavsund et al., 2003; Rolandsen et al., 2011). Furthermore, knowledge of spread of disease in moose population is now much in focus after chronic wasting disease (CWD) which was first seen in wild reindeer (Benestad et al., 2016) and then moose in Norway (Pirisinu et al., 2018). Handling these management challenges require an understanding of individual movement patterns, including the likelihood to revisit areas. Until now, moose management has focussed on managing population density through setting harvesting quotas. However, hunting only in one particular area can impact on the population size of partially migratory populations. Likewise, age and sex specific hunting strategies impact the age- and sex-structure of the populations, which also can affect movement patterns as I found site fidelity to increase with age. Therefore, having good strategies, tools and techniques is a must and understanding movement ecology and finding out how site fidelity aids in animals persistence opens possibilities for guiding conservation efforts.

The results of my study suggest that different factors could cause variation in site fidelity which might be relevant to achieve management goals. Knowledge about site fidelity and migration patterns can help us with habitat conservation and management by allowing the identification of essential sites that moose regularly prefer. In addition, this knowledge can also help wildlife managers in regulating hunting pressure in different areas based on moose space use to achieve management goals.

The age effect on site fidelity that prevailed in my study provides good evidence of age being important in managing and conserving moose populations, as it may suggest that moose needs years of experience to utilize an area optimally. They should be allowed to do so, both by becoming old and reducing disturbance during critical periods. Particularly this can be important because they transfer knowledge to their offspring.

As my study found, females with calves are more faithful to the previously occupied site than females without calves. This information can help managers in prioritizing their protection and assuring the availability of necessary supplies throughout crucial

reproduction seasons by identifying important habitats. This can aid in making management plans regarding hunting which reduce disruption in essential breeding and calving sites.

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>
- Aronsson, M., Low, M., López-Bao, J. V., Persson, J., Odden, J., Linnell, J. D. C., & Andrén, H. (2016). Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. *Ecology and Evolution*, 6(9), 2957–2967. <https://doi.org/10.1002/ece3.2032>
- Ball, J. P., Nordengren, C., & Wallin, K. (2001). Partial migration by large ungulates: Characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology*, 7(1), 39–47. <https://doi.org/10.2981/wlb.2001.007>
- Bartoń, K. (2023). *MuMIn: Multi-Model Inference* (1.47.5). <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beletsky, L. D., & Orians, G. H. (1991). Effects of Breeding Experience and Familiarity on Site Fidelity in Female Red-Winged Blackbirds. *Ecology*, 72(3), 787–796. <https://doi.org/10.2307/1940581>
- Benestad, S. L., Mitchell, G., Simmons, M., Ytrehus, B., & Vikøren, T. (2016). First case of chronic wasting disease in Europe in a Norwegian free-ranging reindeer. *Veterinary Research*, 47(1), 88. <https://doi.org/10.1186/s13567-016-0375-4>
- Bjørneraas, K., Herfindal, I., Solberg, E. J., Sæther, B.-E., van Moorter, B., & Rolandsen, C. M. (2012). Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia*, 168(1), 231–243. <https://doi.org/10.1007/s00442-011-2072-3>
- Bjørneraas, K., Solberg, E. J., Herfindal, I., Moorter, B., Rolandsen, C., Tremblay, J.-P., Skarpe, C., Saether, B.-E., Eriksen, R., & Astrup, R. (2011). Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology*, 17, 44–54. <https://doi.org/10.2981/10-073>

