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Movement patterns of golden eagles in relation to distribution of reindeer and sheep in Fennoscandia

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An adult golden eagle male in Fosen, Trøndelag. Photo captured by a wildlife camera and used in agreement with NINA.

Preface

This thesis completes my five years of studying at the Norwegian university of life sciences (NMBU), where the last two have been spent finishing a master's in Natural Resource Management. I would first of all like to direct a big thank you to Leif Egil Loe at the Faculty of Environmental Sciences and Natural Resource Management (MINA) for his guidance and support throughout this whole process, and for always helping and responding no matter the size of the issue. I would also like to thank Jennifer Stien and Jenny Mattisson from the Norwegian Institute of Nature Research (NINA) and Audun Stien from the University of Tromsø (UiT) for allowing me to work on the GPS-data and a memorable month of field work, as well as all the help, feedback and tips I have received along the way.

A big thanks is directed towards NMBU for five amazing study years filled with invaluable knowledge and practical experiences. I also want to direct a special thanks to my family and all my classmates from both the bachelor's and master's program for all support, thoughtfulness, and fun throughout the studies. Finally, I would like to thank Sangkoret Lærken for being my family away from home, and for functioning as a much-needed distraction and break during this year of thesis work.

Ås, 16.05.2022



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Abstract

Predator-livestock conflicts are a big problem worldwide, and usually result in big ethic and economic difficulties. Even though a lot of research has been done on the matter, there are still many uncertainties connected to the subject. For the golden eagle the main challenges are connected to the lack of information regarding territoriality, and how it affects depredation of livestock and both small- and large-scale movements. Territorial individuals, on the other hand, are believed to stay in their territory throughout the year without the ability to track resources over large spatial scales. Non-territorial individuals roam larger areas and are therefore believed to be the main tortfeasor on livestock, since they presumably are driven by food availability.

My thesis is based on data from nine eagles, three territorial and six non-territorial individuals, that carried GPS transmitters in a harness on their backs. The data has been collected through the NINA project called “Loss of lambs to Golden Eagles on the Fosen Peninsula,” a five-year-long project investigating the role of golden eagles in the loss of domestic sheep as well as the eagles’ diet and movement behavior. Home range size was estimated for the breeding- and non-breeding season for the territorial eagles. Upon finding that territorial individuals largely stay within or close to their breeding territories throughout the year, I continued investigating if patch residency time for the non-territorial individuals was affected by presence of reindeer and sheep. This was done on three different radii: 1000, 5000 and 10 000 meters. I hypothesized that both prey species are attractive for young golden eagles and that patch residency time would increase in their presence.

I found that two out of the three territorial individuals made small-scale movements during the non-breeding season. This could be explained by an abundance of prey at the location visited, as well as the need to recharge after an energy-demanding breeding period. For the non-territorial individuals, the patch residency analysis for all three radii revealed that the eagles tended to spend more time in patches with reindeer than without, but less time in patches with sheep present than without. An explanation could be a preference for reindeer over sheep. Reindeer is a prey type that can be found naturally in Norway, and therefore have been an available food source for a long period of time. Lastly, the results show large seasonal and individual variations in patch residency time. This could be explained by the fluctuations in the population of the eagles’ main prey species, hare, and ptarmigan. According to the

alternative prey hypothesis, the depredation of livestock will increase when the access to the eagles' main prey is low. This might explain the big monthly and yearly variations for each individual.

My study indicates that non-territorial golden eagles stay longer in an area if reindeer are present. Based on these results, I see culling as an unsuitable management measure, mainly because the patch residency within a 10 000-meter radius is as low as approximately eight days, but also because of large individual and temporal variation, making this result hard to generalize.

This thesis gives insight into the movement behavior of golden eagles and is relevant to future management, especially regarding the realism of catching the culprit doing the livestock damage. Going forward, it will be necessary to do more research on the subject to gather an even deeper understanding of movement behavior and motivations for the eagles, but also to move towards obtaining loss rates of reindeer and lambs in a range of study sites.

Key words: golden eagle, predator – prey conflict, livestock depredation, semi-domesticated reindeer, domestic sheep, patch residency time, home range, movement

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Introduction

Predator – livestock conflicts are a big problem worldwide (Zimmermann et al., 2010). They result in economic difficulties and many management issues that ethically are difficult to solve, mainly because livestock have high economic value, but also because the predators involved often are protected legally (Graham et al., 2005). Much research has been done on the matter worldwide (Zimmermann et al., 2010), but lack of information is still one of the main drivers of the conflict.

Territoriality, defined in Britannica as “the monopolization of space by an individual or group” (Koenig & Dickinson, 2018), is a well-known phenomenon in the animal kingdom. Territoriality is highly variable between species, populations, groups and individuals (Kaufmann, 1983). Some will allow individuals from other family groups to utilize parts of their home range, while others will chase away intruders as soon as they cross territory borders. It is common to spend many of the juvenile years as a non-territorial with the flexibility of resource search over large areas. Conversely, year-round territoriality has the cost of not ranging for food sources beyond territorial borders. When related to the potential for depredation of livestock, a non-territorial individual will be able to take advantage of aggregations of livestock over larger areas than a territorial individual.

The golden eagle (*Aquila chrysaetos*) is highly territorial but will usually not claim a territory before it reaches five years or older (Heggøy & Øien, 2015). When it does, it stays in and defends this area for the rest of its life with its partner. Territories vary in quality and size but need to encompass one or several hunting areas and either a forest patch or a mountainside suitable for nesting and raising of young (Katzner et al., 2020). Up until the eagles find a territory to inhabit, they roam larger areas in search for available territories and food. It is believed that non-territorial eagles mainly are driven by food availability when they decide where to go or where to stop for short or long periods (Watson, 1997). During this period of their life, they can travel more than hundred kilometers in 24 hours (Stokmo, 2021) and utilize the food sources they encounter. They are therefore thought to be important tortfeasors on livestock, especially domestic sheep (*Ovis aries*) and semi-domestic reindeer (*Rangifer tarandus*) (Watson, 1997). Watson also suggests that non-territorials will hunt for larger mammals than the territorial ones simply because they can eat at the scene and do not have to carry their whole prey back to a nest. Territorial eagles have young to feed during the

breeding season and will not be able to carry their whole prey back to the nest if it is too heavy or too far away. On the other hand, they will be able to do damage to the livestock populations within their territory border.

Farmers in Norway claim high livestock losses to golden eagles yearly (Stien, 2016). However, quantitative information is missing, both on direct loss rates and which type of individuals that are overrepresented for any damage done. There are seasonal and large-scale variations in livestock distribution of sheep and semi-domestic reindeer in Fennoscandia because of changes in pastures and grazing areas. Sheep are let out on uncultivated pasture in early June and will stay out until early September. Reindeer are out year-round, but on summer- and late-summer pasture from May until September (Busterud, 2015).

One of the main problems is the lack of knowledge concerning the territoriality of individuals and if the culprit is a territorial or non-territorial individual. Free-ranging livestock may overlap spatially with resident predators like territorial eagles but may also serve as attractors for highly mobile predators. Non-territorial eagles can be expected to track these resources, while territorial individuals may not, especially if they are confined to their territory year-round. Actions for reducing predator-livestock conflicts such as culling or relocations may have highly different outcomes if the culprit is a resident predator or a predator in transit.

The Norwegian Institute for Nature Research (NINA) started a five-year project in Fosen in 2018 named “Loss of lambs to Golden Eagles on the Fosen Peninsula”. The project, funded by the Norwegian Environment Agency (Miljødirektoratet), collaborates with livestock farmers, the Norwegian Nature Surveillance (SNO), Norwegian Veterinary Institute, and several research universities. The project found high losses of lambs to golden eagles in 2014-2015 (Stien, 2016), and the farmers in Indre Fosen municipality received compensations for almost 240 000 Norwegian kroner in 2021 (Rovbase.no, 2021). The project’s primary goal is to investigate the role of golden eagles in the loss of lambs in Rissa beitelag. Part of the studies involves increasing knowledge of movement patterns of both non-territorial and territorial individuals and whether GPS position data could be used to indicate predation of lambs. By equipping golden eagles caught in Fosen with GPS transmitters, the researchers can follow their movement and map their diet by seeking out clusters of coordinates.

