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NINA Report

Movement patterns and diurnal activity of golden eagles in Norway

Jennifer Stien, Jenny Mattisson, Audun Stien



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Movement patterns and diurnal activity of golden eagles (*Aquila chrysaetos*) in Norway

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Adult golden eagle in Steinkjer municipality © NINA

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Abstract

Stien, J., Mattisson, J. & Stien, A. 2025. Movement patterns and diurnal activity of golden eagles (*Aquila chrysaetos*) in Norway. NINA Report 2557. Norwegian Institute for Nature Research.

The golden eagle (*Aquila chrysaetos*) is the only large raptor in Norway with a national monitoring program aimed at species conservation and management. It is also the only large avian carnivore where economic compensation for losses due to predation is paid to Norwegian livestock owners. In the current report we use GPS-position data from nine golden eagles to contribute to the general knowledge of the movement ecology of golden eagles and to evaluate whether there is evidence for golden eagles to be attracted spatially to domestic prey. We describe the seasonal movement patterns of the GPS-tagged individuals, including evaluating whether natal site philopatry is common, the diurnal patterns of movement and the seasonal use of areas in relation to livestock presence and / or density.

The territorial birds stayed within their relatively small territories throughout the year, while non-territorial individuals showed large-scale movements, including movement across the national borders to Sweden and Finland and covering both coastal and inland areas. Non-territorial individuals were fairly consistent between years with respect to both latitudinal distance covered and, at a crude scale, the area that they used. Daily movement distances varied considerably between individuals but monthly mean straight line daily distances were typically less than 23 km. All non-territorial individuals showed behavior indicative of natal philopatry as they returned to the same area in early summer every year. However, they did not spend prolonged periods in these areas. Both territorial and non-territorial birds showed a strong diurnal pattern of activity and movement, being most active and travelling longest distances during the middle of the day. There was no strong evidence for individuals to be attracted to either reindeer calving areas or sheep grazing lands in late spring and early summer, when calves and lambs are small and most vulnerable for eagle predation. Thus, large-scale movements of non-territorial birds do not appear to actively involve tracking of livestock prey at these times of the year.

It is well established that golden eagles kill both reindeer and sheep, and that small calves and lambs are particularly vulnerable to eagle predation. Future work should focus on obtaining unbiased estimates of the extent of livestock losses, and in situations when losses are high, find efficient methods to reduce them. We believe GPS-tracking of both non-territorial and territorial birds may contribute towards this work. GPS-tracking more non-territorial birds will allow a better evaluation of whether they are attracted to reindeer calving lands around the time of calving and also to sheep grazing areas early on in the grazing season, while tracking a larger number of both territorial and non-territorial birds will enable a more complete picture of golden eagle diet to be documented.

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Sammendrag

Stien, J., Mattisson, J. & Stien, A. 2025. Movement patterns and diurnal activity of golden eagles (*Aquila chrysaetos*) in Norway. NINA Report 2557. Norwegian Institute for Nature Research.

Kongeørnen (*Aquila chrysaetos*) er den eneste store rovfuglen i Norge med et nasjonalt overvåkingsprogram rettet mot bevaring og forvaltning av arten. I tillegg er det den eneste fuglearten hvor tap som følge av predasjon gis rett til erstatning til norske husdyreiere av sau og rein. I denne rapporten analyserer vi flere års GPS-posisjonsdata fra ni kongeørner for å få bedre kunnskap om bevegelsesøkologien kongeørn. En hovedmålsetning med analysene er å evaluere om kongeørner blir tiltrukket til områder med husdyr. Først beskriver vi de sesongmessige bevegelsesmønstrene til de GPS-merkede individene. Deretter evaluerer vi om de synes å returnere til området de ble født hver sommer, døgnvariasjon i aktivitet og bevegelses-mønstre og den sesongmessige bruken av områder i forhold til tilstedeværelsen og tettheten av husdyr.

De territorielle kongeørnene holdt seg innenfor sine relativt små territorier gjennom hele året, mens de ikke-territorielle individene viste storskala bevegelser gjennom året, inkludert bevegelser over landegrensene til Sverige og Finland og bruk av både kyst- og innlandsområder. Ikke-territorielle individer var relativt konsistente mellom år med hensyn til både de breddegradene de forflyttet seg og, grovt sett, området de brukte. Daglige bevegelsesdistanser varierte betydelig mellom individer, men i gjennomsnitt forflyttet de seg mindre enn 23 km i rett linje per dag. Alle ikke-territorielle individer viste atferd som indikerte at de returnerte til området de ble født. De returnerte til det samme området på forsommeren hvert år, men de tilbrakte ikke lengre perioder i disse områdene. Både territorielle og ikke-territorielle fugler viste et sterkt døgnmønster i aktivitet og bevegelse; de var mest aktive og fløy de lengste avstandene midt på dagen. Det var ingen sterke bevis for at kongeørnindividene ble tiltrukket til beiteområder for sau eller kalvingsområder for rein under kalvingstidene. Bevegelsesmønsteret til ikke-territorielle fugler synes derfor ikke ut til å aktivt oppsøke områder husdyr i den perioden de er relativt lett tilgjengelige byttedyr.

Det er vel etablert at kongeørner kan drepe både rein og sau, og at små kalver og lam er særlig utsatt for predasjon fra ørn. Fremtidig arbeid bør fokusere på å skaffe gode estimater på omfanget av husdyrtap, og i situasjoner hvor tapene er store, finne effektive metoder for å redusere dem. Vi mener GPS-sporing av både ikke-territorielle og territorielle fugler vil bidra til dette. Ved å spore flere ikke-territorielle fugler vil man få en bedre evaluering av om de trekker mot sauebeiteområder og kalvingsland for rein rundt kalvingstidspunktet. I tillegg kan en bedre forståelse av kongeørnens diett oppnås ved å studere GPS-merkede ikke-territorielle og territorielle fugler.

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Contents

Abstract	3
Sammendrag	4
Contents	5
Foreword	6
1 Introduction	7
2 Methods	9
2.1 GPS-tagged golden eagles	9
2.2 Data processing and analyses	9
2.3 Seasonal movement patterns and natal philopatry	9
2.4 Diurnal activity patterns	10
2.5 Time spent in livestock areas	10
2.5.1 Time spent in sheep summer rangelands and reindeer calving lands	11
2.5.2 The effect of sheep density on time spent in sheep summer rangelands	11
3 Results	12
3.1 Seasonal movement patterns and natal philopatry	12
3.2 Diurnal activity patterns	20
3.3 Time use in livestock areas	22
3.3.1 Time spent in sheep summer rangelands and reindeer calving lands	22
3.3.2 Effect of sheep density on time spent in sheep rangelands	23
4 Discussion	24
4.1 Seasonal and diurnal patterns	24
4.2 Use of livestock areas	25
5 Appendix	27
6 References	35

Foreword

During the research project “The role of golden eagles in the loss of lambs on Fosen Peninsula” (Kongeørn som skadevolder på lam på Fosen), carried out between 2017-2022, ten adult golden eagles and two adult sea eagles were caught and fitted with GPS-devices. GPS data gives a unique insight into the area use of both territorial and non-territorial golden eagles and inference of their behavioural activity and diet. Initial reporting of area use from analyses of the movement data (in Stien et al. 2023 and Mattisson et al. 2023), indicated that territorial individuals remained in their territories year-round while non-territorial individuals used large areas and also crossed into Sweden and Finland.

In the current report we investigate the movement data of these marked golden eagles in greater detail, focusing on seasonality of movements, diurnal activity and time spent in sheep and reindeer rangelands of territorial and non-territorial individuals. The work for this report was financed by a predator-livestock conflict reduction grant from the Norwegian Environment Agency.

We would like to thank Jan Ove Gjershaug and Alv Ottar Folkestad for help in ageing the individuals we caught and GPS-marked, from pictures taken at the time of capture.

20.01.2025 Jennifer Stien

1 Introduction

The golden eagle (*Aquila chrysaetos*) has a worldwide distribution, occurring across the Palearctic and north America (Katzner et al. 2020). It is a long-lived, territorial species and populations consist of both a breeding segment, largely consisting of individuals that are four years old or older, and a non-breeding segment, largely consisting of immature individuals (Katzner et al. 2020).

The golden eagle is highly flexible in terms of seasonal movements. In northern latitudes of North America territorial individuals have seasonal southward winter migrations, while studies across its range at more temperate latitudes, including central Sweden and Norway, indicate that territorial individuals are mostly permanent residents (Watson et al. 2010, Moss et al. 2014, Katzner et al. 2020, Stien et al. 2023, but see Singh et al. 2021). During the breeding season, territorial individuals tend to stay within their home range. Territory size varies from 20 km² to 320 km², depending on the food resources available. Non-territorial individuals disperse from their natal territory in their first autumn (Whitfield et al. 2023, Katzner et al. 2020, Watson 2010). Thereafter they roam widely, over distances from hundreds to several thousand kilometres, with latitude playing a part in the scale and seasonal pattern of movement (Nygård et al. 2016, Singh et al. 2021, Sidiropoulos et al. 2024, Whitfield et al. 2024). Immature individuals from nests in Finnmark, northern Norway, have been shown to migrate south each winter and return to the north in the summer (Nygård et al. 2016). In both Scotland and United States, immature individuals have been documented returning to their natal area in subsequent summers and also to establish territories as adults close to their natal territory (Steenhof et al. 1984, Grant et al. 1999, Murphy et al. 2018). However, the frequency of philopatry is unknown.

In common with other large raptors, the golden eagle is regarded as mainly being active during the daytime with little activity during the night (Dunstan et al. 1978, Natake 2013). During daylight hours, they spend a large amount of time perching and walking short distances (Katzner et al. 2020). Flying activity has been reported as most frequent during the middle of the day, partly making use of thermals for effective transport (e.g. Singh et al. 2021). However, there are few detailed studies regarding diurnal activities and daily time budgets.

Golden eagles are food generalists, exhibiting shifts in diet (Reynolds et al. 1969), and often predating the most abundant small and medium sized mammals and birds available (0.5 kg – 4 kg, Crandall et al. 2017, Watson 2010), but also scavenge on carcasses, especially during the winter (Mattisson et al. 2022, Singh et al. 2021). In Norway, their prey includes domestic livestock, mainly in the form of lambs and reindeer calves. Documented and estimated losses of both sheep and reindeer are compensated by the Norwegian government (rovbase.no). Lambs are typically born indoors and become vulnerable to golden eagle predation when they are let out on summer rangelands together with their mothers. Young, small lambs (< 8 kg) are more vulnerable to golden eagle predation than larger ones (Stien et al. 2023) but predation can also occur late on in the grazing season when the lambs have grown larger (20 - 35 kg, Stien et al. 2016, rovbase.no). The outdoor grazing season typically starts in late May, initially inside fenced pastures close to farm buildings, before animals are released onto grazing rangelands largely above the treeline in early June. Reindeer calves are also particularly vulnerable to golden eagle predation, and particularly during the calving period, which typically occurs in May and in remote mountainous areas.

In this report, we use GPS-position data from nine golden eagles that were GPS-tagged as part of a project to investigate the role of golden eagles on the loss of lambs in the Fosen peninsula in Trøndelag (Stien et al. 2023). Data is from four territorial-, and five non-territorial GPS-tagged individuals between 2018 and 2023, consisting of 13 bird-years. The main objectives with our analyses are to contribute to the general knowledge of the movement ecology of golden eagles and evaluate whether there is evidence for golden eagles to be attracted spatially to domestic prey. We first describe the seasonal movement patterns of the GPS-tagged individuals, focusing mainly on non-territorial individuals. This includes evaluating whether natal site philopatry is

common, expecting non-territorial individuals to return and remain in the same area in subsequent summers if they exhibit strong natal philopatry. We then investigate the diurnal patterns of movement of territorial and non-territorial individuals, expecting both groups to exhibit a strong diurnal pattern in their activity, with peak activity during the middle of the day and low activity during the night. In terms of daily activity, we expect territorial individuals to be more active throughout the year due to territory defense, and provisioning of food to offspring, and in the case of males to their mate during incubation and early chick rearing. We expected non-territorial individuals on average to fly longer distances when active, as they use much larger areas than territorial individuals. Finally, we investigate the seasonal use of areas in relation to livestock presence and/ or density. If individuals specialise on predation of young livestock (lambs and reindeer calves), we expect individuals to spend more time in reindeer calving lands in May, and sheep grazing lands in June when the young of these livestock are small and at their most vulnerable to predation. Furthermore, we expect the time spent in areas to increase with increasing density of livestock. We discuss the results in context of the wider literature, limitations with the current data and recommend ways forward to increase ecological knowledge of the species and its role as a predator of livestock.