- Bose, S., Forrester, T. D., Brazeal, J. L., Sacks, B. N., Casady, D. S., & Wittmer, H. U. (2017). Implications of fidelity and philopatry for the population structure of female black-tailed deer. *Behavioral Ecology*, 28(4), 983–990. <https://doi.org/10.1093/beheco/ax047>
- Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F., & Godley, B. J. (2007). Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society B: Biological Sciences*, 274(1617), 1533–1539. <https://doi.org/10.1098/rspb.2007.0211>
- 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>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed). Springer.
- Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2157–2162. <https://doi.org/10.1098/rstb.2010.0107>
- Cagnacci, F., Focardi, S., Ghisla, A., van Moorter, B., Merrill, E. H., Gurarie, E., Heurich, M., Mysterud, A., Linnell, J., Panzacchi, M., May, R., Nygård, T., Rolandsen, C., & Hebblewhite, M. (2016). How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. *Journal of Animal Ecology*, 85(1), 54–68. <https://doi.org/10.1111/1365-2656.12449>
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197(3), 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Cameron, R. D., Whitten, K. R., & Smith, W. T. (1986). Summer range fidelity of radio-collared caribou in Alaska’s Central Arctic Herd. *Rangifer*, 51–55. <https://doi.org/10.7557/2.6.2.582>

- Cederlund, G. N., & Sand, H. K. G. (1992). Dispersal of subadult moose (*Alces alces*) in a nonmigratory population. *Canadian Journal of Zoology*, *70*(7), 1309–1314. <https://doi.org/10.1139/z92-183>
- Clobert, J., Baguette, M., Benton, T. G., & Bullock, J. M. (2012). *Dispersal Ecology and Evolution*. OUP Oxford.
- Colson, K. E., White, K. S., & Hundertmark, K. J. (2016). Parturition site selection in moose (*Alces alces*): Evidence for social structure. *Journal of Mammalogy*, *97*(3), 788–797. <https://doi.org/10.1093/jmammal/gyw006>
- Denoël, M., Dalleur, S., Langrand, E., Besnard, A., & Cayuela, H. (2018). Dispersal and alternative breeding site fidelity strategies in an amphibian. *Ecography*, *41*(9), 1543–1555. <https://doi.org/10.1111/ecog.03296>
- Forrester, T. D., Casady, D. S., & Wittmer, H. U. (2015). Home sweet home: Fitness consequences of site familiarity in female black-tailed deer. *Behavioral Ecology and Sociobiology*, *69*(4), 603–612. <https://doi.org/10.1007/s00265-014-1871-z>
- Friedrich, M. J., Hunt, K. L., Catlin, D. H., & Fraser, J. D. (2015). The importance of site to mate choice: Mate and site fidelity in Piping Plovers. *The Auk*, *132*(1), 265–276. <https://doi.org/10.1642/AUK-14-100.1>
- Fryxell, J. M., Greever, J., & Sinclair, A. R. E. (1988). Why are Migratory Ungulates So Abundant? *The American Naturalist*. <https://doi.org/10.1086/284822>
- Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T., & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences*, *105*(49), 19114–19119. <https://doi.org/10.1073/pnas.0801737105>
- Fryxell, J. M., & Sinclair, A. R. E. (1988). Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, *3*(9), 237–241. [https://doi.org/10.1016/0169-5347\(88\)90166-8](https://doi.org/10.1016/0169-5347(88)90166-8)
- Garfelt-Paulsen, I. M., Soininen, E. M., Ravolainen, V., Loe, L. E., Hansen, B. B., Irvine, R. J., Stien, A., Ropstad, E., Veiberg, V., Fuglei, E., & Pedersen, Å. Ø. (2021). Don't go chasing the ghosts of the past: Habitat selection and site fidelity during calving

in an Arctic ungulate. *Wildlife Biology*, 2021(2), wlb.00740.
<https://doi.org/10.2981/wlb.00740>

Gehr, B., Bonnot, N. C., Heurich, M., Cagnacci, F., Ciuti, S., Hewison, A. J. M., Gaillard, J.-M., Ranc, N., Premier, J., Vogt, K., Hofer, E., Ryser, A., Vimercati, E., & Keller, L. (2020). Stay home, stay safe—Site familiarity reduces predation risk in a large herbivore in two contrasting study sites. *Journal of Animal Ecology*, 89(6), 1329–1339. <https://doi.org/10.1111/1365-2656.13202>

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28(4), 1140–1162. [https://doi.org/10.1016/S0003-3472\(80\)80103-5](https://doi.org/10.1016/S0003-3472(80)80103-5)

Hansen, B. B., Aanes, R., & Sæther, B.-E. (2010). Partial seasonal migration in high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Canadian Journal of Zoology*, 88(12), 1202–1209. <https://doi.org/10.1139/Z10-086>