In this thesis, I want to investigate to which extent GPS-marked golden eagles track large-scale distributions of sheep and reindeer. I start by classifying the marked individuals in Fosen as territorial and non-territorial. Upon finding that territorial eagles only show a small range expansion in the non-breeding season, I explore if sheep and reindeer are attractors of non-territorial golden eagles. I quantify patch residency time within areas of 1000-, 5000- and 10 000-meter radius and predict that residency time increases when eagles encounter areas with sheep and reindeer present. Because I calculate the expected time use of immature eagles in sheep and reindeer areas and that culling of ‘problematic individuals’ has been suggested as a management action, my findings are relevant to the feasibility of removal of individuals that have caused the death of a lamb.

Method

Study species

The golden eagle (*Aquila chrysaetos*) is the second-largest raptor in Norway, with a wingspan of 190 to 225 cm (Svensson et al., 2011), with only the white-tailed eagle (*Haliaeetus albicilla*) being bigger. In Norway, the golden eagle usually inhabits mountainous areas with some open ground suitable for hunting, in addition to Scots pine (*Pinus sylvestris*)- and Norway spruce (*Picea abies*) dominated forests. The nests are built in either a steep mountainside or in trees (usually pine or spruce), all dependent on the territory, disturbances, and dangers. Golden eagles are shy and will therefore avoid human contact if possible. They prefer areas with topography that creates updrafts since they need these for their soaring flight (Katzner et al., 2020)

Golden eagles are monogamous and strongly territorial and usually establish in a territory with a mate when they reach five to seven years of age (Katzner et al., 2020). The rest of their life will usually be spent in this area, where they defend it from intruders and competitors. The territory borders are marked with undulating flight, and intruders (especially non-territorial individuals) will be chased, in particular during the breeding season. Finding a territory can be challenging, and non-territorial eagles will roam large areas trying to find one where they can establish and reproduce. While territorial eagles have limited and (mostly) short-distance movements within their territory borders, the non-territorial ones can travel long distances during their first years. It is assumed that the non-territorial eagles’ movements mainly are driven by food availability (Katzner et al., 2020).

Golden eagles are predators and prefer smaller mammals and medium-sized birds like ptarmigan (*Lagopus spp.*), hare (*Lepus timidus*), black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao urogallus*), but can also hunt calves and young of bigger ungulates like roe deer (*Capreolus capreolus*), reindeer and domestic sheep (Watson, 1997). The golden eagle catches and kills its prey with its big talons by either going in through the side and puncturing the prey's lung or by going for the frontal lobe. There are variations and specializations in diet, affected by location and fauna. For instance, Sidiropoulos et al. (2022) mention tortoises as an essential part of the eagles' diet during the breeding season in Greece. In Norway and Scandinavia, ptarmigan and hare are the most important food sources (Tjernberg, 1981).

Study area

The project was conducted on the Fosen peninsula. The landscape consists of mountainous areas and large areas of bog and forests, with altitudes varying between 0 and 600 meters above sea level. In addition to Norway spruce, there is deciduous forest growing on the southern parts facing the fjords, with species that are uncommon this far north because of their temperature requirements (Rosvold, 2021). Because of the steep outcrops, Fosen makes a highly suitable habitat for golden eagles.

Although captured and marked at the Fosen peninsula, some eagle individuals ranged widely. Therefore, the extended study area consists of the western parts of Norway and all the way up to Finnmark, in addition to northern Finland and central and northern Sweden.



Picture taken from a perch spot used by a golden eagle at the Fosen peninsula, June 2021

Capture protocol and data collection

A total of nine golden eagles were captured in Fosen between November and February 2017-2021 as part of the NINA-led collaborative research project “Loss of lambs to Golden Eagles on the Fosen Peninsula”. The instrumentation and capture method was approved by the Norwegian food safety authority (Stien, 2022). Eagles were captured with a bow net with a manually controlled remote firing system. GPS transmitters (3rd generation CTT ®-1000-BT3 series from Cellular Tracking Technologies) were fitted on the eagles’ backs in a specially designed harness. The harness was fastened at the top of the breastbone in a cross with four to six bio-stitches with an expected lifespan of three years to ensure that the eagles would not carry the GPS for the rest of their lives. GPS transmitters used in this project were solar-driven, reducing battery size, thereby reducing the weight of the device and potential negative impacts of carrying a device on the eagles. Since they were solar-driven, the total number of positions during periods of little or no sunlight (spring and autumn night-time and most of the winter season) was limited. In summertime, position interval was usually every 15 minutes throughout the day to gather data during the sheep grazing season, which lasted between early

June and late September. Outside of the grazing season and during periods of low light, they were programmed to take positions once every hour between sunrise and sunset. The positions were sent via GSM to the Dyreposisjoner database.

A metal ring with a unique identification number was fitted to each eagle's right leg to make it possible to identify the eagles later on. A blood and/or a feather sample was collected for DNA-analysis. This made it possible to analyze feathers and pellets found after the transmitter fell off, in addition to identifying the gender. Pictures of wing- and tail feathers were taken to give a rough identification of age (adult/immature), since plumage varies with age.

Data used in this thesis are GPS data sent directly from transmitters carried by the eagles. Although data is available for the whole year, only data received during the summer months have been used for the patch residency analysis in this thesis, since the aim of the research was to study movement behavior and differences in areas with and without domestic animals (sheep are free-ranging only in summer). 'Summer' consists in this case of the months May, June, July and August, the same time that reindeer have calves and sheep are out on pasture. In summertime, golden eagles are expected to do most damage on livestock, both reindeer and sheep, since both lambs and calves are small and easy targets. For the home range analysis, all locations within the interval from May 2019 to August 2021 have been included.

Data handling and preparations

All data handling and -analysis were done in RStudio (version 1.4.1103). Different transmitter settings during the start of the project made it necessary to choose an interval from May 5th 2019 to August 31st 2021 to work with for the patch residency analysis, since all transmitters had the same 15-minute interval GPS-fix during this period. This resulted in the removal of one non-territorial eagle from this specific analysis, GE02.

The sampling period varied considerably between individuals. There were more positions included in the analysis for the territorial eagles (males GE01, GE03 and GE07) than for the non-territorial ones (GE04, GE05, GE06, GE08 and GE09). This is because locations from all seasons have been included, not just from the summer months. GE01 carried a transmitter from November 2017 until April 2019 and had varying transmitter settings, like GE02. GE01 was still included in the home range analysis since this analysis is less sensitive to sampling

frequency than the patch residency analysis. For GE03, positions from November 2018 to August 2021 were included, while GE07 was sampled from February 2020 to February 2021 (Table 1).

The non-territorial individuals were only sampled from May 5th to August 31st within the interval, and therefore also had big variations in sampling periods. GE04 was sampled from May 2019 to August 2021. GE05 only sent positions during winter and was therefore excluded from the analysis. GE06 was sampled from May to August in both 2020 and 2021, while both GE08 and GE09 was sampled from May to August 2021 (Table 1).

Table 1: Summary of the data period used for analysis of gps-marked golden eagle movement, with non-territorial individuals marked in green and territorial individuals marked in blue.

*GE05 was non-territorial and only sent positions for one winter period, which resulted in the positions not being included.

