

Demographic patterns in winter carcass use by Golden Eagle and White-tailed Eagle in Finnmark, Norway



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BIO-3910 Master`s thesis in Biology

Februar 2012

In collaboration with

Norwegian Institute of Nature Research (NINA) Tromsø

Cover photo from one of the automatic cameras.
Golden Eagle at carcass and White-tailed Eagle standing by

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Acknowledgements

First of all I would like to especially thank my supervisor, Audun Stien for all his great work and support during the whole process. I thank my other supervisors, Karl-Otto Jacobsen and Rolf Anker Ims for their reviews, good advises and comments as well as I apologize for the last minute work. I would further like to express my gratitude to the following people:

Trond Johnsen and Bård Jörgen Bårdsen for advising and pointing out literature and references to me.

- My friends; Xabier Ancin Murguzur, Lorena Munoz and Tore Nordstad for their support, assistance and most of all taking my mind off of my studies once in a while.
- My family, for their mental and financial support during my whole university studies.
- My love, Hálfván Helgi Helgason, for his great support, help, understanding and inspiration during my whole studies.
- All the people that gathered the data by going around Finnmark putting out and collecting photo-boxes and carrions.

I'd also like to thank the other people who played a large role in nurturing my interest and knowledge of biology, knowingly or unknowingly: My dad Páll Halldór Benediktsson, my grandparents Elínborg S. Pálsdóttir and Benedikt S. Þorsteinsson†, Gunnar Þór Hallgrímsson, Páll Hersteinsson†, Ester Rut Unnsteinsdóttir, Skarphéðinn Þórisson, Saga Svavarsdóttir and Hallvard Strøm.

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Abstract

The carcass use of juveniles, subadults and adults of the two eagle species in Norway, the White-tailed Eagle (*Haliaeetus albicilla*) and the Golden Eagle (*Aquila chrysaetos*) was studied in Finnmark, the northernmost county of Norway for two winters, in 2009 and 2010. Artificial carrion was laid out as bait on four peninsulas, along with automatic digital cameras which took picture on 5-15 minutes interval. The pattern of carcass use was evaluated in relation to distance from coast and forest, altitude, peninsula, year and day of the year. Furthermore, I investigated whether there were differences in the time spent scavenging each day. Juvenile eagles of both species and subadult White-tailed Eagles were rare on the carcasses, while subadult Golden Eagles and adults of both species occurred at similar, but overall, rather low frequencies. In general, occupancy on carcass decreases with distance from coast for both species, most clearly so for adult White-tailed Eagles. Subadult Golden Eagles were fairly evenly distributed across the peninsulas. Adult Golden Eagles were more common on the Sværholt and Varanger peninsulas, while adult White-tailed eagles were most common on the Nordkinn and Sværholt peninsulas. I detected no differences between the age groups in time period spent scavenging per day. The intensity of use of the carrion was too low in both eagle species for interference competition for such food resources to be a likely determinant of the spatial and temporal distribution of eagles during the winters in Finnmark.

Keywords

Golden Eagle, *Aquila chrysaetos*, White-tailed eagle, *Haliaeetus albicilla*, scavengers, carcass, tundra, arctic, winter

Introduction

Arctic areas are generally quite species-poor compared to more southerly areas because of the low and highly seasonal productivity (Begon et al. 1986). During the winter these areas get even species poorer because of the southern autumn migration of various species, mainly birds (Begon et al. 1986). Still other prey species may be present but not reachable for instance, because lakes are often frozen during winter making non-migrant fish unreachable and snow covers species like lemmings and other small rodents (Sonerud 1986). Thus food scarcity can make the winter season hard time for carnivorous species, especially raptors in inland areas. The coastline of open seas, on the other hand, is likely to provide more resources in winter (Willgoos 1961, 1984). Moreover, carrion can be an important but spatially scattered food source many scavenging animals can exploit (e.g. Jędrzejewski and Jędrzejewska 1992; DeVault et al. 2003; Selva and Fortuna 2007), not at least in the arctic areas in wintertime. The two largest raptors in Norway, the Golden Eagle (*Aquila chrysaetos*) and the White-tailed Eagle (*Haliaeetus albicilla*) are known to scavenge and scavenging has been noted to be more important in the wintertime when live prey is scarce (Willgoos 1961, Halley and Gjershaug 1998, Watson 2010). In northern Norway, semi-domesticated reindeer are the most numerous ungulates and important for the scavenger community during winter when higher natural mortality occurs than in the summer.