2 Methods

2.1 GPS-tagged golden eagles

Golden eagles were caught during winter, at baits with bow nets and tagged with a solar charged GPS device (CTT-1000-BT3 3rd Gen, Cellular Tracking Technology) fitted using a backpack harness as part of the project “The role of golden eagles as predators of lambs on Fosen” (Stien et al. 2023). The catching period was between autumn and the end of winter 2017 – 2022. The battery charging capacity of the GPS devices depends on the intensity of sunlight exposure. Due to limited sunlight most of the year, and the energetic cost of obtaining and sending position data, the GPS devices were programmed to take positions once an hour between sunrise and sunset between September and May. In the summer sheep grazing season, positions were taken more frequently, once every 15 minutes from June to the end of August in 2017 - 2019, and from around 1 May to the end of August in 2020 -2023 to include the reindeer calving period.

2.2 Data processing and analyses

The data consisted of position data from nine individuals between 2017 and 2023, four territorial individuals and five non-territorial, and tracking periods for individuals between 116 days and five years (**Table 1**). At a daily scale this data covers all seasons for at least one individual bird-year (**Table 2**). Missing data in the tracking periods occurred mostly due to seasonal loss of battery charge. In addition, six months of missing data existed for GE07 as he lost the device on 29 May and was thereafter refitted with the same device in December of the same year. We standardized position data into equal time intervals dependent on the analysis (see each section). All analyses were performed in R Statistical Software (v4.1.2; R Core Team 2021).

Table 1. Summary of characteristics of individual golden eagles included in this study.

ID	Sex	Year hatched	Ter-ritorial	Tracking period
GE01	Male	≤ 2014	Yes	23.11.2017 – 22.04.2019
GE02	Male	2017	No	23.02.2018 – 14.03.2020
GE03	Male	≤ 2013	Yes	30.11.2018 – present
GE04	Male	2015	No	23.02.2019 – 26.03.2020
GE06	Male	2018	No	17.12.2019 – 14.03.2024
GE07	Male	≤ 2014	Yes	03.02.2020 – 24.02.2021*
GE08	Female	2019	No	06.12.2020 – 20.10.2023
GE09	Male	2020	No	08.12.2020 – present
GE10	Male	≤ 2014	Yes	09.12.2021 – 13.04.2023

*Captured twice. First device dropped off on 29.02.2020 and was refitted with the same device on 15.12.2020.

2.3 Seasonal movement patterns and natal philopatry

In the study of seasonal movement patterns and natal philopatry, we focused on non-territorial individuals as the territorial individuals stayed predominantly within their home ranges throughout the year.

The data from non-territorial individuals was filtered to one position per 24 hours to standardize the position frequency across seasons (**Appendix Table 1**) while maintaining sufficient resolution to describe the large-scale movement behaviour of these individuals.

Thereafter, the data was grouped by individual bird-year giving four individuals and 13 bird-years. We used net square displacement (NSD) in the R package 'amt' to investigate degree of natal philopatry. Net square displacement is the square of the distance from the first position of each bird-year and each subsequent position (i.e. is non-directional). We set the start of the bird year to June 1 as a previous study in Norway found that most individuals had returned to their natal area by this date (Nygård et al. 2016). Seasonal natal philopatry is suggested by NSD distances close to zero at the start of each bird year, indicating that the individual has returned to the area at which it was located on 1 June the previous year. As we do not have a priori knowledge of the position or extent of natal territories of the study birds, we interpreted a return within 50 km of the position on 1 June in the initial year of GPS-tagging as suggesting a return to the natal territory.

2.4 Diurnal activity patterns

In the study of the diurnal activity patterns of the eagles we included both territorial and non-territorial individuals but focused on the months with position intervals of 15 minutes. Furthermore, as the devices were programmed to collect data between the hours of sunrise and sunset, we only included hours with similar numbers of observations for each month. The resulting data included positions from May to September for four territorial and four non-territorial individuals covering a total of 19 bird-years. There were many observations of very short movement distances per 15-minute interval in the dataset. These short distance movements were likely to be due to walking or very short flights and possibly GPS measurement error in stationary birds. To distinguish these behaviors from active longer distance flights we categorized the movement distances according to whether they were less than, or more than 50 m and interpreted movements of less than 50 m as indicative of low activity such as walking, or short flights, and movement distances of more than 50 m as active birds.

We used generalized linear models (GLMs), assuming a binomial distribution and a logit link function, to model the diurnal pattern in the proportion of the time the birds were active throughout the day. In the analysis the categorical variable indicating whether movement was less than 50 m or more than 50 m was fitted as the response variable, while hour of the day was fitted as a categorical predictor variable. We explored patterns in activity using this approach with respect to months over the summer and bird territoriality. In addition, the average movement distance per 15-minute position interval was analysed for the subset of data when the birds were active (more than 50 m movement). The average movement distance was modelled using a GLM assuming a Gamma distribution and log link function, and hour of the day, territory status (territorial and non-territorial) and month were fitted as categorical predictor variables. The impact of temporal autocorrelation in movement distances was evaluated using a model incorporating first order temporal autocorrelation in residuals (AR1). The temporal autocorrelation was small and its effect on results were of no biological significance and therefore ignored in the final analyses.

2.5 Time spent in livestock areas

We used NIBIO's "beitelag" (grazing layer) shape files from 2018 to 2023 to define the spatial polygons for sheep rangeland (<https://kilden.nibio.no>). This data describes the distribution of organized sheep summer rangelands, and the number of the sheep breed Norwegian white sheep (Norsk kvit sau; NKS) in each polygon. NWS is the breed which accounts for the majority of sheep on rangelands and the main income for Norwegian sheep farmers. In addition, we used official shape files describing reindeer seasonal grazing areas in Norway (<https://kilden.nibio.no>) and Sweden (GIS data Länsstyrelserna© 2000-2008, SWECO) to define reindeer calving lands. We included golden eagle position data with intervals of 15 minutes from May to the end of August in the analyses. This included the main calving and summer period for reindeer, and the summer rangeland season for sheep (typically June – August). To be included in the analysis,

at least 10 days of data from a given month and individual had to be available. This gave data for the whole period May – end of August for the non-territorial individuals GE06, GE08 and GE09 (nine bird-years), and for the period June and July for GE04 (one bird-year). In months with sufficient data, none of our territorial individuals moved between sheep polygons or used reindeer calving lands so territorial individuals were excluded from this analysis. We used the package *sf* to classify the observed eagle positions with respect to the different sheep grazing districts and reindeer calving areas, using number of observations as a proxy for time spent in different areas.

2.5.1 Time spent in sheep summer rangelands and reindeer calving lands

We classified livestock polygons into four categories: sheep summer rangeland, reindeer calving land, both sheep summer rangeland and reindeer calving land, and livestock absent (i.e. areas not registered as used for sheep summer rangeland or reindeer calving land). We calculated the proportion of position observations in each livestock polygon category each month and then used this as the dependent variable in a GLM assuming the variance to be proportional to $\mu(1-\mu)$, where μ is the predicted proportion (a “quasi-binomial” distribution), and a logit link function. Livestock area category, eagle individual and month were included as independent variables. We expected that individuals would spend more time in polygons with sheep in June when the sheep are released on the rangelands and the lambs are at their smallest and most vulnerable to predation by golden eagles. Similarly, we expected individuals to spend more time in polygons with calving lands during the main calving period in May and early June, than post calving in July and August.

2.5.2 The effect of sheep density on time spent in sheep summer rangelands

We then investigated the effect of sheep density on time spent in the sheep rangeland polygons using the number of eagle position as a proxy for time spent in areas of different densities of sheep. We used a negative binomial GLM with a log-link function to model the number of eagle positions within a sheep rangeland polygon as a function of the density of sheep in the rangelands. In addition, we included the size of sheep rangeland polygon and the factor variable golden eagle individual as covariates. We expected that if eagles had a preference for lambs, individuals would spend more time in rangeland polygons with higher densities of sheep.

3 Results

3.1 Seasonal movement patterns and natal philopatry

All non-territorial individuals showed large-scale movements during the course of the year (**Figure 1**) including movement across the national border to Sweden and the use of both coastal and inland areas (**Figure 2, 3 and 4**). However, there was substantial individual variation in their movement patterns. One individual, GE06, was a long-distance mover, undertaking seasonal migration between Lebesby municipality in Finnmark in the summer, and Sande municipality in southern Møre og Romsdal in the winter, a north-south straight-line distance of 950 km and start to end point distance of 1274 km. Immediately after marking in December 2020, GE06 went south to Molde municipality in Møre og Romsdal before heading north again. The other non-territorial individuals moved over much shorter latitudinal distances (**Figure 5**), with the shortest range being carried out by GE08 which had an annual north-south distance of 160 km (**Table 2**) between Vefsn municipality in Nordland and Krokoms kommun in Jämtland, Sweden. However, data was lacking between October and February for GE08 this year (**Appendix, Table A1**) so that winter migration distance could have been longer. Individuals were fairly consistent between years with respect to both latitudinal distance covered and, at a crude scale, the spatial area that they used (**Table 2, Figure 2, 3 and 4**). Timing of movements was also fairly consistent for the long-distance migrator GE06 (**Figure 5**), heading north towards the end of March, and after the first autumn in which it headed south in mid-July, consistently headed south during the end of June or start of July in subsequent years. GE09 moved north consistently during February and March in all years, a seasonality similar to GE06. All individuals used both coastal and inland areas.

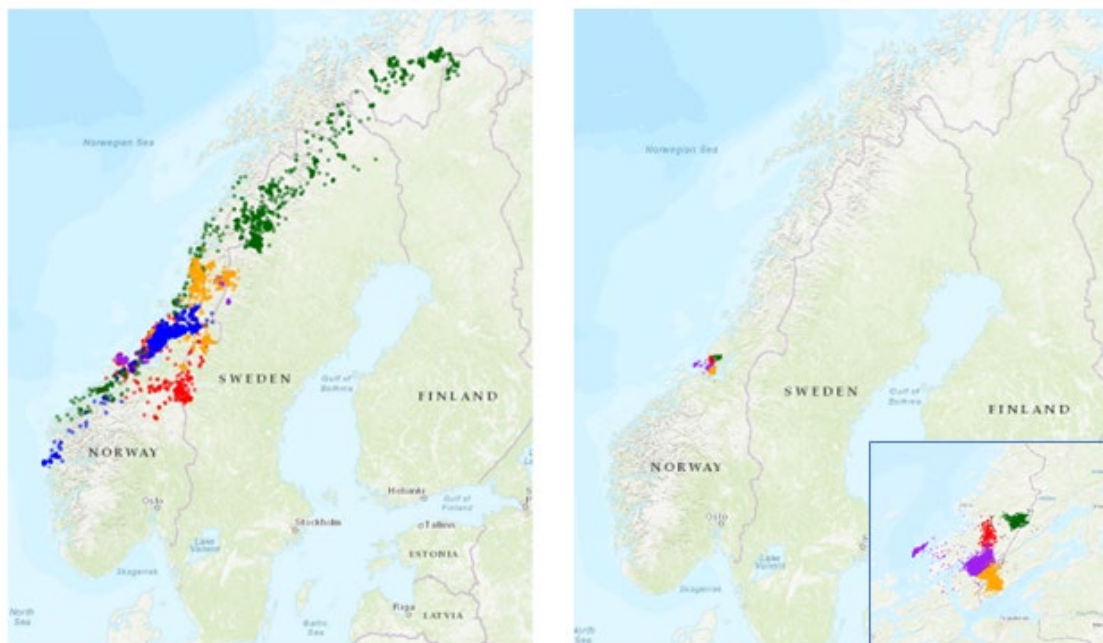


Figure 1. Movement of non-territorial individuals (left) between February 2018 and December 2023 from Stien et al. 2023. GE02: Red, GE04: purple, GE06: green, GE08: yellow, GE09: blue; and territorial individuals (right) GE01: Red, GE03: purple, GE07: green, and GE10: yellow between 2017 and 2023.

Daily movement distances varied considerably between individuals. Monthly mean straight line daily distances were typically less than 23 km (**Figure 6**). The longest consecutive daily distances occurred typically during months of the year with few observations due to lack of battery charge, however, this was also the time of year that individuals made the longest journeys with maximum daily distance varying from 115 km (GE04) to 355 km (GE09). The turning angle between daily movements varied widely and showed no elevated frequency close to the no change in angle of movement (turning angle = 0, **Figure 7**), suggesting that the direction of movement was in general not consistent between consecutive days.