Harestad, A. S., & Bunnell, F. L. (1979). Home Range and Body Weight—A Reevaluation. *Ecology*, 60(2), 389–402. <https://doi.org/10.2307/1937667>

Hebblewhite, M., & Merrill, E. H. (2007). Multiscale wolf predation risk for elk: Does migration reduce risk? *Oecologia*, 152(2), 377–387. <https://doi.org/10.1007/s00442-007-0661-y>

Herfindal, I., Sæther, B.-E., Solberg, E. J., Andersen, R., & Høgda, K. A. (2006). Population characteristics predict responses in moose body mass to temporal variation in the environment. *Journal of Animal Ecology*, 75(5), 1110–1118. <https://doi.org/10.1111/j.1365-2656.2006.01138.x>

Herfindal, I., Tremblay, J.-P., Hansen, B. B., Solberg, E. J., Heim, M., & Sæther, B.-E. (2009). Scale dependency and functional response in moose habitat selection. *Ecography*, 32(5), 849–859. <https://doi.org/10.1111/j.1600-0587.2009.05783.x>

Lavsund, S., Nygrén, T., & Solberg, E. J. (2003). STATUS OF MOOSE POPULATIONS AND CHALLENGES TO MOOSE MANAGEMENT IN FENNOSCANDIA. *Alces: A Journal Devoted to the Biology and Management of Moose*, 39, 109–130.

- Lidgard, D. C., Bowen, W. D., & Iverson, S. J. (2020). Sex-differences in fine-scale home-range use in an upper-trophic level marine predator. *Movement Ecology*, 8(1), 11. <https://doi.org/10.1186/s40462-020-0196-y>
- Linnell, J. D. C. (2005). [PDF] *Spatial aspects of managing natural resources and conserving biodiversity. Integrating the global and the local by John Durrus Linnell · 2737808553 · OA.mg*. <https://oa.mg/work/2737808553>
- LINNELL, J. D. C., ANDERSEN, R., KVAM, T., ANDRÉN, H., LIBERG, O., ODDEN, J., & MOA, P. F. (2001). Home Range Size and Choice of Management Strategy for Lynx in Scandinavia. *Environmental Management*, 27(6), 869–879. <https://doi.org/10.1007/s002670010195>
- 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/>
- McLaren, A. A. D., & Patterson, B. R. (2021). There’s no place like home—Site fidelity by female moose (*Alces alces*) in central Ontario, Canada. *Canadian Journal of Zoology*, 99(7), 557–563. <https://doi.org/10.1139/cjz-2021-0010>
- Merkle, J. A., Abrahms, B., Armstrong, J. B., Sawyer, H., Costa, D. P., & Chalfoun, A. D. (2022). Site fidelity as a maladaptive behavior in the Anthropocene. *Frontiers in Ecology and the Environment*, 20(3), 187–194. <https://doi.org/10.1002/fee.2456>
- Milner-Gulland, E. J., Fryxell, J. M., & Sinclair, A. R. E. (2011). *Animal Migration: A Synthesis*. OUP Oxford.
- Moen, A. (1999). National atlas of Norway. *Vegetation. Norwegian Mapping Authority, Hønefoss, Norway*.
- 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>
- 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>
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052–19059. <https://doi.org/10.1073/pnas.0800375105>
- Nikula, A., Heikkinen, S., & Helle, E. (2004). Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. *Wildlife Biology*, *10*(2), 121–135. <https://doi.org/10.2981/wlb.2004.017>
- Ofstad, E. (2013). Seasonal Variation in Site Fidelity of Moose (*Alces alces*) [Master thesis, Institutt for biologi]. In 37. <https://ntnuopen.ntnu.no/ntnu-xmlui/handle/11250/245241>
- Ofstad, E. G., Herfindal, I., Solberg, E. J., Heim, M., Rolandsen, C. M., & Sæther, B.-E. (2019). Use, selection, and home range properties: Complex patterns of individual habitat utilization. *Ecosphere*, *10*(4), e02695. <https://doi.org/10.1002/ecs2.2695>
- 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>
- Pirisinu, L., Tran, L., Chiappini, B., Vanni, I., Di Bari, M. A., Vaccari, G., Vikøren, T., Madslie, K. I., Våge, J., Spraker, T., Mitchell, G., Balachandran, A., Baron, T., Casalone, C., Rolandsen, C. M., Røed, K. H., Agrimi, U., Nonno, R., & Benestad, S. L. (2018). Novel Type of Chronic Wasting Disease Detected in Moose (*Alces alces*), Norway. *Emerging Infectious Diseases*, *24*(12), 2210–2218. <https://doi.org/10.3201/eid2412.180702>
- Puehringer-Sturmayr, V., Krejci, J., Schuster, R., Kleindorfer, S., Kotrschal, K., Frigerio, D., & Loretto, M.-C. (2023). Space use and site fidelity in the endangered Northern Bald Ibis *Geronticus eremita*: Effects of age, season, and sex. *Bird Conservation International*, *33*, e10. <https://doi.org/10.1017/S0959270922000053>
- Pyke, G. (1983). Animal movements: An optimal foraging approach. In *Encyclopedia of Animal Behavior* (pp. 7–31). <https://doi.org/10.1016/B978-0-12-809633-8.90160-2>

- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. URL <https://www.R-project.org/>.
- Rolandsen, C. M., Solberg, E. J., Bjørneraas, K., Heim, M., Van Moorter, B., Herfindal, I., Garel, M., Pedersen, P. H., Sæther, B.-E., Lykkja, O. N., & Os, Ø. (2010). Elgundersøkelsene i Nord-Trøndelag, Bindal og Rissa 2005—2010. Sluttrapport. In 142. Norsk institutt for naturforskning. <https://ntnuopen.ntnu.no/ntnu-xmlui/handle/11250/2437410>
- Rolandsen, C. M., Solberg, E. J., Heim, M., Holmstrøm, F., Solem, M. I., & Sæther, B.-E. (2008). Accuracy and repeatability of moose (*Alces alces*) age as estimated from dental cement layers. *European Journal of Wildlife Research*, 54(1), 6–14. <https://doi.org/10.1007/s10344-007-0100-8>
- Rolandsen, C. M., Solberg, E. J., Herfindal, I., Van Moorter, B., & Sæther, B.-E. (2011). Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density? *Ecosphere*, 2(10), art113. <https://doi.org/10.1890/ES11-00169.1>
- Rolandsen, C. M., Solberg, E. J., Sæther, B.-E., Moorter, B. V., Herfindal, I., & Bjørneraas, K. (2017). On fitness and partial migration in a large herbivore – migratory moose have higher reproductive performance than residents. *Oikos*, 126(4), 547–555. <https://doi.org/10.1111/oik.02996>
- Rutberg, A. T. (1983). Factors Influencing Dominance Status in American Bison Cows (*Bison bison*). *Zeitschrift Für Tierpsychologie*, 63(2–3), 206–212. <https://doi.org/10.1111/j.1439-0310.1983.tb00087.x>
- Schieck, J. O., & Hannon, S. J. (1989). Breeding site fidelity in willow ptarmigan: The influence of previous reproductive success and familiarity with partner and territory. *Oecologia*, 81(4), 465–472. <https://doi.org/10.1007/BF00378953>
- Schmidt, K. A. (2004). Site fidelity in temporally correlated environments enhances population persistence. *Ecology Letters*, 7(3), 176–184. <https://doi.org/10.1111/j.1461-0248.2003.00565.x>
- Schneider, D. C. (2001). The Rise of the Concept of Scale in Ecology: The concept of scale is evolving from verbal expression to quantitative expression. *BioScience*, 51(7), 545–553. [https://doi.org/10.1641/0006-3568\(2001\)051\[0545:TROTCO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0545:TROTCO]2.0.CO;2)