The Golden Eagles in Finnmark exploit mainly terrestrial habitats, feeding mostly on Mountain hares (*Lepus timidus*) and ptarmigans (*Lagopus spp.*) (Johnsen et al. 2007, Watson 2010) while the White-tailed Eagle is more restricted to coastal areas and inland areas with lakes since its diet consists mainly of fish and seabirds (Willgoos 1961, 1984). However, both intra- and inter-specific competition may occur linked to the exploitation of carcasses in wintertime (Halley and Gjershaug 1998). During winter immature Golden Eagles from Finnmark usually disperse southward into Sweden and Finland (Jacobsen et al. 2011), leaving nest area in September/October (McIntyre et al. 2008, Jacobsen et al. 2011), returning to their natal site in late March-April (Jacobsen et al. 2011). Most adult Golden Eagles in Finland are sedentary, staying at their territory whole year around, to protect it and skip a potentially risky migration (Fremming 1980, Watson 2010). The same may be true for the adult Golden Eagle population in Finnmark (K.-O. Jacobsen pers. comm.) Adult White-tailed Eagles from inland areas most likely move to the outer coastal areas in wintertime when lakes start to freeze (Willgoos 1961, Nygård et al. 2003). If so this may reduce competition between White-tailed Eagles and Golden Eagles in inland areas during the winter, but increase competition close to the coast. However, Golden Eagle territories in Scotland tend to cover areas at higher altitudes than territories used by White-tailed eagles (Evans et al. 2010), which might reduce competition along the coast.

A general problem in estimating the distribution and abundance of species is that we seldom are able to detect and count all individuals within an area. Many individuals will be undetected because individuals differ in their activity levels, or because it is difficult to design a survey that fully cover all of the potential area used by the species. This implies that a species is not necessarily absent when not detected (Yoccoz et al. 2001, MacKenzie et al. 2005). If the uncertainty associated with detection is not accounted for during modeling, it can be assumed that species is not present when it is, and conclusion on species associations and interactions can be wrong (MacKenzie et al. 2004). This has led to an increasing focus on modeling the detection process when interpreting ecological survey data (MacKenzie et al. 2002).

In 2005, a research project was initiated to monitor the winter scavenger community in Finnmark, northern Norway. Automatic digital camera-boxes were positioned along with bait on 6-11 transects (different between years), at 2-4 peninsulas, during a period of two months (March - April) approximately, with pictures taken every 5-15 minutes over the study periods. The transects covered a gradient from coast to inland. To get a better insight into the spatial and temporal use of carcasses by eagles in the wintertime, I analyzed pictures from 2009 and 2010 with eagles on the bait, and distinguished between three different age groups of eagles; juvenile, subadult and adult eagles.

The aim of this study was to get an estimate of the relative abundance of the different age groups of the two eagle species, White-tailed and Golden Eagles, in Finnmark, and how they exploit carcasses. More specifically I will:

1. Evaluate the observation from satellite marked immature eagles (juvenile and subadults), that they leave Finnmark for the winter;
2. Investigate whether immature eagles use carcasses more than adult eagles(Halley and Gjershaug 1998)(Halley and Gjershaug 1998)(Halley and Gjershaug 1998)(Halley and Gjershaug 1998), due to their lack of hunting skills and since exploiting carcass is easier;
3. Investigate whether the two eagle species and the different age groups of eagles affect each others carcass use;
4. Investigate whether both White-tailed Eagles and Golden Eagles are associated with the coast in the winter, or whether Golden Eagles use more inland and higher altitudinal areas than the White-tailed Eagle;

Methods

Study area

The study was conducted in Finnmark, northern Norway (fig. 1) where the vegetation in Finnmark consists mainly of low shrub tundra (Walker et al. 2005) and mountain tundra areas (Oksanen and Virtanen 1995, Virtanen et al. 1999) separated by relatively narrow stretches of sub-arctic mountain birch forests. The low shrub tundra is dominated by dwarf birch (*Betula nana*) and willow shrubs (*Salix spp.*) but bilberries (*Vaccinium myrtillus*), heather (*Calluna vulgaris*), grasses (*Graminoids*) and mosses (*Bryopsida*) are also common (Oksanen and Virtanen 1995, Virtanen et al. 1999, Killengreen et al. 2007). In the mountain tundra, the vegetation can be quite sparse, dwarf shrubs are the dominating vascular plants and mosses and lichens are the common cryptogams. In coastal tundra areas the crowberry (*Empetrum hermaphroditum*) is the dominating vascular plant (Oksanen and Virtanen 1995, Virtanen et al. 1999, Killengreen et al. 2007, Isaksen et al. 2008).

By the coast of Finnmark the winters are quite mild, because of the warm Atlantic Ocean currents, but with high precipitation (Tveito et al. 2000, 2001). The further inland you get the less precipitation and colder it gets. In Finnmark the average mean temperature in January/February, by the coast, is about -6 to -4°C but decreases to -20 to -16°C inland. In March and April the mean temperature starts to increase again, reaching plus degrees in May, and the differences in temperature between inland and coast reduces (Tveito et al. 2000, 2001).