All individuals showed evidence of returning to the area they were in on June 1 the first year after capture. This suggests that they may return to their natal area. However, overall, the timing of the return and period of time they stayed in the area varied considerably. While one individual passed through the area in May-June in subsequent years (GE06, **Figure 8**), others used an extended area nearby in the summer months and dropped back to what is likely to be their natal area several times in this period (GE08 and GE09, **Figure 8**). Also, some individuals spent a longer time period in what is likely to be their natal area, e.g. March-May (GE04) or June-August (GE02, **Figure 8**).

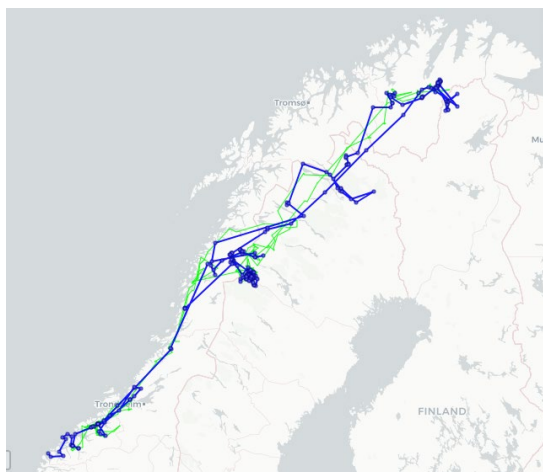
Table 2. Annual maximum north – south movement distance (km) for non-territorial individuals between 2018 and 2023.

ID	Maximum distance (km)
GE02_2018	257
GE02_2019	232
GE04_2019	296
GE06_2020	866
GE06_2021	950
GE06_2022	765
GE06_2023	776
GE08_2021	228
GE08_2022	160
GE08_2023	178
GE09_2021	477
GE09_2022	417
GE09_2023	471

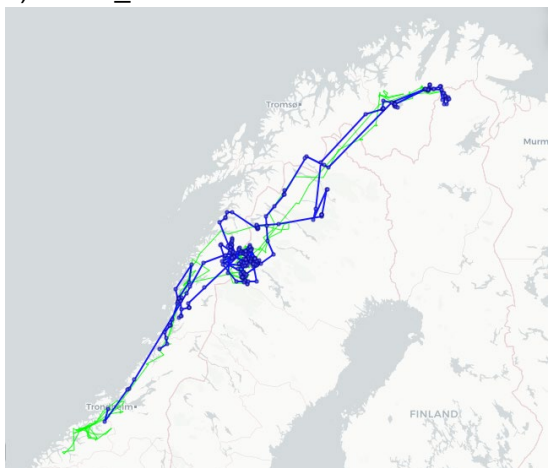
a) GE06_2020



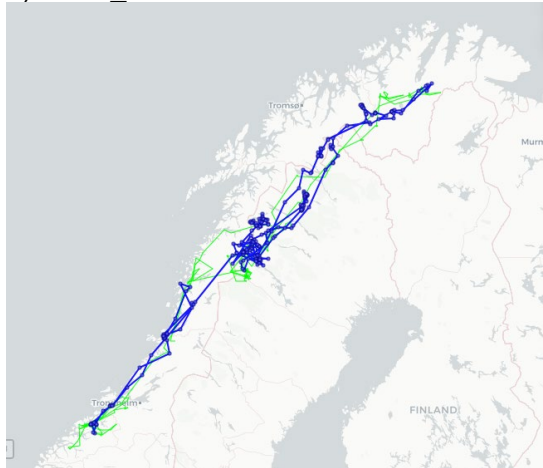
b) GE06_2021



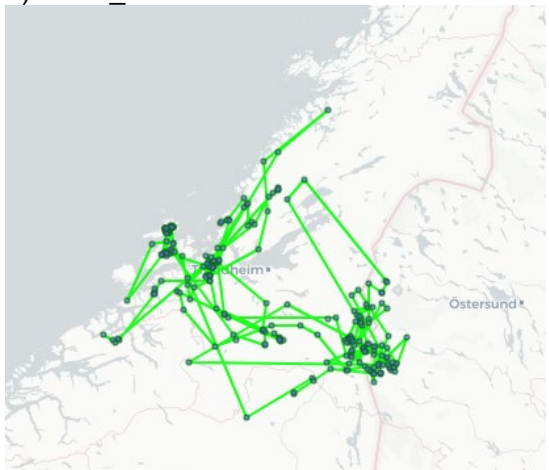
c) GE06_2022



d) GE06_2023



e) GE02_2018



f) GE02_2019

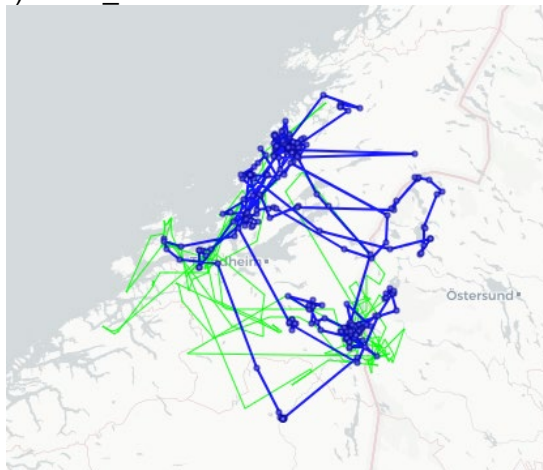
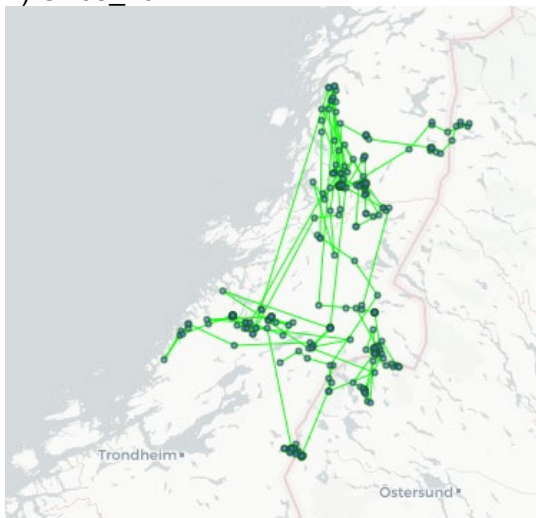


Figure 2. Annual daily movement of a – d) GE06 (2020-2023) and e – f) GE02 (2018-2019). The movement trajectory from the first year of data is plotted as a thin green line in subsequent years to aid visualisation of area covered.

a) GE04_2019



b) GE08_2021



c) GE08_2022



d) GE08_2023

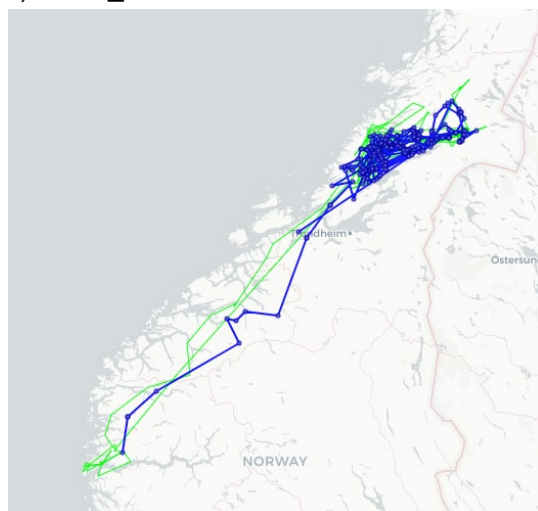


Figure 3. Annual daily movement of a) GE04 (2019), b – d) GE08 (2021-2023) where the movement trajectory from the first year is plotted as a thin green line in subsequent years to aid visualisation of area covered

a) GE09_2021



b) GE09_2022



c) GE09_2023

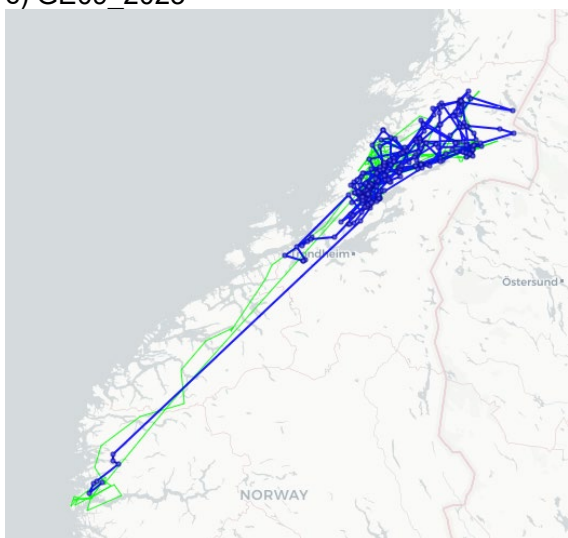


Figure 4. Annual daily movement of a) – c) GE08 (2021-2023) where the movement trajectory from the first year is plotted as a thin green line in subsequent years to aid visualisation of area covered.

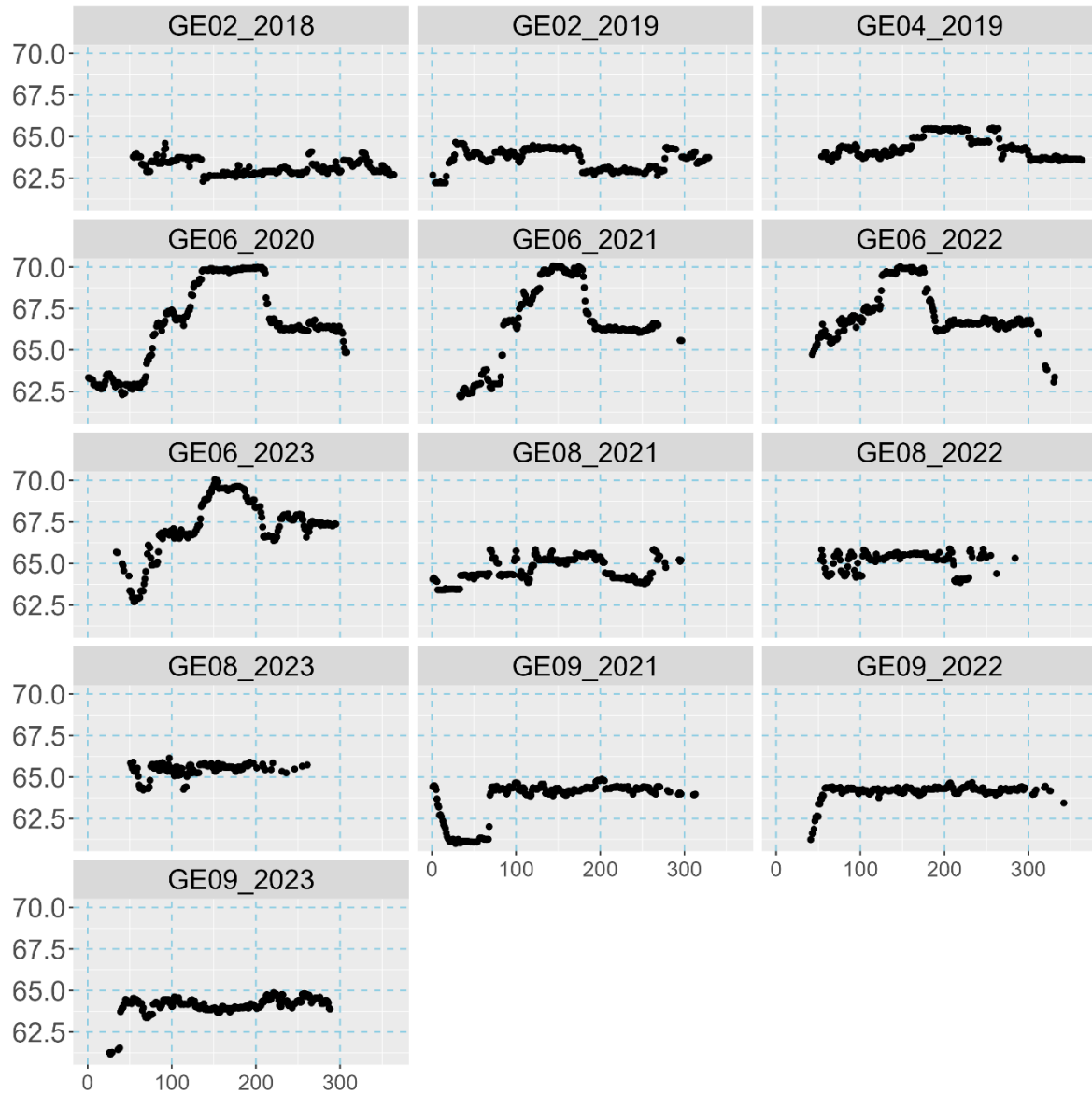


Figure 5. Plot of north-south movement for non-territorial individuals where the y-axis is latitude and the x-axis is julian day (100 = April 10, 200 = July 19, and 300 = Oct 27).