Individual	Data sampled	Period used for analysis	Number of positions
GE01	23.11.17 – 22.04.19	Whole period	9306
GE03	30.11.18 – 31.08.21	Whole period	34399
GE04	05.05.19 – 11.03.20	05.05.19 – 31.08 2019	1035
GE05	16.12.19 – 15.01.20	None*	22
GE06	18.12.19 – 31.08.21	05.05.20 – 31.08 2020 05.05.21 – 31.08 2021	3140
GE07	03.02.20 – 24.02.21	Whole period	3018
GE08	06.12.20 – 31.08.21	05.05.21– 31.08 2021	1390
GE09	10.12.20 – 31.08.21	05.05.21 – 31.08 2021	1489

Maps

To investigate interactions between eagles, grazing areas of domestic animals and terrain, spatial information on golden eagle GPS locations was extracted from digital maps. All maps were rasterized in ArcGis (version 10.8) before being loaded into R as raster layers. A map of the tree line border (Mattisson & Odden, 2016) was used to investigate if the eagles spent more time in or outside of mountainous areas. For Norway, information concerning the distribution of sheep and domesticated reindeer were derived from Kilden (NIBIO, 2021). For Sweden, only distribution of reindeer was used (GIS data Länsstyrelserna© 2000-2008) since

all sheep graze in fenced pastures. In Norway, sheep graze in uncultivated pasture during the summer months. The sheep map contains information about the different uncultivated areas and sheep density (NIBIO; NIBIO, 2021). The reindeer maps used for Norway and Sweden include information about spring- and summer pasture, calving- and collection areas and migration routes (GIS data Länsstyrelserna© 2000-2008; Landbruksdirektoratet). Only information and location about the summer pastures were extracted for this thesis.

The sheep density data and the reindeer data were transformed from numeric values to a binary variable where 1 = presence and 0 = absence from the area where the GPS position was registered. This was done to harmonize the Norwegian and Swedish maps in case of methodological differences.

Statistical analysis

Home range analysis

A home range analysis was run for the breeding and non-breeding season for the territorial individuals through the Kernel method from the `adehabitatHR` package. The `kernelUD`-function allows you to estimate the utilization distribution, which is defined as “the bivariate function giving the probability density that an animal is found at a point according to its geographical position” (Calenge et al., 2020a). I estimated the 95% kernel area for each territorial eagle in the breeding- and non-breeding seasons. The breeding season was defined as May to August (based on the duty cycles of the transmitter settings to ensure a 15-minute interval setting), while the non-breeding season was defined as the rest of the year (September to April). These estimates were used to report the mean home range size of the territorial eagles in my study, seasonal difference in home range size (and potential documentation of year-round residency) and finally plotted to visualize the difference in range use of territorial and non-territorial eagles.

Patch residency analysis

I wanted to investigate how much time the eagles spent in each patch they visited and what motivated them to stop in the first place. The `residenceTime` feature from the `adehabitatLT` package is a trajectory analysis based on the residence time method created by Barraquand and Benhamou (2008). Residence time, in this case, is how long the eagles stay at a location before they leave. This is measured by registering the time of arrival at a given relocation, in

addition to registering the time of arrival at both relocations registered before and after the current one. A time limit threshold for how long the eagles can stay outside the given radius before it counts as a new relocation is set through the `maxt`-function (Calenge et al., 2020b)

To run a patch residency analysis, a radius and a maximum time the eagles can spend outside a point before it counts as a new relocation must be defined. In this case, the maximum time allowed to spend outside the circle was set to four hours. This means that if the eagle returned within four hours, it would still count as being within the same patch. I was mainly interested in what caused variation in intermediate to large scale movement on a relevant scale for spatial variation in sheep and reindeer. Therefore, three different radii were chosen: 1000, 5000 and 10 000 meters. The selection of radii was guided by exploration of the data in the Dyreposisjon database (www.dyreposisjon.no) to facilitate that different movement processes were captured at each spatial scale.

To see how patch residency time was affected by reindeer- and sheep presence/absence, as well as terrain type (above or below the tree line), I went through the following analytical steps. First, the correlation between the candidate fixed effects (sheep, reindeer, month and mountainous area) was checked through the `hetcor`-function from the `polycor` package (Fox & Dusa, 2022). The `hetcor` creates a matrix with values for each variable. If variables correlated with an absolute value of less than 0.6, they could be included in the same model (Tabachnick & Fidell, 1996). Thereafter, candidate linear mixed models fitted with the `lmer` function in the `lme4` package (Bates et al., 2007) were subjected to backward selection using likelihood ratio test (Pinheiro & Douglas, 2000). As the response variable, I used patch residency time (separate models for each of the three radii). Candidate fixed effects in the starting model consisted of sheep (presence/absence), reindeer on summer pasture (presence/absence), month, habitat (above or below the tree line) and the two-way interactions between sheep and month and reindeer and month. Individual was fitted as a random intercept. Model selection ended when all included variables were significant at a $p = 0.05$ level. This selection procedure was completed for all three radii and resulted in a final model for each scale.

Results

Home range analysis for territorial individuals

All three eagles that defended a breeding territory mostly remained in the Fosen region throughout the year (Figure 1). During the breeding season, the home range of the three

eagles was respectively 112 km² (GE01), 102 km² (GE03) and 68km² (GE07). During the non-breeding season, the size increased by 37%, 75% and 85% to 178 km², 414 km² and 428 km². GE01 stayed in his territory throughout the year, but both GE03 and GE07 traveled outside their territory during the non-breeding season. GE03 travelled to the Tarva island group in Ørland between September and November in both 2019 and 2021 (Dyreposisjoner, 2022). GE07 travelled to a spot further south on the Fosen peninsula. Although the territories on average increased by 35% from the breeding season to non-breeding season, the scale of movement was minor compared to the non-territorial eagles (Figure 1 and 2).

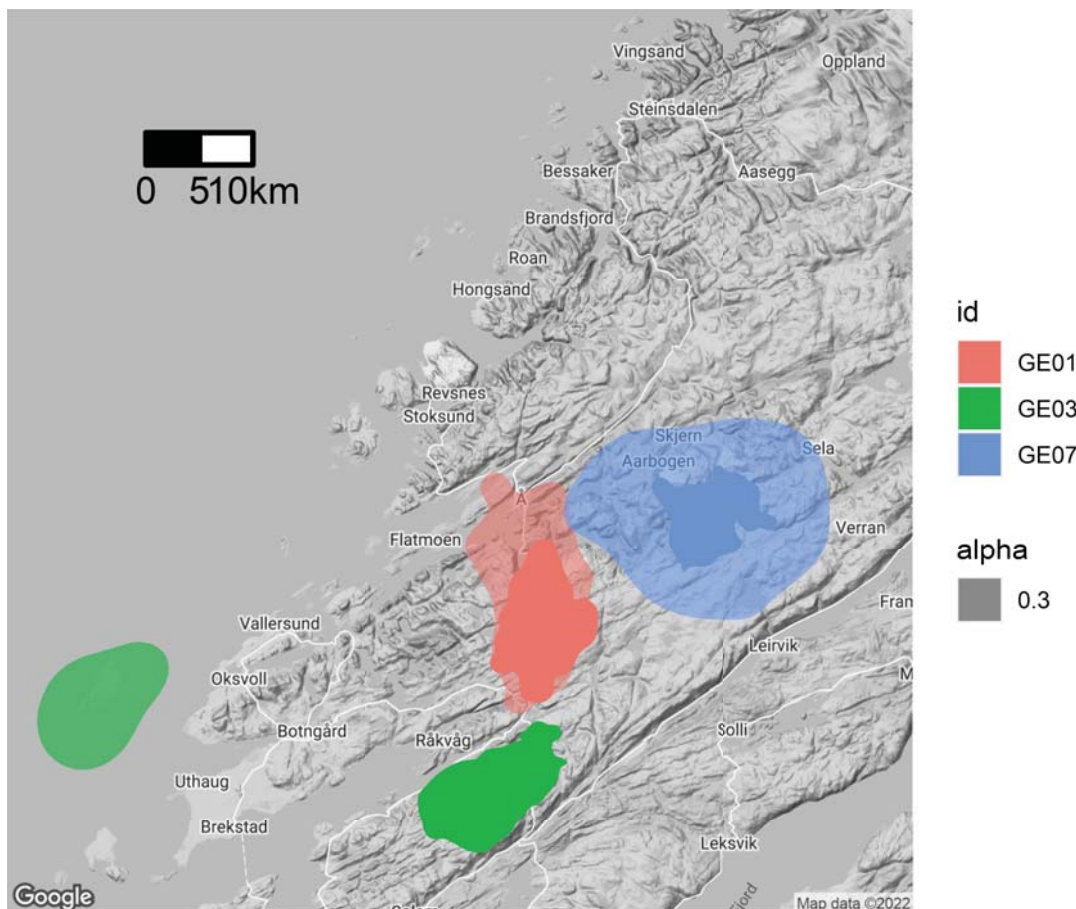


Figure 1: Home ranges of the three male territorial eagles GE01 (red), GE03 (green) and GE07 (blue) during the breeding season (full color) and the non-breeding season (transparent). The plot shows how the home ranges expand during the non-breeding season.