- 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>
- Skonhoft, A. (2005). The costs and benefits of a migratory species under different management schemes. *Journal of Environmental Management*, 76(2), 167–175. <https://doi.org/10.1016/j.jenvman.2005.01.016>
- Storaas, T., Gundersen, H., Henriksen, H., & Andreassen, H. P. (2001). THE ECONOMIC VALUE OF MOOSE IN NORWAY - A REVIEW. *Alces: A Journal Devoted to the Biology and Management of Moose*, 37(1), Article 1.
- Sweanor, P. Y., & Sandegren, F. (1988). Migratory behavior of related moose. *Ecography*, 11(3), 190–193. <https://doi.org/10.1111/j.1600-0587.1988.tb00800.x>
- Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, 7(6), 533–555. <https://doi.org/10.1007/BF01237820>
- Switzer, P. V. (1997). Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology*, 40(5), 307–312. <https://doi.org/10.1007/s002650050346>
- Testa, J. W., Becker, E. F., & Lee, G. R. (2000). MOVEMENTS OF FEMALE MOOSE IN RELATION TO BIRTH AND DEATH OF CALVES. *Alces: A Journal Devoted to the Biology and Management of Moose*, 36, 155–162.
- Timmermann, H. R., & McNicol, J. G. (1988). Moose Habitat Needs. *The Forestry Chronicle*, 64(3), 238–245. <https://doi.org/10.5558/tfc64238-3>
- Townsend, T. W., & Bailey, E. D. (1981). Effects of Age, Sex and Weight on Social Rank in Pinned White-tailed Deer. *The American Midland Naturalist*, 106(1), 92–101. <https://doi.org/10.2307/2425138>
- Tremblay, J.-P., Solberg, E. J., Sæther, B.-E., & Heim, M. (2007). Fidelity to calving areas in moose (*Alces alces*) in the absence of natural predators. *Canadian Journal of Zoology*, 85(8), 902–908. <https://doi.org/10.1139/Z07-077>
- Valenzuela, L. O., Sironi, M., Rowntree, V. J., & Seger, J. (2009). Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales

- (*Eubalaena australis*). *Molecular Ecology*, 18(5), 782–791. <https://doi.org/10.1111/j.1365-294X.2008.04069.x>
- van Beest, F. M., Vander Wal, E., Stronen, A. V., Paquet, P. C., & Brook, R. K. (2013). Temporal variation in site fidelity: Scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. *Oecologia*, 173(2), 409–420. <https://doi.org/10.1007/s00442-013-2647-2>
- van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., & Sæther, B.-E. (2013). Understanding scales of movement: Animals ride waves and ripples of environmental change. *Journal of Animal Ecology*, 82(4), 770–780. <https://doi.org/10.1111/1365-2656.12045>
- van Moorter, B., Singh, N. J., Rolandsen, C. M., Solberg, E. J., Dettki, H., Pusenius, J., Månsson, J., Sand, H., Milner, J. M., Roer, O., Tallian, A., Neumann, W., Ericsson, G., & Myrsterud, A. (2021). Seasonal release from competition explains partial migration in European moose. *Oikos*, 130(9), 1548–1561. <https://doi.org/10.1111/oik.07875>
- Veiberg, V., Nilsen, E. B., Rolandsen, C. M., Heim, M., Andersen, R., Holmstrøm, F., Meisingset, E. L., & Solberg, E. J. (2020). The accuracy and precision of age determination by dental cementum annuli in four northern cervids. *European Journal of Wildlife Research*, 66(6), 91. <https://doi.org/10.1007/s10344-020-01431-9>
- Welch, I. D., Rodgers, A. R., & McKinley, R. S. (2000). TIMBER HARVEST AND CALVING SITE FIDELITY OF MOOSE IN NORTHWESTERN ONTARIO. *Alces: A Journal Devoted to the Biology and Management of Moose*, 36, 93–103.
- Wittmer, H. U., McLellan, B. N., & Hovey, F. W. (2006). Factors influencing variation in site fidelity of woodland caribou (*Rangifer tarandus caribou*) in southeastern British Columbia. *Canadian Journal of Zoology*, 84(4), 537–545. <https://doi.org/10.1139/z06-026>
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer. <https://doi.org/10.1007/978-0-387-87458-6>



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