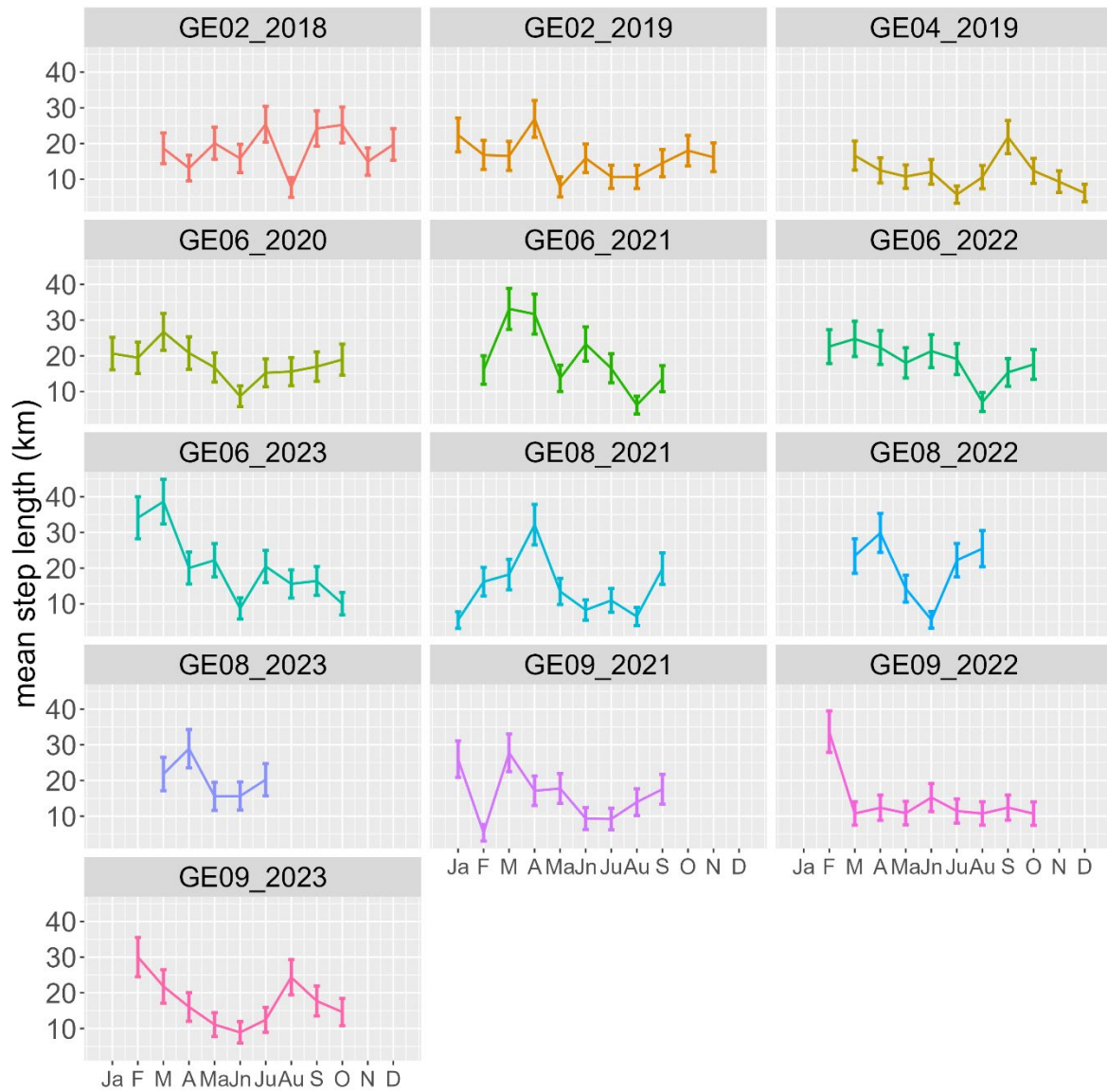


Figure 6. Mean daily step length each month for straight-line distances travelled by non-territorial golden eagles.

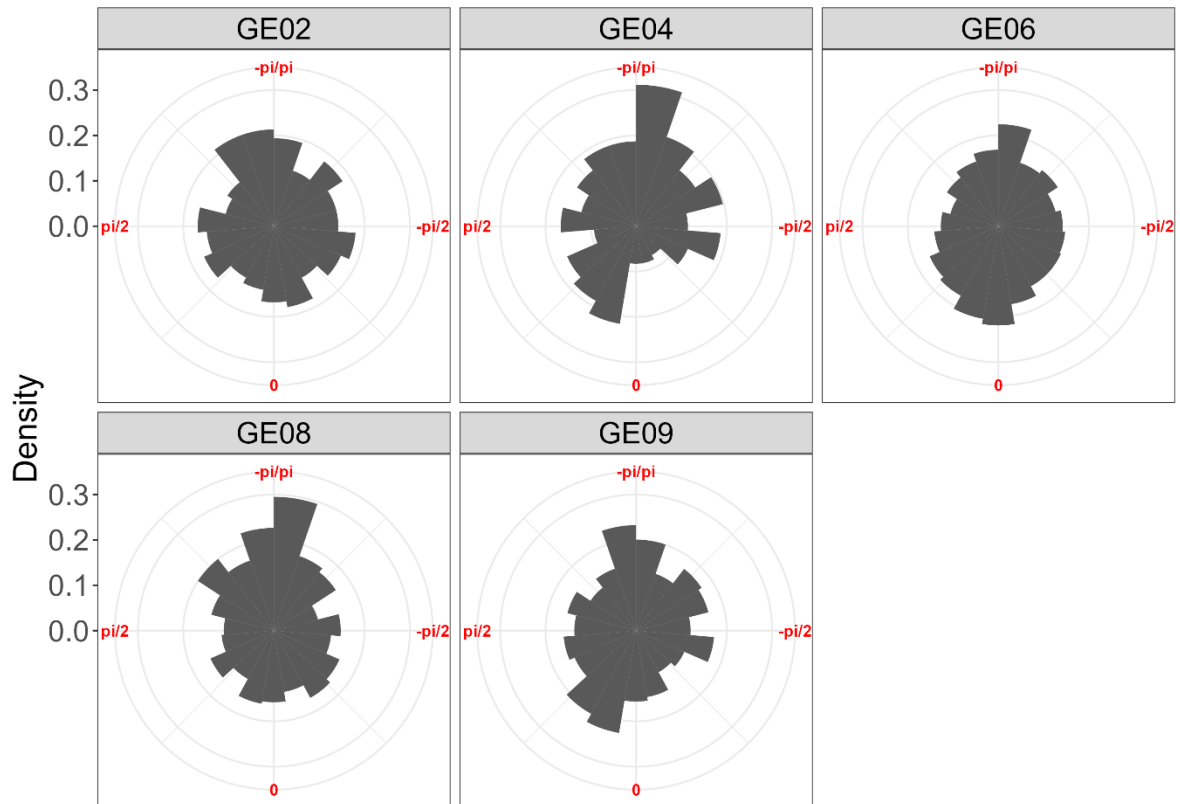


Figure 7. Turning angle between consecutive daily movements for non-territorial individuals between 2018 and 2023. Angles with value = 0 denote that the individual continued to move in the same direction as the previous day whereas $\pi/2$ and $-\pi/2$ denote degrees of turning. $-\pi/\pi$ denotes that they turned 180 degrees compared to the previous day. The density distribution (rings) of the proportion of angles is shown on the y-axis.

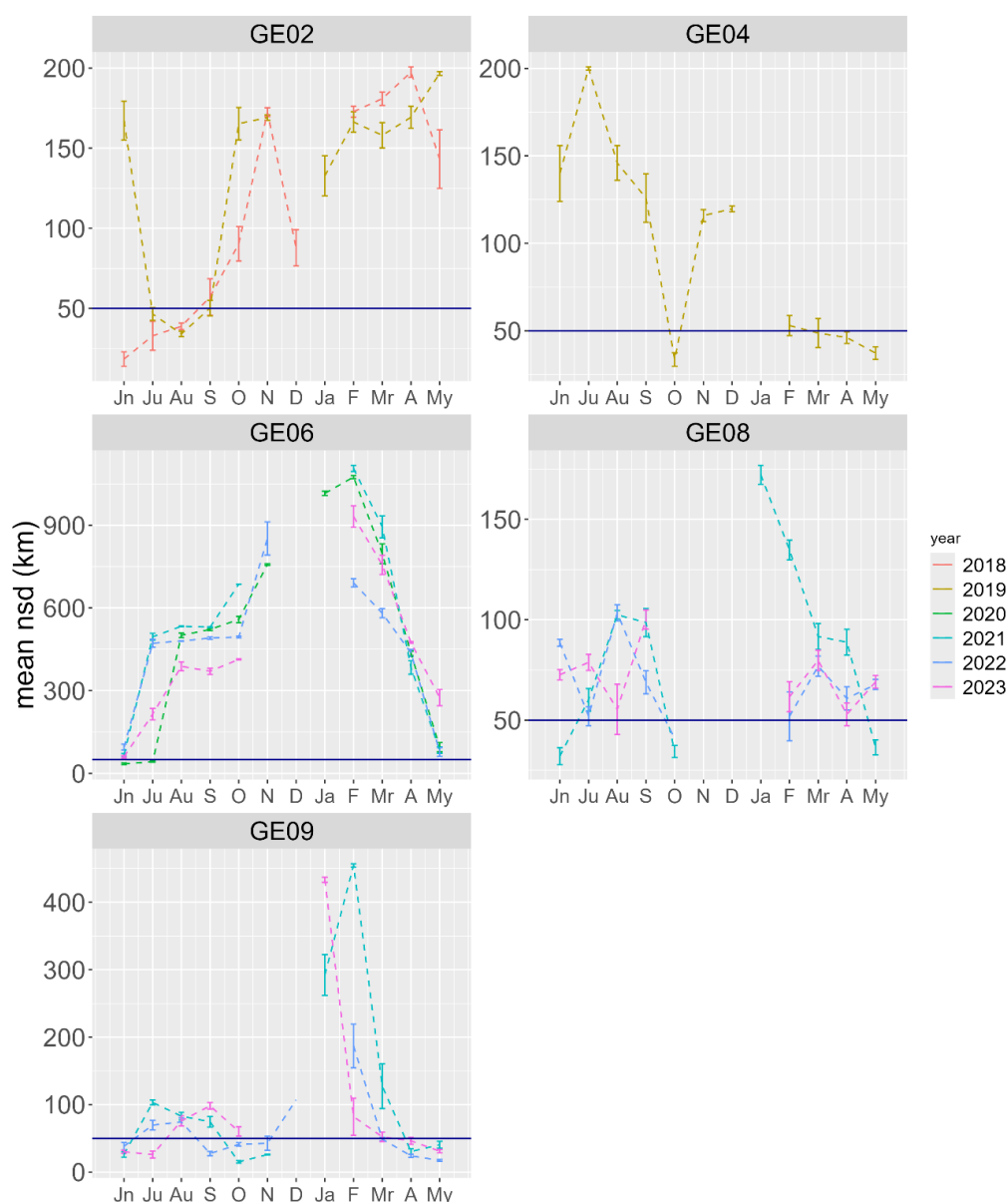


Figure 8. Mean annual net square displacement (NSD ± 1 SE) per month (June to May) and year for non-territorial golden eagle individuals with start date June 1.

3.2 Diurnal activity patterns

Between May and September, both territorial and non-territorial individuals were most active between roughly 08:00 and 17:00 and with activity peaking between 11:00 and 16:00 (**Figure 9**). Territorial individuals were in general more active in the day than non-territorial individuals in May and June, and also to a lesser degree in September, while territorial and non-territorial showed more similar diurnal patterns of activity in July and August (**Figure 9**).

Average movement distances when active (i.e. movement > 50 m) were very similar between territorial and non-territorial individuals, both having a mean diurnal distance of 1.3 km per 15 minutes (**Figure 10**). However, there were some seasonal differences in movement. Compared to territorial individuals, non-territorial individuals moved on average longer distances per 15 minutes when active in June (mean = 2 km, range = 1.9 – 2.2 km) and July (mean = 1.8 km,

range = 1.7 – 1.8 km) than territorial individuals (June mean = 1.5 km, range = 1.4 - 1.5 km; July mean = 1.3 km, range = 1.2 – 1.4 km) (**Figure 10**). In May, August and September movement distances were similar per 15 min in territorial and non-territorial birds (**Figure 10**).