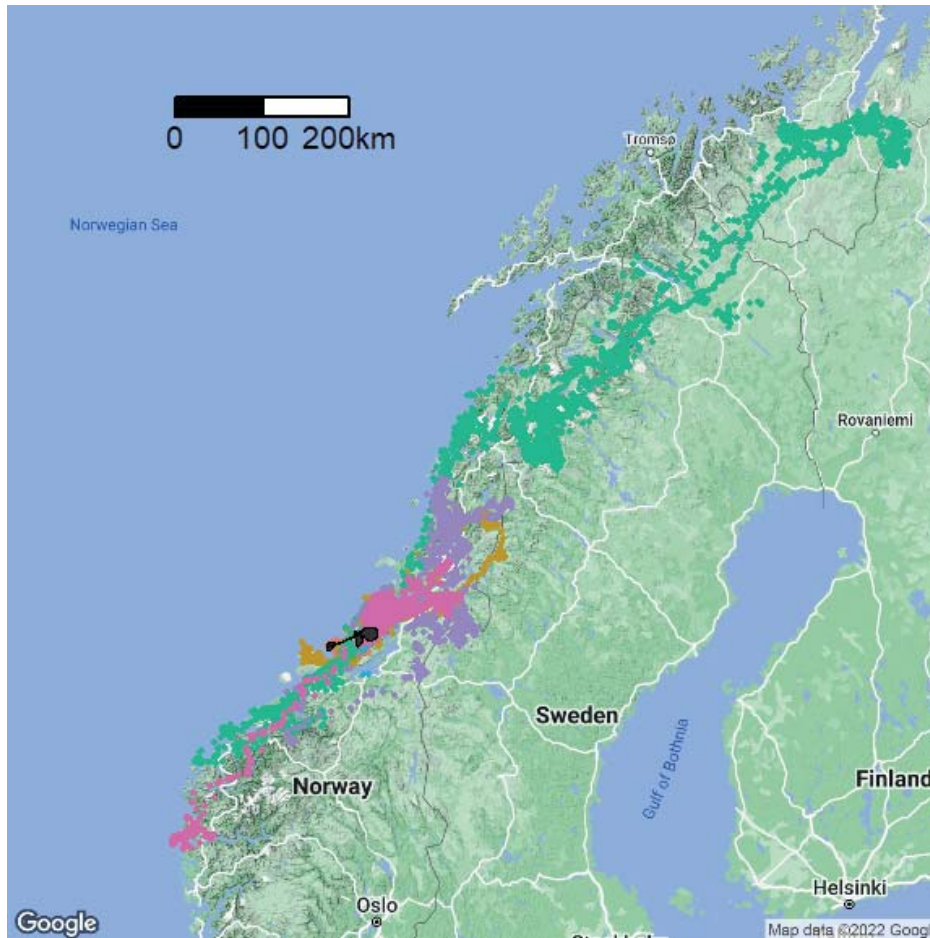


Figure 2: Points representing the large-scale movements of the six non-territorial eagles (GE04, GE05, GE06, GE08 & GE09) compared to the small-scale movements of the territorial eagles (GE03 & GE07, represented in black).

Patch residency analysis for non-territorial individuals

The percentage of GPS locations falling within reindeer grazing areas was on average 67%, while it was 27% within areas with sheep (range between individuals 37% to 85% for reindeer and 5,5% to 62% for sheep). A total of 62% of the time was spent in mountainous areas (range individually from 25% to 84%). There was low correlation between the three different variables (Table 2), enabling the inclusion of both mountain/forest and reindeer presence in the same model to tease apart their relative influence. The mean residency time across all eagles and seasons was one day for 1000 meters, three days for 5000 meters and seven days for 10 000 meters.

Table 2: Correlation matrix from the hetcor-function in the polycor package in Rstudio. Numbers between 0.6 and -0.6 indicates low correlations and allows the variables to be included in the same model. The diagonal 1 pattern means that everything is 100% correlated with itself, while 'Polychoric' is a categorical correlation coefficient.

	Sheep presence	Reindeer presence	Month	Above/below the tree line
Sheep presence	1	Polychoric	Polychoric	Polychoric
Reindeer presence	-0.37	1	Polychoric	Polychoric
Month	-0.20	0.38	1	Polychoric
Above/below the tree line	-0.48	0.49	0.26	1

Model selection resulted in three different models for the three different radii. For the 10 000-meter radius, the final model included sheep and reindeer presence, month (June, July and August), mountainous area (if it was above or below the tree line) and the interaction between month and sheep presence. Only the interaction between reindeer presence and month fell out during the LRT. For the 5000-meter radius, the full model was selected as the best. For the 1000-meter radius, the final model included all variables except the two interaction variables between month and reindeer presence and month and sheep presence.

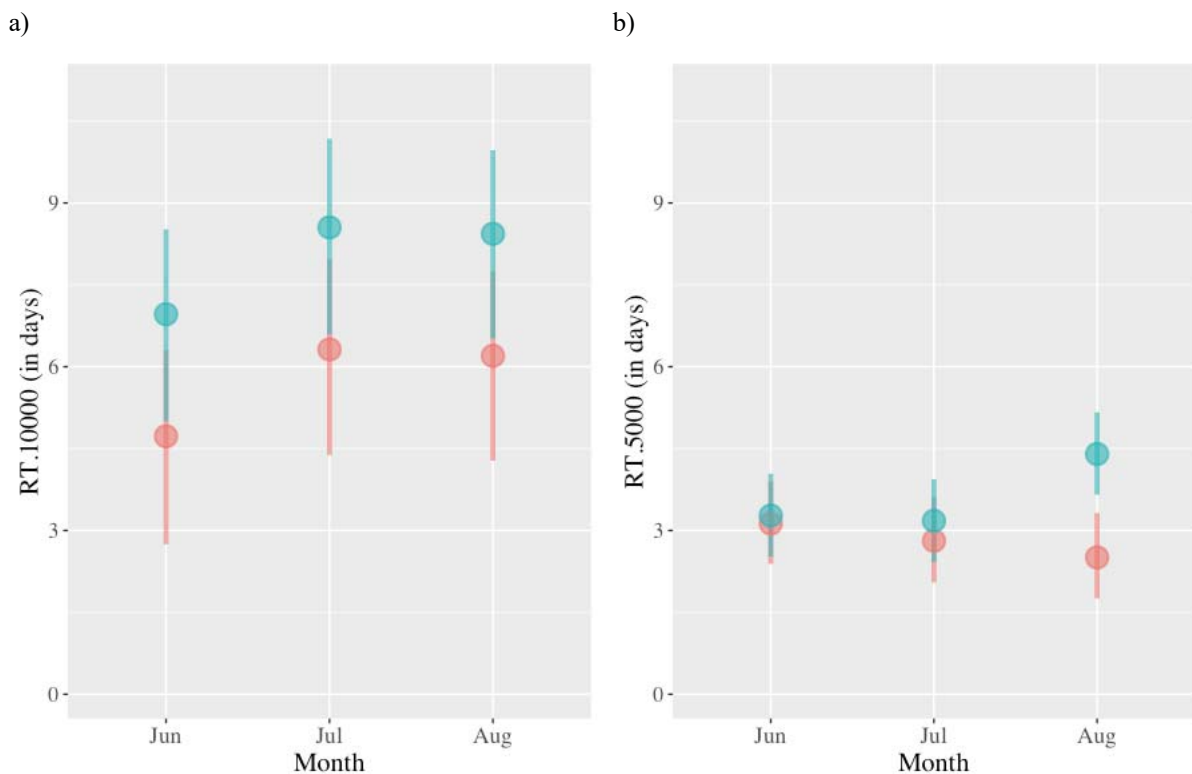
Reindeer

The final models for all three scales found that eagles spent more time in patches with reindeer present than in patches without, but the interaction with month depended on spatial scale. For the 10 000-meter radius, the eagles spent less time at each patch in June than in July and August but still stayed longer in patches with reindeer (seven days) than without (four and a half days). In July and August, the mean patch residency was eight days if reindeer were present in the patch, while it dropped to six days if reindeer was absent (Figure 3).

For the 5000-meter radius, the pattern changed. Here the eagles spent around three days in each patch in both areas with and without reindeer present, with close to no difference between the two in June and July. An increase in patch residency was spotted in August, where the eagles stayed in patches with reindeer present for almost four and a half days while they left patches without reindeer after two and a half (Figure 3). For the 1000-meter radius,

the eagles spent a little more than one day in patches with reindeer present and a little less than one day in patches without in June. They had shorter visits in July and August, where they spent a little less than a day in patches with reindeer and only around half a day in patches without (Figure 3).

Despite the significant statistical effects of reindeer, there was high individual and temporal variation in response to reindeer presence (Figure 4). The confidence limits in the parameter estimates for patch residency time are overall large, implying that there is much variation in the response to presence of reindeer over time. This view is corroborated when looking at the raw data. Although a statistically significant effect, it is no strong increase when flying into reindeer areas or no strong visual signal of sudden drops in patch residency time when flying out at any of the scales considered.



c)

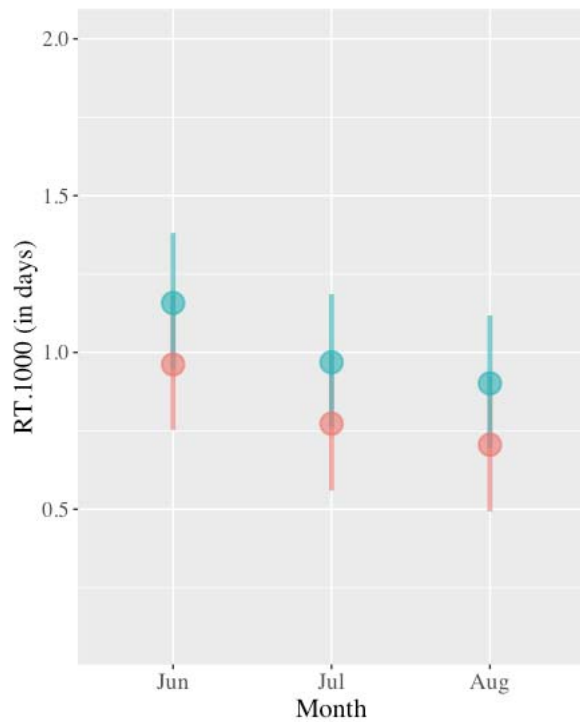


Figure 3: Patch residency time at three different radii for non-territorial eagles during summer: 10 000 meters (a), 5000 meters (b) and 1000 meters (c). Blue dots represent areas with reindeer present while red dots represent areas without reindeer present. Error bars are 95% confidence limits.

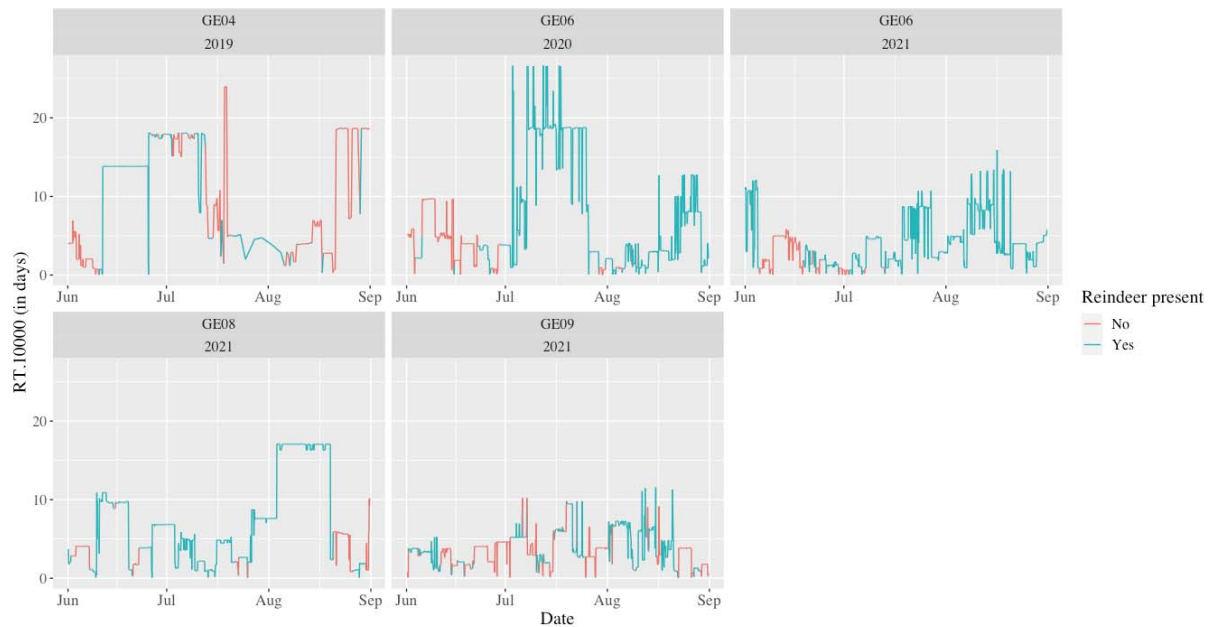


Figure 4: Patch residency time for non-territorial individuals in areas with (blue) and without reindeer (red) present, with radius 10 000 meters. The plot shows big yearly, monthly and individual variation.

Sheep

The effect of sheep presence on patch residency time was much less consistent than for reindeer. The final models for all three scales show that patch residency increased and decreased depending on the radii investigated, but the interaction with month also depended on spatial scale. In June, for the 10 000-meter radius, the eagles spent about four days in both patches with and without sheep, while it stayed for six days in patches with and without sheep present in July. August was the only month with a significant difference, where the eagles on average spent five days in patches without sheep present and three in patches with sheep (Figure 5).

For the 5000-meter radius, the patch residency was lower in general, although the pattern was similar to the 10 000-meter radius. The eagles spent three days in patches both with and without sheep in June and July. In August, they spent less time at each stop in general, with three days in patches without sheep and one and a half day in patches with sheep (Figure 5). The 1000-meter model was in this case not significant and is therefore excluded.

There was individual and temporal variation in areas with sheep present. For example, GE04 had a patch residency of more than 20 days mid-July in 2019 while GE02 barely stayed in a spot for five days during the same period, both at a 10 000-meter radius (Figure 6).