The lack of observations during the night were a result of the GPS-device programming which was set to take locations between the hours of sunrise and sunset. However, with the sparse data available, there was evidence for both territorial and non-territorial individuals sometimes being active. Several longer flights were documented at more than 5 km in 15 minutes in June and July, mostly between 22:00 and 23:00.

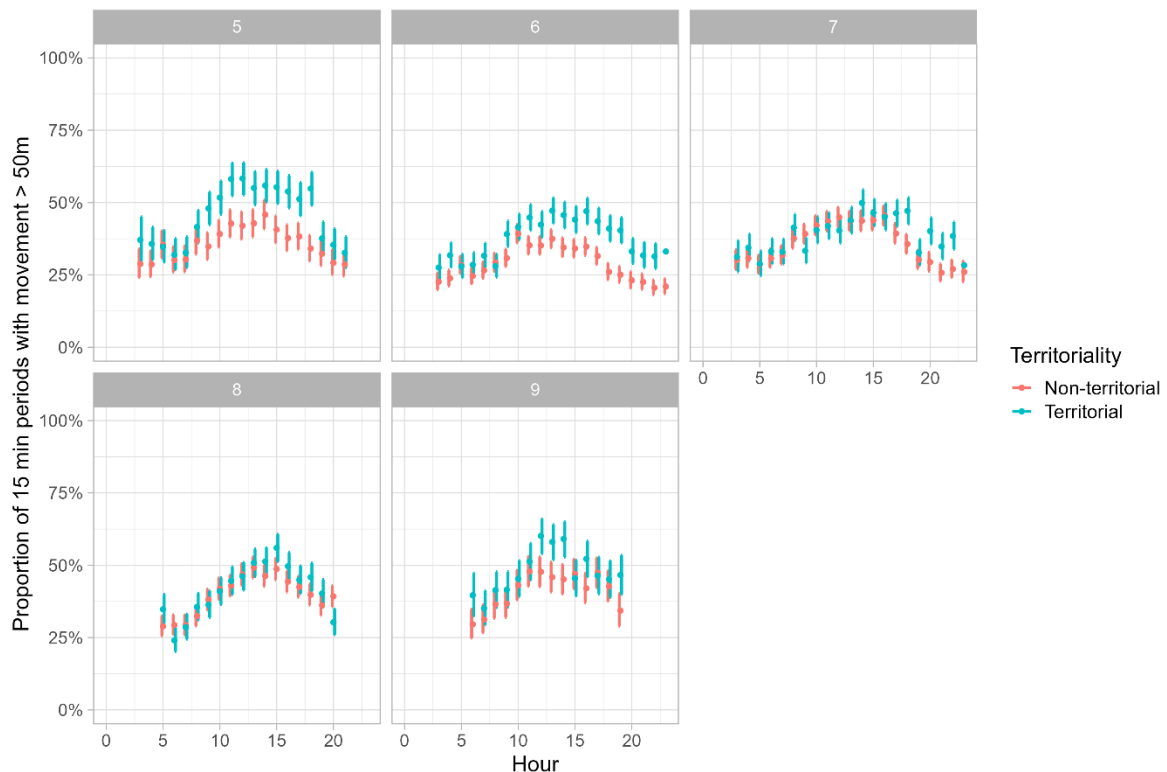


Figure 9. Proportion of 15 min periods with movement > 50 m \pm 95 % CI by territorial and non-territorial individuals between 2018 and 2023 for each hour in the day (Central European Time) and month between May (5) and September (9).

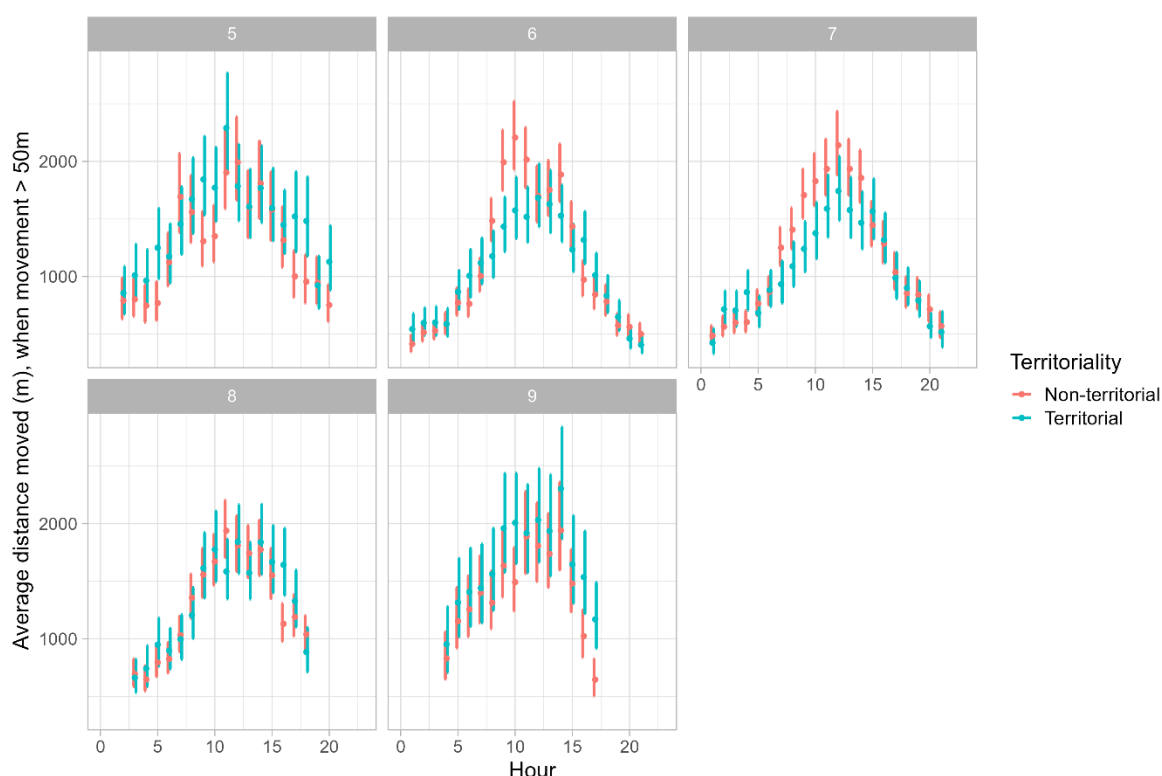


Figure 10. Average distance moved (m) in active periods (movement distances > 50 m) \pm 95 % CI for territorial and non-territorial individuals between 2018 and 2023 for each hour and month between May (5) and September (9).

3.3 Time use in livestock areas

3.3.1 Time spent in sheep summer rangelands and reindeer calving lands

There were substantial differences between the different individuals in their use of sheep summer rangelands and reindeer calving areas. These differences reflected the distribution of the different habitats in the area the eagles lived, e.g. the eagle moving to northern Norway in the summer, (GE06) used reindeer calving land proportionately more than eagles staying in more sheep dominated areas in Trøndelag in the summer (**Appendix Figures A1 - A7**). All individuals spent roughly between a quarter and a third of the time outside registered livestock areas during the summer (**Figure 11**). Statistical analyses suggested no evidence for variation between months in the use of sheep summer rangelands or reindeer in the different eagles, i.e. there was no evidence in these data for any of the eagles to use reindeer calving land more in May and June, and sheep summer grazing land more in June than in July and August. Only in the relatively small dataset from GE04 from June and July was there a distinct monthly difference in use of livestock areas. This individual used a mixture of habitats in June, while in July it spent most of its time in an area that was both sheep grazing land and reindeer calving land (0.98, **Figure 11**). All three non-territorial individuals spent time in both Norwegian and Swedish calving grounds (**Appendix Figures A1 - A7**).

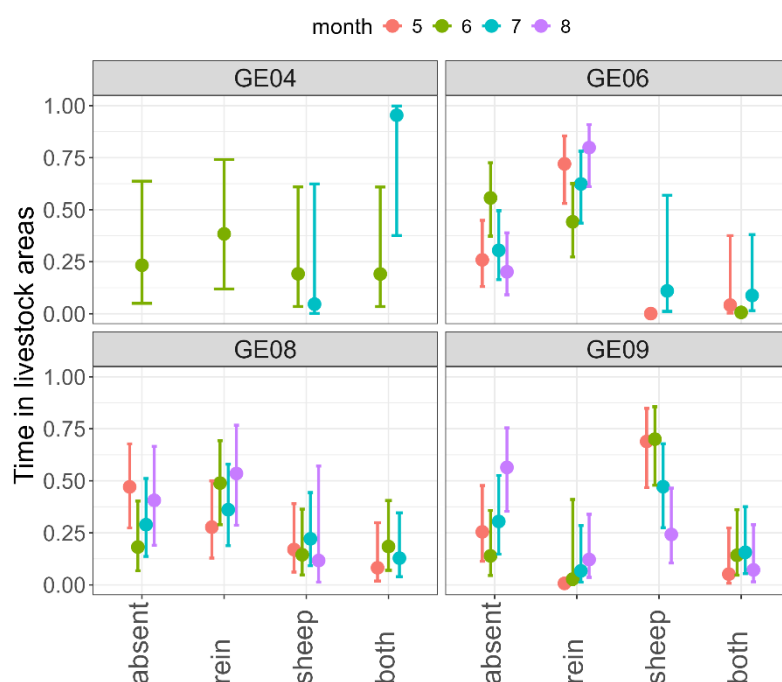


Figure 11. Proportion of time spent in different livestock areas for GE04, GE06, GE08 and GE09 between May and August.

3.3.2 Effect of sheep density on time spent in sheep rangelands

The time eagles spent in sheep rangeland polygons increased significantly with increasing area of the polygon. However, when controlling for the area of the polygon there was no evidence for a significant positive effect of sheep density on time use (**Table 4**).

Table 4. Coefficient estimates for the model estimating the effects of sheep density and sheep rangeland polygon area on the time spent (number of positions measured per 15 minutes) in grazing districts by non-territorial individuals. The model was fitted using a log link function and grazing area was log transformed before being entered in the model.

Co-efficient	Coefficient estimate	Standard error	P
Intercept	1.41	0.68	0.04
Sheep density	0.02	0.03	0.33
Sheep rangeland polygon area	0.71	0.12	< 0.001

4 Discussion

4.1 Seasonal and diurnal patterns

All of the non-territorial golden eagles showed a seasonal north-south pattern in their movement but at very different scales. As all but one were males, this variation cannot be due to sex alone which has been reported to explain differences in area use of non-territorial golden eagles in some studies, with males generally covering a larger area than females (e.g. Whitfield et al. 2023). Although in our study, the female covered the smallest area, this individual also had the shortest time span of data. Therefore, we cannot rule out that the reported area use would have been larger with more positions available. Overall, the areas observed used by the non-territorial individuals are within the range documented in other studies from Scandinavia and North America. However, in contrast to previous studies in Sweden (Singh et al. 2021) and northern Norway (Nygård et al. 2016), only one individual undertook annual movements of more than 1000 km. Even though we do not know the exact natal area for the non-territorial individuals, as all were caught in the wintertime on the Fosen peninsula, their consistent seasonal area use over multiple years, combined with young age of capture, indicates they are likely to originate from areas north of the capture area on Fosen, from Northern Trøndelag to Finnmark. Accordingly, genetic analyses have showed that none of the captured non-territorial birds were related to individuals from known territories near the area of capture (Stien et al. 2023). Our results are consistent with the study by Nygård et al. (2016) that found partial and full migration strategies among non-territorial individuals from Finnmark. All individuals migrated south for the winter and returned northwards to broadly similar areas in the spring. Interestingly, our results suggest that the seasonal latitudinal migration distance is not necessarily positively related to the latitude of the native area. One individual (GE09) spent its summers in northern parts of Trøndelag and winters in Vestland, a north-south distance at well over 400 km, while the individual that spend its summers in Nordland (GE08) had the shortest north-south migration distance of only 200 km.

In common with Nygård et al. (2016) we find patterns of movement that are consistent with a return to natal area. However, the use of the natal area is only apparent at a coarse spatial scale. The areas used by non-territorial golden eagles in the summer were much larger than the range of territory sizes reported for territorial golden eagles. This suggests that the offspring do not spend much time within the territory of the parents in the summer, even if they pass by every year.