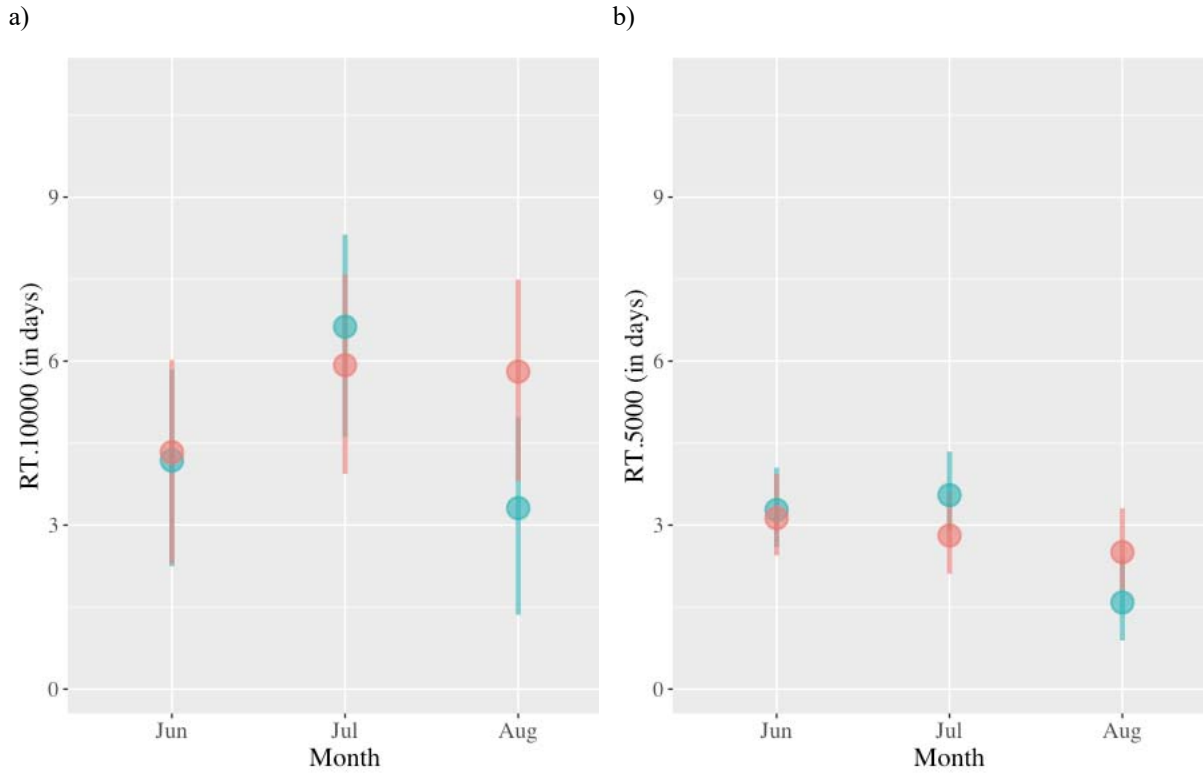


Figure 5: Patch residency time at two different radii for non-territorial eagles during summer: 10 000 meters (a) and 5000 meters (b). Blue dots represent areas with sheep present while red dots represent areas without sheep present. Error bars are 95% confidence limits.

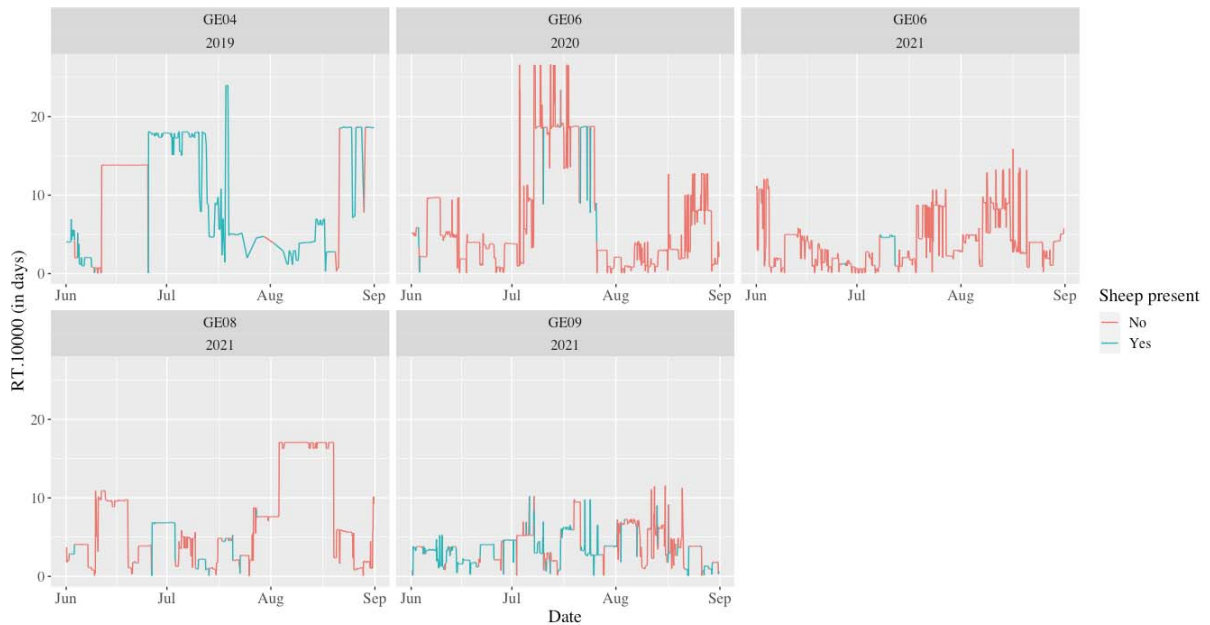


Figure 6: Patch residency time for non-territorial individuals in areas with (blue) and without (red) sheep present, for radius 10 000 meters. The plot shows big individual, monthly and yearly variation.

Mountainous areas

Eagles spent the same number of days in patches above and below the tree line for all three months, with only minor differences. In June, the eagles spent around four and a half days in each patch, while the patch residency increased in July and August. During these months the eagles spent around six days in each patch (Figure 7). Although there was a significant effect of mountainous habitat, it was much less than the effect of livestock presence.

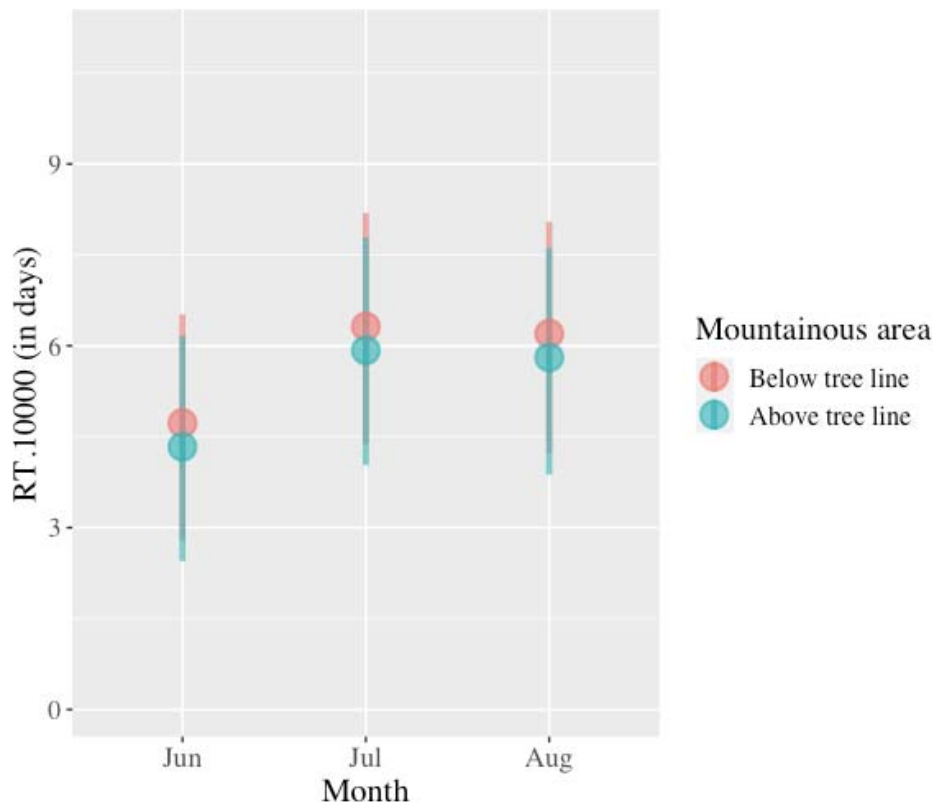


Figure 7: Patch residency time at a 10 000-meter radius for non-territorial eagles during summer, with patches above the tree line (blue) or below the tree line (red). The presence values of mountainous areas was set to 1 for above and 0 for below the tree line. Error bars are 95% confidence limits.