All individuals indicated movements across borders into Sweden and one individual into Finland, but not, in contrast to Nygård et al. (2016) and Singh et al. (2021), to Russia. These two studies marked fledglings in their nests in Finnmark and Northern Sweden, closer to the Russian border than our study which may explain this difference. Trans-country movements may result in exposure to a wider range of pressures than experienced within Norway. This can be due to different national policies with respect to e.g. windfarms, transport networks (Ecke et al. 2017, Singh et al. 2021, Singh et al. 2024), as well as a wider range of environmental conditions including contaminants, and inter- and intra-specific ecological interactions. The frequent occurrence of trans-country movements suggest that collaboration on a Scandinavian scale is relevant for management.

The daily activity level of the golden eagles showed a peak in the middle of the day, but they were also inactive for much of the time during this peak. This is consistent with previous findings (Dunstan et al. 1978, Natake 2013, Katzer et al. 2020, Singh et al. 2021). The hourly activity of non-territorial individuals was not much different from that of territorial individuals. In May and June territorial birds were more often active than non-territorial birds, and in June and July there was evidence for non-territorial birds to move slightly further than territorial birds when active. The observed patterns suggest that the large-scale movement pattern of non-territorial birds, with their use of large areas, does not translate into elevated daily activity budgets when compared to territorial birds. The elevated activity level of territorial birds may suggest that territoriality

is demanding in the latter part of the breeding period, probably due to territory defense and food provisioning for chicks and partners.

The lack of territoriality among the marked young birds is consistent with an age of first breeding of 4 years or older expected for populations with a high density of territorial birds (Watson 2010, Heggøy & Øien 2015). Several of the non-territorial birds were followed for several years, and accordingly grew older. By 2024, GE06 was an adult (7th calendar year, i.e. 6 y. o.), but showed no signs of territoriality. The other three non-territorial individuals were between 4 - 5 years old by the end of their GPS monitoring periods and did not show any sign of territoriality either. In contrast, GE04 showed signs of territorial behavior in its fifth calendar year (4 y.o) in 2020 but his GPS-device dropped off in March, making it uncertain whether he became territorial or not.

Our study lacks data for part of the winter for most individuals and has lower GPS-sampling during the dark hours of the day as a consequence of choosing GPS-devices charged by solar cell batteries with limited storage capacity. However, these devices were the best we found at the time considering animal welfare (low enough weight to minimize disturbance for the bird). Technological developments for GPS-devices are progressing rapidly and future studies are likely to be able to use GPS-devices which have better battery capacity, enabling improved winter data coverage, while being significantly lighter than those we used in this study and thereby decreasing disturbance to the birds which are GPS-tagged. Improved data collection during the winter months will increase our basic knowledge about variation in annual movement patterns which is currently lacking. Thus, GPS-tagging is still highly relevant for improving knowledge regarding the ecology of this species and on golden eagle-livestock conflicts.

4.2 Use of livestock areas

A study from Sweden (Singh et al. 2021), based on tracking data of 27 eagles over eight years suggests that individual eagles track the spring reindeer migration and are more likely to be found in calving lands during calving than at other times of the year. We were not able to detect a similar pattern but in contrast to Singh et al. (2021) we only investigated the pattern in the summer months while they covered the whole year. However, all our birds spent at least some time in calving lands during the summer and some spent most of the time in calving lands. Although we focused on calving rangelands in the analyses, these areas overlap to varying degrees with summer grazing areas, so reindeer may have been available in these areas during all summer months. In general, we found little variation between months in livestock area use with respect to calving lands. This suggests that the eagles were not more attracted to reindeer during the calving period than during the rest of the summer. Presence in livestock areas can imply a risk of predation but as eagles also scavenge, habitat use can also result from attraction to carcasses or merely attraction to mountain habitat, which is the specie's favored habitat (Katzner et al. 2020). Predation studies of some of the included individuals show that they all occasionally kill reindeer calves and/ or lambs but that the majority of prey taken is small game such as hares and ptarmigan (Mattisson et al 2023). One of the eagles that we followed in predation studies (GE09) spent approximately half of its time in sheep grazing areas and approximately a fifth of its time in calving areas. Still, during 124 days of predation studies, conducted over two summers, it was only involved in one lamb kill and 1 - 4 reindeer calf kills, indicating that it was not an attraction to sheep grazing areas that determined his whereabouts.

Singh et al. (2021) suggested that immature individuals are more likely to track reindeer movements and be inside calving grounds than adults. Observations by reindeer herders also suggest that individuals with white underwing and tail plumage, a coarse method of categorizing an individual as immature, are dominant in reindeer grazing lands. All non-territorial individuals in our study were immature (non – adult plumage), being in their first or second year of life at time of capture. Since the territorial birds included in our study did not leave their territories, they clearly did not track food sources outside of their territories. This suggests that only the non-territorial birds could track migratory food resources, and clearly, with their extensive area use have

potential to do so. However, we found no evidence for the non-territorial birds to target calving lands around calving, lending no support to Singh et al.'s (2021) hypothesis in Norway. We note that the degree of white plumage is not a reliable method of ageing individuals, with some immatures showing little or no white underwing plumage, whilst some adults retain white plumage (<https://www.orrhult.eu/projekt/orn/aldersbest.kungs/5.femte%20drakt/5.dr.index.htm>) and ageing from observations in the field rather than detailed observation in the hand can be difficult.

We did not find any pattern suggesting non-territorial birds were attracted to sheep grazing areas in the period after sheep are released on the rangelands, or to rangelands with high sheep densities. Also, all eagles spent a considerable amount of time (> 25 %) in areas not registered as sheep or calving rangelands. Overall, we interpret our analysis as lending no support to the hypothesis that the large-scale spring/ summer movements of non-territorial eagles are driven by a search for domestic livestock.

There are several factors that may have contributed to our conclusion that we find little support for large-scale movements of non-territorial eagles being driven by a search for domestic livestock. Firstly, we have high quality data from only a small number of golden eagles. Even though we have several years of data from some of them, we cannot reach a robust and general conclusion based on the behavior of only four birds. Non-territorial birds may have different individual preferences, and we may have studied a biased sample of the larger population of non-territorial golden eagles in Norway. Secondly, the spatial polygons describing reindeer calving land and sheep rangelands give a crude representation of the spatial distribution of sheep and reindeer calves. The polygons may not cover all areas used by reindeer for calving or used by sheep each year. Domestic livestock may have been available also in areas categorized as having neither sheep nor reindeer calving. Furthermore, the sheep and reindeer utilizing these polygons are likely to be heterogeneously distributed within these areas, leaving parts of them unused by the domestic prey. The use of position data of the livestock could therefore improve the analyses, but such data are not available for the extended areas used by the eagles.

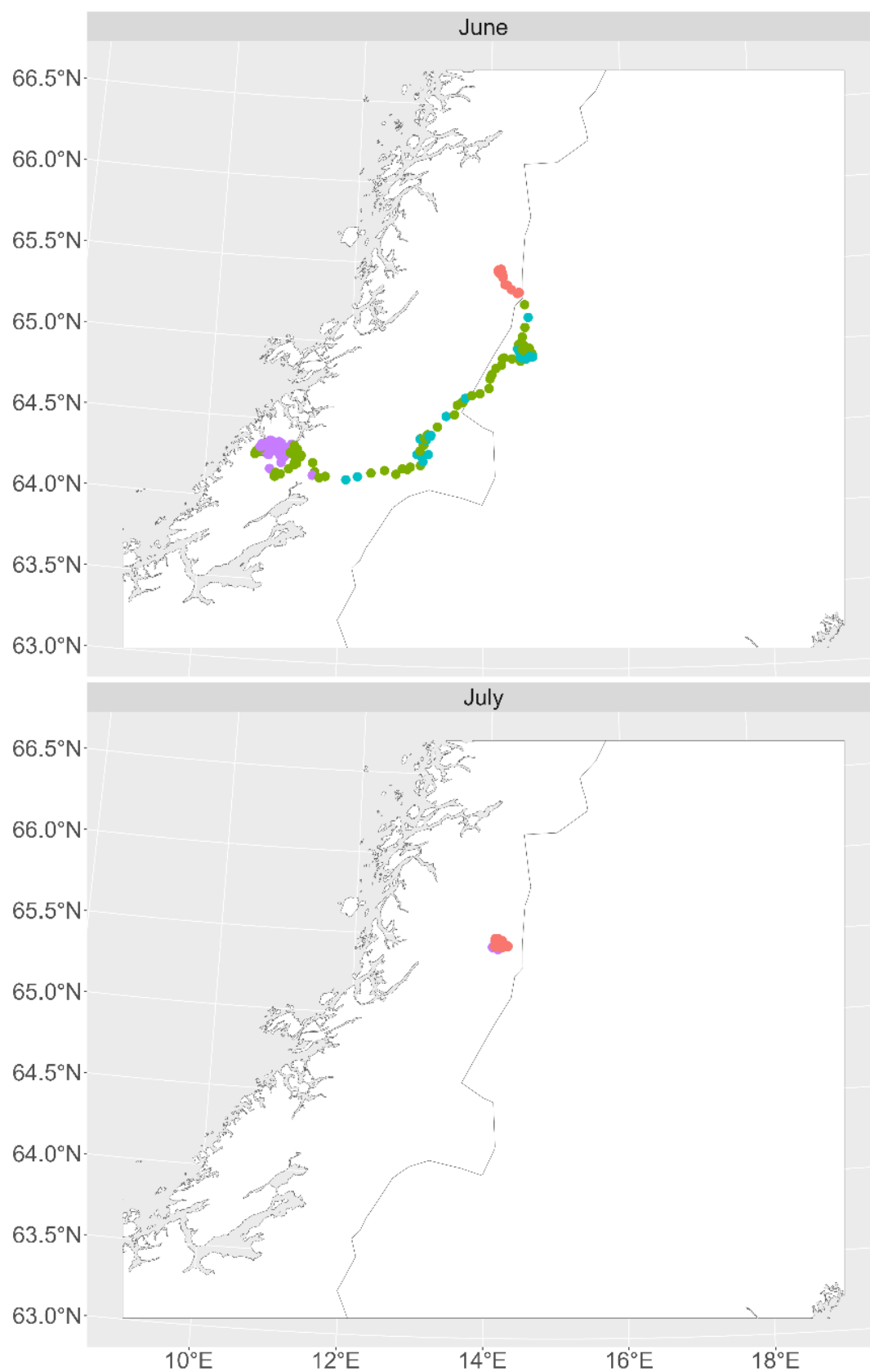
Thirdly, it is very likely that there are many factors that affect the area use of non-territorial golden eagles. In our predation studies of individual GPS-marked eagles we found that smaller prey, such as ptarmigan and hare, were the most common prey types. This suggests that the availability of these smaller prey species may be more important for the area use of the eagles than the larger domestic prey. In addition, territorial golden eagles are known to be aggressive to conspecifics. The distribution and density of occupied golden eagle territories is therefore likely to play an important role in the space use of non-territorial birds. Parts of the calving areas that are within the boundaries of territorial birds may therefore be less available for non-territorial birds. Such ecological behaviour would reduce the strength of the signal in the data with respect to attraction to domestic prey.

It is well established that golden eagles kill both reindeer and sheep, and that small calves and lambs are particularly vulnerable to predation. Future work should focus on obtaining unbiased estimates of the extent of the losses, and in situations when losses are high, find efficient methods to reduce them. By GPS-marking more non-territorial golden eagles, it will be possible to conclude with more confidence whether non-territorial Norwegian golden eagles are attracted to calving lands. However, this approach is likely to continue to suffer from coarse data on the distribution of domestic livestock within the area used. GPS-marking of territorial individuals that have territories that overlap reindeer calving lands, may therefore be a good supplement, as the restricted area of such studies would allow more detailed information to be obtained on the distribution of reindeer calves. The restricted area use of territorial eagles is also likely to make behavioral responses to calving easier to detect. Furthermore, a main strength of studying GPS-marked territorial and non-territorial eagles is that the approach allows for accompanying predation studies that quantify the prey of the marked eagles.

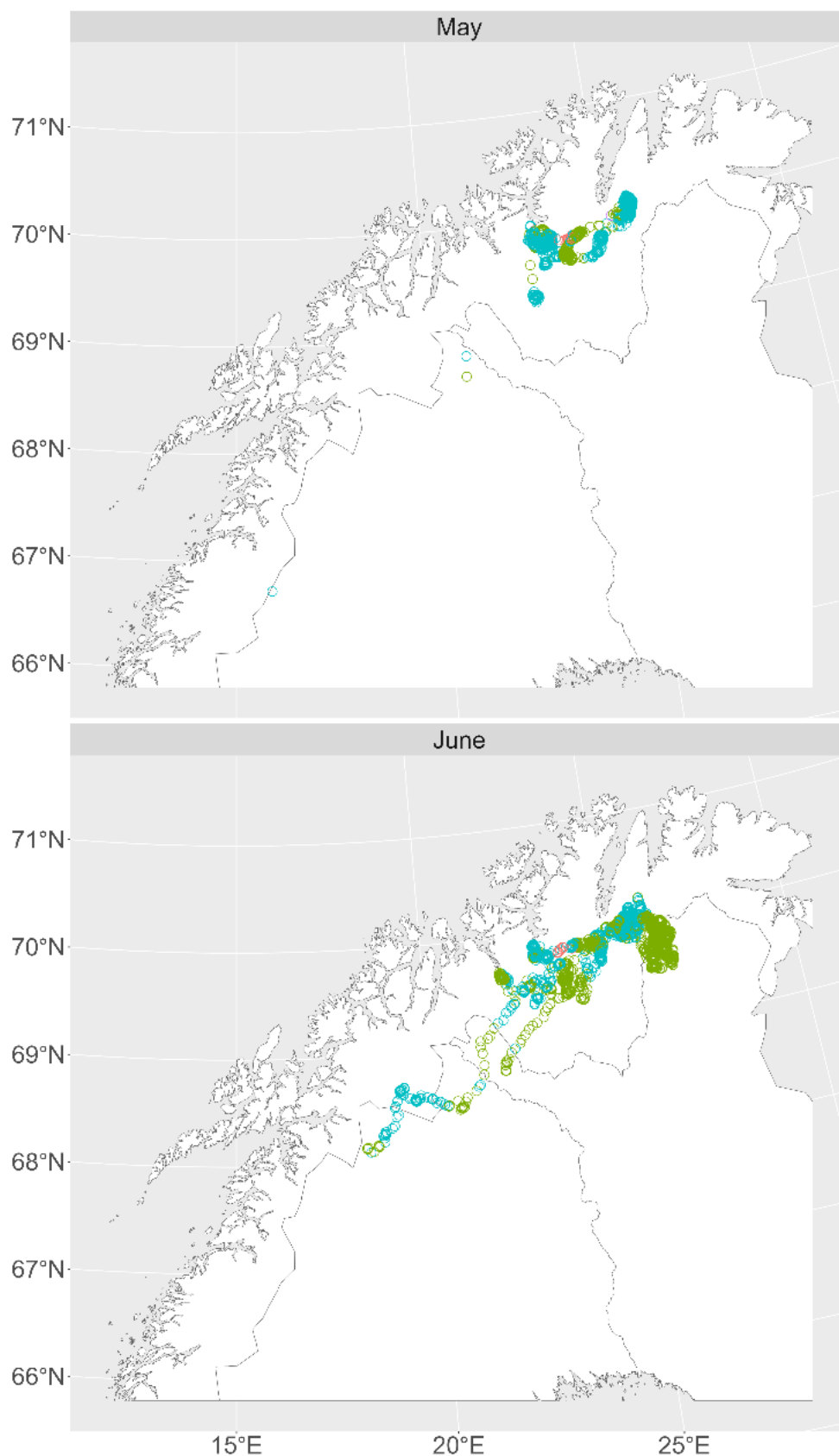
5 Appendix

Appendix Table A1. Number of daily positions per month for non-territorial golden eagles tagged between 2018 and 2023.

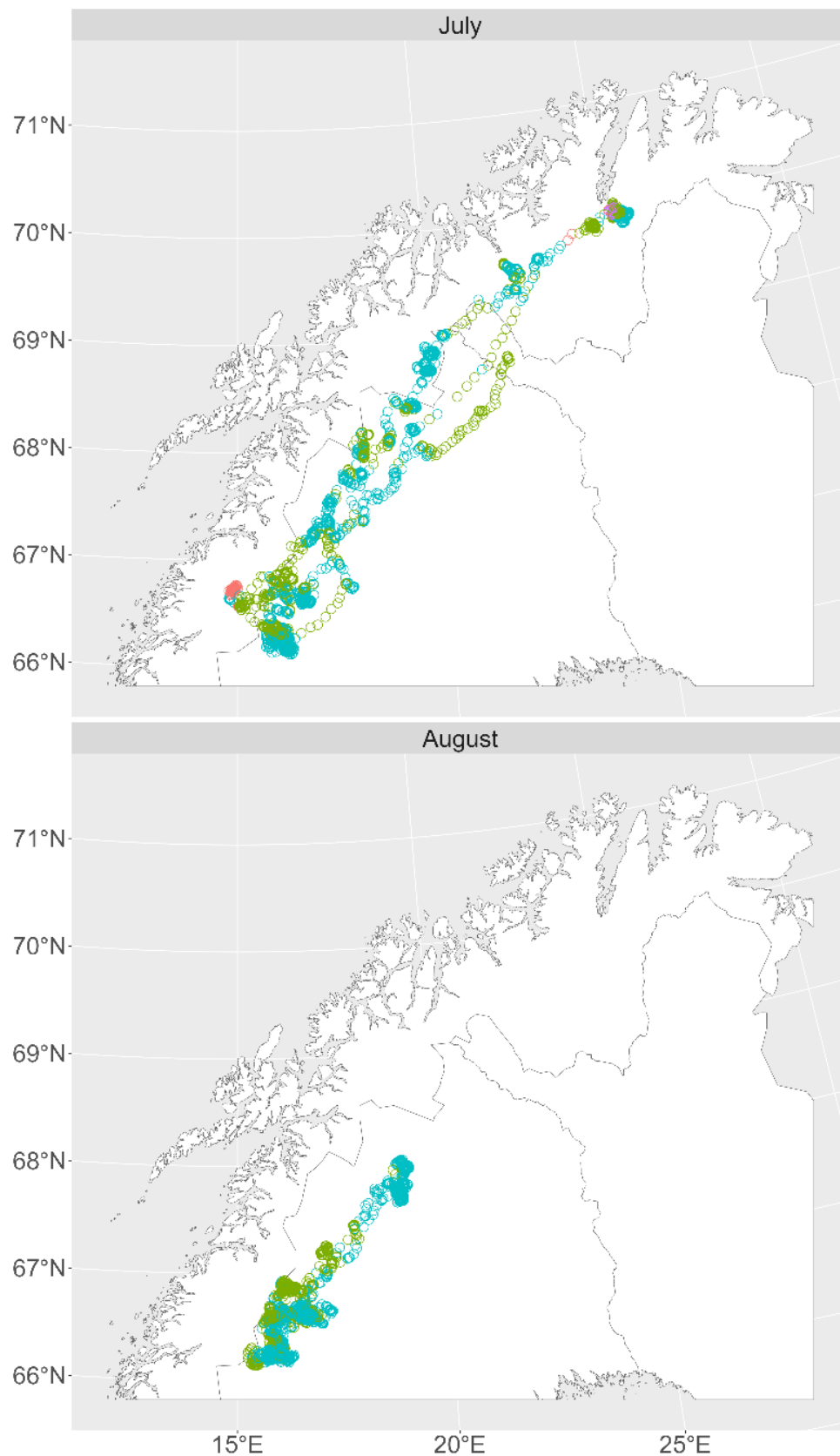
Month	GE02_2018	GE02_2019	GE04_2019	GE06_2020	GE06_2021	GE06_2022	GE06_2023	GE08_2021	GE08_2022	GE08_2023	GE09_2021	GE09_2022	GE09_2023
Jan	0	22	0	31	0	0	0	31	0	0	29	0	4
Feb	6	21	6	29	26	15	16	27	6	9	25	17	22
Mar	31	22	27	28	29	28	30	30	30	30	27	29	29
Apr	30	24	30	30	29	30	30	27	28	28	26	29	28
May	22	23	30	30	31	31	31	31	26	29	31	31	30
Jun	20	20	28	30	29	29	30	29	25	27	27	29	29
Jul	20	25	31	31	28	29	26	28	26	17	30	30	30
Aug	26	23	31	29	31	29	29	31	22	4	30	28	30
Sep	17	20	26	30	26	30	30	26	7	3	28	29	29
Oct	20	19	29	31	3	30	22	5	1	0	8	23	15
Nov	22	19	29	3	0	7	0	0	0	0	3	9	0
Dec	24	0	29	0	0	0	0	0	0	0	0	1	0



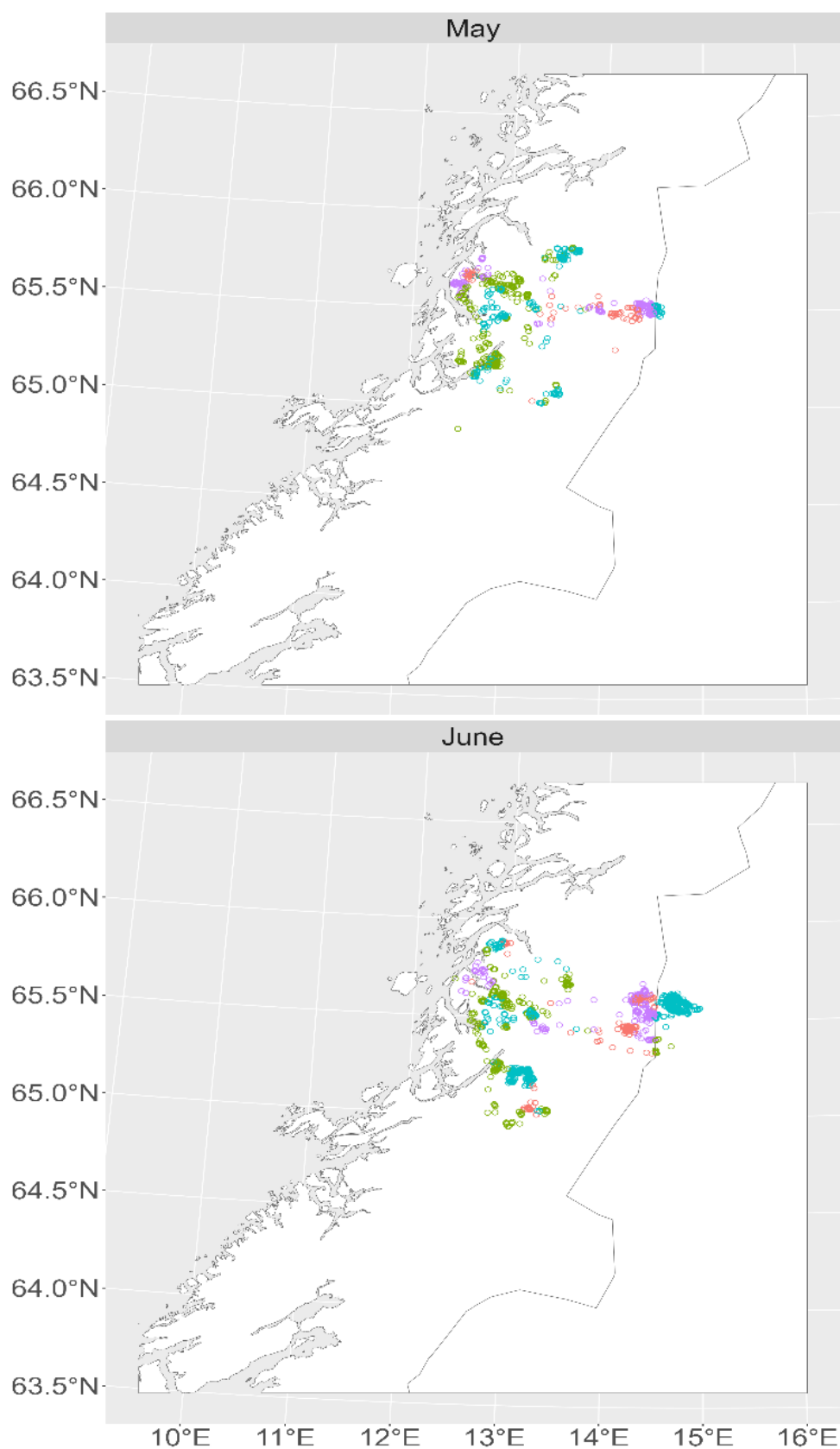
Appendix Figure A1. Use of livestock areas for GE04 in 2019 (green = absent from livestock areas, purple = sheep grazing rangelands, blue = calving grounds, pink = both sheep grazing rangelands and calving grounds).