Discussion

In my thesis I have studied the ranging behavior of territorial versus non-territorial GPS-marked golden eagles and the effect of reindeer and sheep presence on patch residency time in summer. I found that territorial eagles, despite expanding their territory during the non-breeding season, remained resident in their territory on a large scale and did not roam inland or north in pursuit of calving areas of reindeer. I also found that non-territorial eagles on average spent more time when entering areas with reindeer present and that the effect of

sheep presence and habitat was much smaller. In reindeer areas, the mean patch residency time within a radius of 10 000 meters was around eight days, but with large individual and monthly variation. Shifts in the main prey populations might cause the variations. My thesis provides bearings for the management of how long a potential culprit normally resides in an area it has conducted loss, and indicates that it will be tough to link a specific individual to a specific damage event.

Home range analysis

Territoriality of golden eagles and to which extent they stay within territory borders vary between locations. In North-America, most eagles breeding in Alaska and Canada migrate to winter grounds. In contrast, the eagles in the south are resident and tend to stay within their territory throughout the year (Katzner et al., 2020). In line with this, I found that adult golden eagles were territorial on a large scale year-round in central Norway. However, the home range analysis show that two out of three individuals expand their territory after the breeding season ended. GE03 (male) flew out to the Tarva island group in Ørland between September and November in both 2019 and 2021. According to Artsdatabanken (2022), there are yearly observations of seabirds and waterfowl in this area, which can be the motivator for GE03 to leave the territory for a certain amount of time during the non-breeding season. Sur et al. (2020) suggests in their research that territory defense and territorial behavior may be more energy demanding than foraging. It is a known phenomenon that resident raptors up their territory defense during the pre-laying period and breeding season (Katzner et al., 2020; Margalida & Bertran, 2005; Watson, 1997). Since the female is more bound to the nest during the breeding season, the male most likely will have the main responsibility regarding the territory. When the breeding season ends and the female no longer is bound to the nest, she can help defend the territory. A possible explanation can be that the female defends the territory while GE03 seeks out aggregations of prey to recharge.

GE01 had varying transmitter settings, with a different number of locations being sent throughout the period he carried the GPS. Sometimes positions were registered hourly, while at other times, positions were registered all the time, several times per minute. This may have affected the accuracy of the estimation of the home range size since many locations would be registered in a spot the eagle stayed at for 20 minutes, and only five positions would be registered at a location where he spent five hours. However, the home range results from

GE01 are relatively similar to those of the two other territorial males. The main difference lays in the non-breeding season, where his territory is smaller than the two others'. Therefore, the results seem to be okay to represent the home range size during the breeding season, but the results from the non-breeding season should be treated with caution.

Patch residency analysis

My results show that the eagles spent more time in areas with reindeer present than in areas with sheep present. A possible explanation for this can be that eagles prefer reindeer over sheep. Reindeer is a food source that naturally can be found in Norway because of the wild reindeer herds, and maybe therefore a natural prey the eagles are adapted to utilize. Not much research has been conducted on golden eagles' preferences between reindeer and sheep. However, research shows that in addition to the golden eagle, the lynx (*Lynx lynx*) also have been reported as a tortfeasor on more reindeer than sheep (Mattisson et al., 2014). On the other hand, although the statistics show a slight preference of sheep over reindeer for wolverines (*Gulo gulo*), Landa et al. (1997) mention that reindeer was the basic prey during the denning period in February – March. This gives an impression of a preference for reindeer (both on a year-round and/or a seasonal basis) for several large carnivores in Norway, possibly including the golden eagle, but more research on the matter is a necessity.

Sheep seem to have no significant impact on patch residency. The patch residency analysis only showed a weak effect for the 10 000-meter radius model in august, where the eagles spent more time in areas without sheep present than in those with. Based on these results, it can be assumed that sheep have little or no impact on whether the eagles slow down or not. However, these findings should be treated with caution, considering that Fosen previously reported high numbers of lambs lost to golden eagles (Stien et al., 2016). Over the past years, the number of losses has decreased (Stien et al., 2021, unpublished), but more research will be necessary to understand these yearly variations.

Even though the results clearly show that patch residency increased in patches with reindeer, there were still big individual and seasonal variations. For example, GE04 spent more than 20 days in patches with sheep available in the middle of July 2019, while around five days were spent in patches with reindeer available. These results contradict my general results, which show that the eagles generally spent more time in areas with reindeer than sheep. GE06, on

the other hand, spent more than 25 days in patches with reindeer in the middle of July 2020, and almost no time in patches with sheep present. As a third example, GE09 generally had a much lower patch residency and spent almost as much time in patches with reindeer present as in patches with sheep. GE09 also had a low seasonal variation compared to the other eagles. These variations could be explained by the alternative prey hypothesis. The alternative prey hypothesis suggests that when the abundance of the predator's main prey is low, it will switch its diet to the alternative prey, which will result in a negative correlation between the density of the main prey and the predation pressure on the alternative prey (Angelstam et al., 1984; Pöysä et al., 2016). Watson (1997) mentions that the golden eagle tends to be a specialist when its main prey is abundant, but that it widens its diet and becomes a generalist in years of low main prey abundances. In Fennoscandia, the main prey for golden eagles is hare and ptarmigan, while livestock is an alternative food source. Many seasonal and individual fluctuations might therefore be explained by variations in the hare- and ptarmigan populations. Hence, the predation on both sheep and reindeer will most likely be higher when the eagles stay in an area with low access to their main prey or in years with bad hare- and ptarmigan abundance.

Culling of problematic individuals has been considered as a management measure in Norway. This has been proven difficult, mainly because you only get permission to kill the exact same individual that has caused the damage (Miljødirektoratet, 2019). The patch residency analysis showed that non-territorial individuals on average spent eight days in patches with reindeer present and four and a half days in patches with sheep present within a 10 000-meter radius. When looking at a livestock loss scenario, the dead animal would first have to be confirmed as a golden eagle kill (with either professional evaluation or photographic proof). Then the owner would have to apply for culling, which has to be evaluated and processed by the county governor (Miljødirektoratet, 2018a; Miljødirektoratet, 2018b), and then mobilize for culling after receiving approval. All in all, it is a long and time-consuming process that could take weeks and months. When looking at the patch residency of non-territorial individuals, it shows that the culprit most likely will be far gone at the time when approval for culling will be given. Therefore, it is an unsuitable management option at this point in time since the uncertainties are too big.

Conclusion and future recommendations

The home range analysis for the three territorial males shows that the territory size increased during the non-breeding season for all three eagles. Two out of three individuals made small-scale movements during the non-breeding season, but on a large scale they remained resident. I suggest that these movements might be motivated by food abundances and the need to recharge after a long and energy-demanding breeding season. One territorial individual had varying GPS settings that might have affected the estimation of home range size. However, the results were evaluated to be representative since they are similar to those of the two other territorial males.

Patch residency analysis shows that eagles spent more time in patches with reindeer present at all three radii and that sheep had almost no effect on whether the eagles slowed down or not. An explanation for this might be a preference for reindeer. I highlight the importance of more research regarding the impact of sheep on patch residency since my results of low to no impact contrast with previous research conducted by Stien et al. (2016). My results show significant seasonal and individual variations in patch residency, which can be explained by fluctuations in the hare and ptarmigan populations. According to the alternative prey-hypothesis, livestock is the alternative prey, and depredation on both reindeer and sheep may therefore be affected by variations in the main prey populations from area to area. Again, more research on the topic is needed to say for sure. Based on the patch residency analysis results, I conclude with that culling of problematic individuals as a management measure is unsuitable. This because of the uncertainties and difficulties connected to finding the culprit.

Why is this thesis relevant to management and livestock farmers? By knowing more about golden eagles' behavior, movement strategies, and preferences it might be easier to find sustainable and effective management options that will benefit both sides of the conflict. With more knowledge about eagles' temporal variation, behavior, territoriality and life strategies, farmers may be able to adjust their daily- and summer pasture routines and possibly prevent some damage and loss of livestock. This thesis has described the residence time of eagles within three different radii, which is relevant when trying to tie specific individuals to losses of sheep and reindeer. It will therefore hopefully contribute to a development of the management of golden eagles.

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Appendix

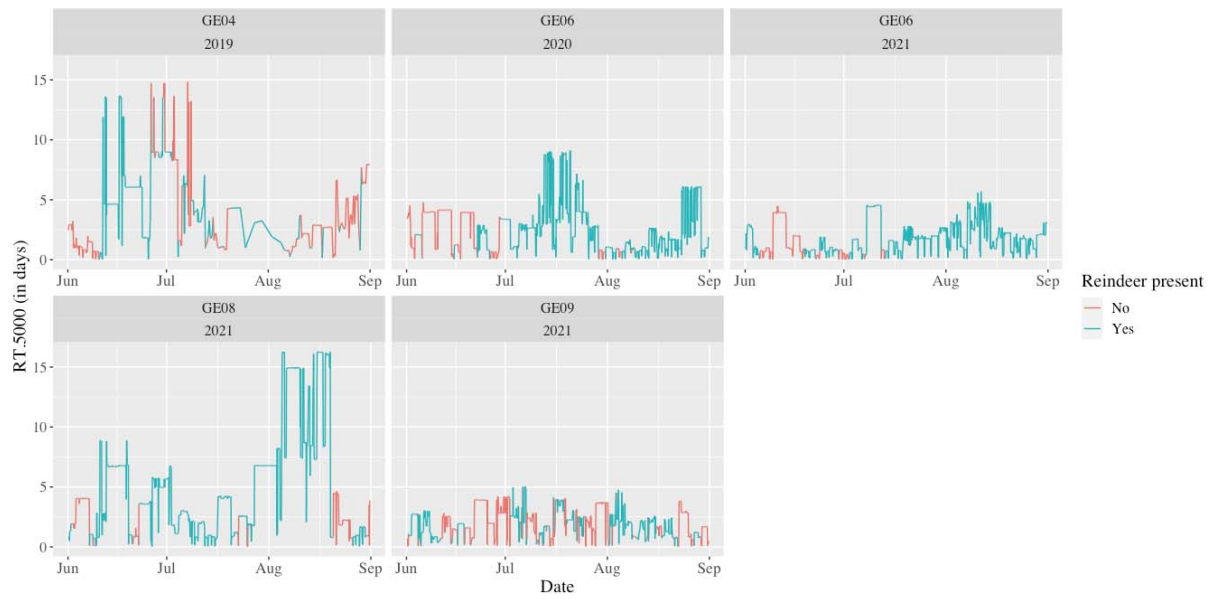


Figure 8: Patch residency time for non-territorial individuals in areas with/without reindeer, with radius 5000 meters.

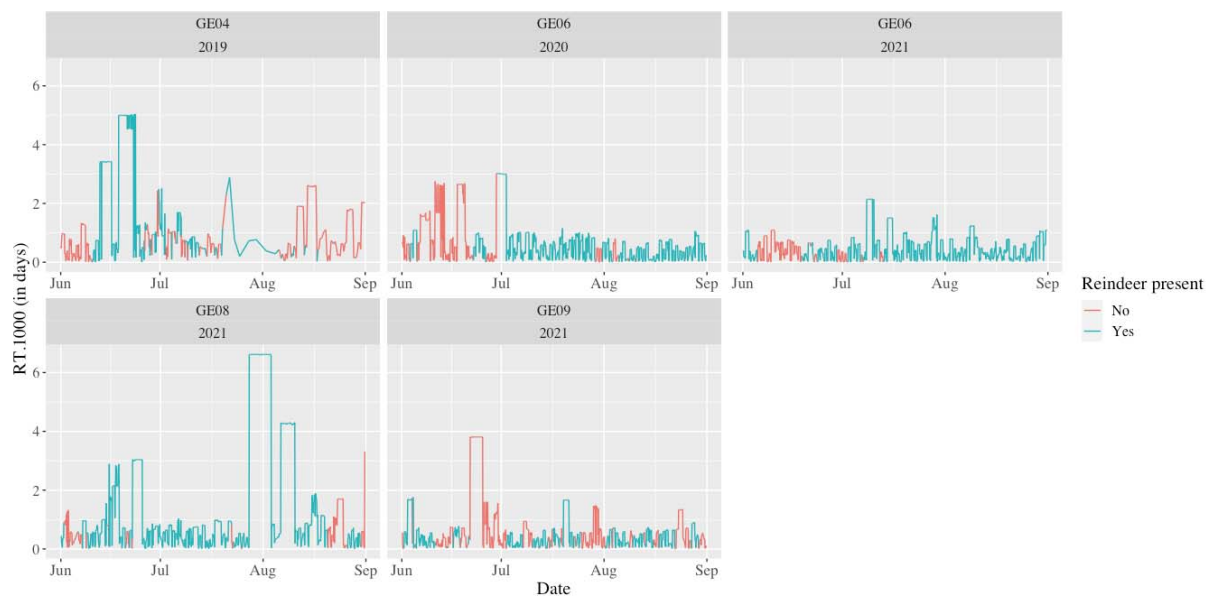


Figure 9: Patch residency time for non-territorial individuals in areas with/without reindeer, with radius 1000 meters.



Figure 10: Patch residency time for non-territorial individuals in areas with/without sheep, with radius 5000 meters.

Table 3: Full table showing the t-values (raw data) for each variable and the interactions between the variables for the 10 000-meter radius model. T-values are significant if they are higher than 2 or lower than -2. A positive significant value means the patch residency time increased, while a negative significant value means that the patch residency time decreased.

Fixed effects	Estimate	Std. Error	t-value
(Intercept)	4.91	1.47	3.34
Reindeer present	1.71	0.09	20.06
Sheep present	-0.34	0.10	-3.42
Month (July)	0.83	0.15	5.75
Month (August)	0.67	0.14	4.86
Above the tree line	-0.39	0.07	-5.82
Interaction: reindeer presence and month (July)	0.90	0.15	5.90
Interaction: reindeer presence and month (August)	0.82	0.16	5.25
Interaction: sheep presence and month (July)	1.07	0.14	7.82
Interaction: sheep presence and month (August)	-1.80	0.19	-9.50

Table 4: Full table showing the t-values (raw data) for each variable and the interactions between the variables for the 5000-meter radius model. T-values are significant if they are higher than 2 or lower than -2. A positive significant value means the patch residency time increased, while a negative significant value means that the patch residency time decreased.

Fixed effects	Estimate	Std. Error	t-value
(Intercept)	1.19	0.19	6.42
Reindeer present	0.12	0.02	6.06
Sheep present	-0.41	0.02	-18.25
Month (July)	-0.34	0.03	-10.34
Month (August)	-0.48	0.03	-15.23
Above the tree line	-0.25	0.02	-16.48
Interaction: Reindeer presence and month (July)	0.19	0.03	5.61
Interaction: Reindeer presence and month (August)	0.25	0.04	7.06
Interaction: Sheep presence and month (July)	0.07	0.03	2.31
Interaction: Sheep presence and month (August)	0.24	0.04	5.60

Table 5: Full table showing the t-values (raw data) for each variable and the interactions between the variables for the 1000-meter radius model. T-values are significant if they are higher than 2 or lower than -2. A positive significant value means the patch residency time increased, while a negative significant value means that the patch residency time decreased.

Fixed effects	Estimate	Std. Error	t-value
(Intercept)	2.98	0.62	4.77
Reindeer present	0.05	0.05	1.17
Sheep present	0.18	0.05	3.30
Month (July)	-0.49	0.08	-6.22
Month (August)	-0.87	0.07	-11.64
Above the tree line	0.10	0.04	2.85
Interaction: Reindeer presence and month (July)	0.27	0.08	3.27
Interaction: Reindeer presence and month (August)	1.20	0.09	23.48
Interaction: Sheep presence and month (July)	0.64	0.07	8.63
Interaction: Sheep presence and month (August)	-1.12	0.10	-10.95



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