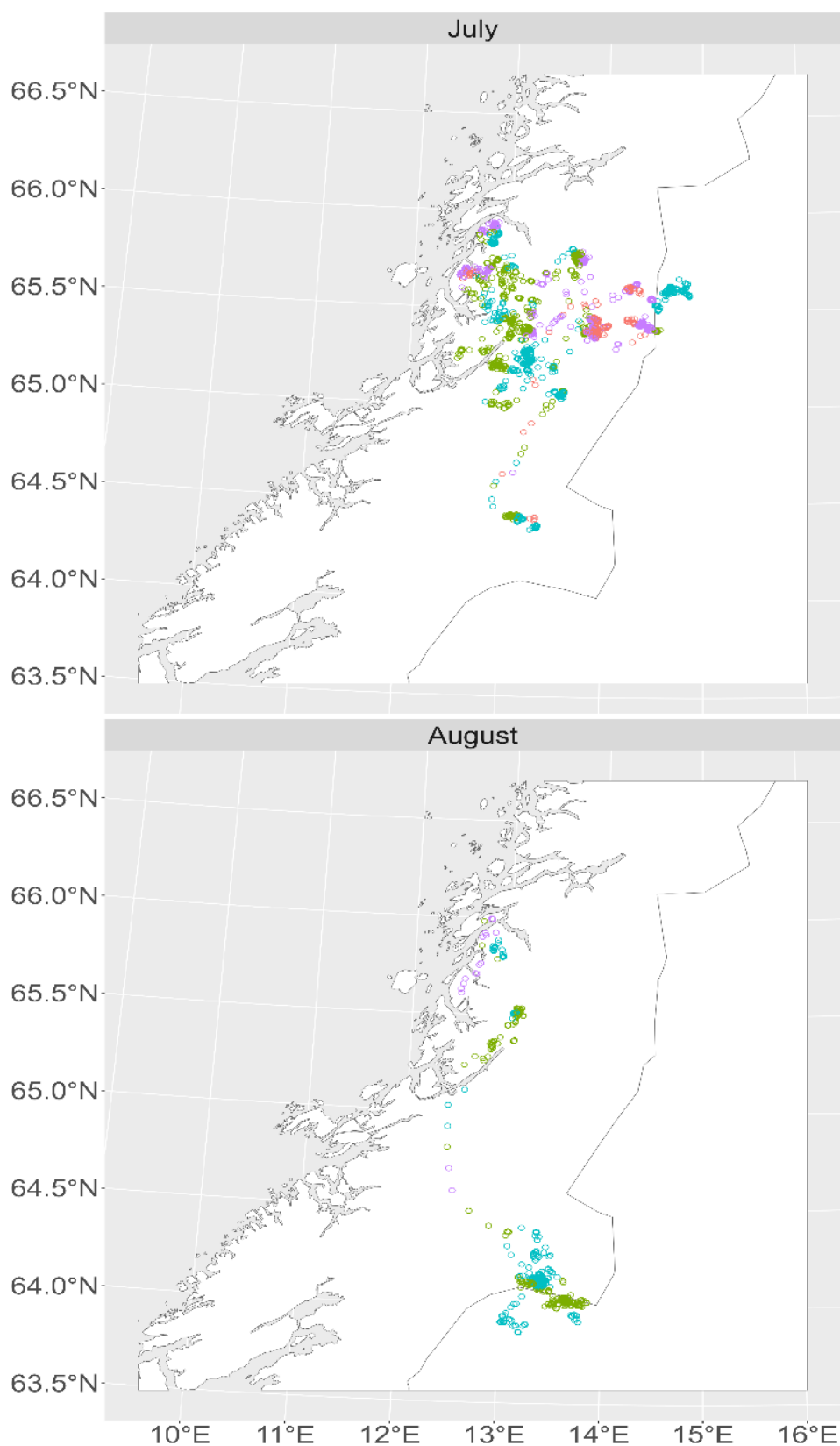
Appendix Figure A2. Use of livestock areas for GE06 2020 - 2023 in May and June (green = absent from livestock areas, blue = calving grounds, pink = both sheep grazing rangelands and calving grounds). Note that potential calving areas in Finland are not accounted for.



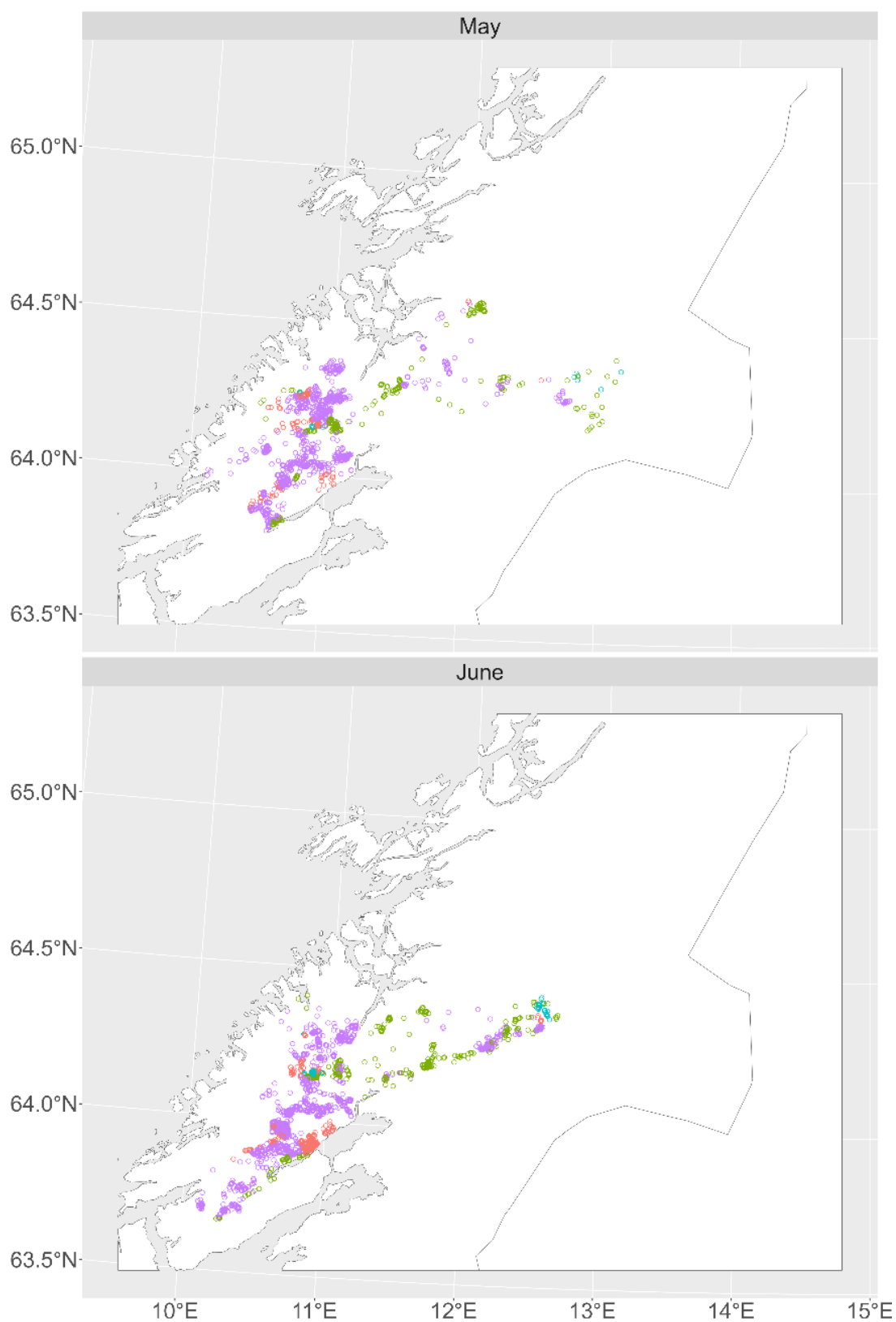
Appendix Figure A3. Use of livestock areas for GE06 2020 - 2023 in July and August (green = absent from livestock areas, purple = sheep grazing rangelands, blue = calving grounds, pink = both sheep grazing rangelands and calving grounds). Note that potential calving areas in Finland are not accounted for.



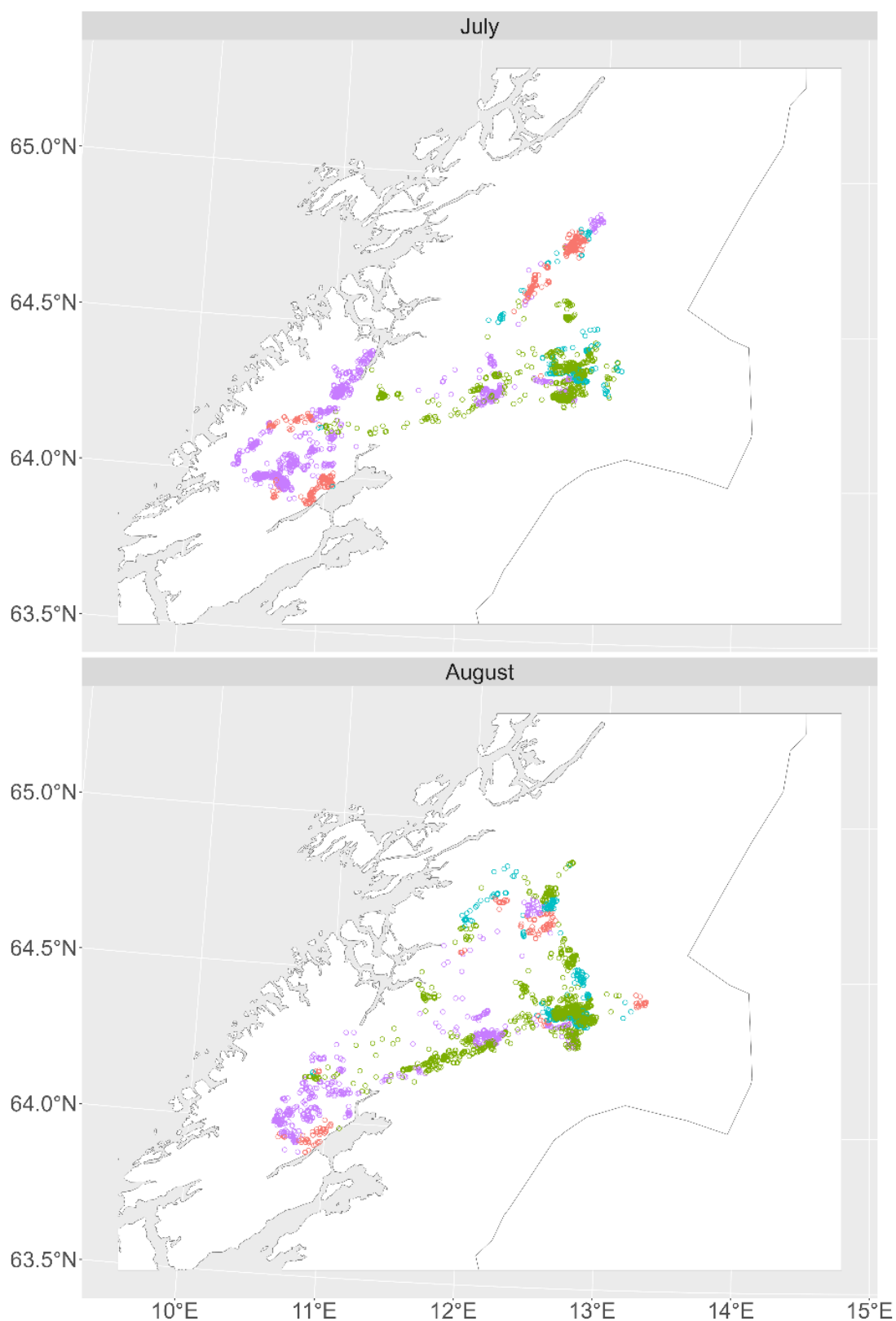
Appendix Figure A4. Use of livestock areas for GE08 2021 - 2023 in May and June (green = absent from livestock areas, purple = sheep grazing rangelands, blue = calving grounds, pink = both sheep grazing rangelands and calving grounds).



Appendix Figure A5. Use of livestock areas for GE08 2021 - 2023 in July and August (green = absent from livestock areas, purple = sheep grazing rangelands, blue = calving grounds, pink = both sheep grazing rangelands and calving grounds).



Appendix Figure A6. Use of livestock areas for GE09 2021 - 2023 in June and July (*green = absent from livestock areas, purple = sheep grazing rangelands, blue = calving grounds, pink = both sheep grazing rangelands and calving grounds*).



Appendix Figure A7. Use of livestock areas for GE09 2021 - 2023 in July and August (green = absent from livestock areas, purple = sheep grazing rangelands, blue = calving grounds, pink = both sheep grazing rangelands and calving grounds).

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