The main scavenging species found on the tundra in Finnmark in wintertime are, beside the eagles, wolverines (*Gulo gulo*), red foxes (*Vulpes vulpes*), arctic foxes (*Vulpes lagopus*), ravens (*Corvus corax*), crows (*Corvus cornix*) and magpies (*Pica pica*). Other predators in wintertime include weasels (*Mustela nivalis*) and stoats (*Mustela erminea*), gyrfalcon (*Falco rusticolus*) (Ims and Fuglei 2005, Killengreen et al. 2011), and the bigger predators; the lynx (*Lynx lynx*) and brown bears (*Ursus arctos*) are found in forested areas. The main prey species would be mainly small mammals such as Norwegian lemmings (*Lemmus lemmus*), grey-sided voles (*Myodes rufocanus*) and tundra voles (*Microtus oeconomus*), but mountain hares (*Lepus timidus*), ptarmigans (*Lagopus spp.*) and semi-domestic reindeer (*Rangifer tarandus*) play an important role for many of the predators in Finnmark (Kaikusalo and Angerbjörn 1995, Ims and Fuglei 2005, Killengreen et al. 2007, Henden et al. 2010).

Reindeer in Finnmark are semi-domesticated, meaning that Sámi people (native inhabitants of Finnmark) own, herd and harvest them. By the coast, the high precipitation in winter is unfavourable for reindeer. Thus the reindeers migrate from their summer pastures, which are in coastal areas, to inland areas during the winter where the season is drier and more stable and they can have easier access to the food (plants and lichens) that lies under the snow (Tveraa et al. 2007). Carcasses are noted to be more important food source for the eagles in the wintertime than in the summertime (Halley and Gjershaug 1998), and reindeer

are the most numerous large mammal in Finnmark making it likely that they are important for the eagle populations in Finnmark.

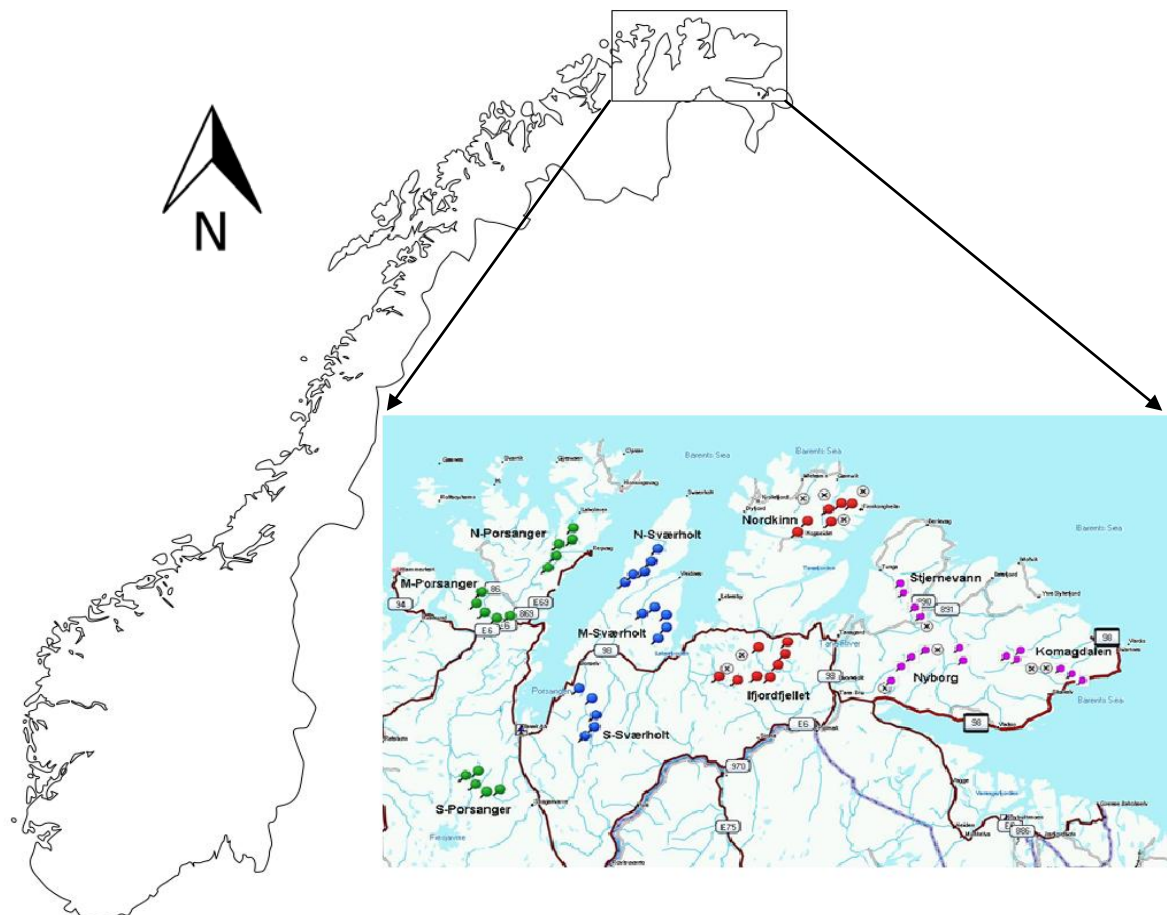


Figure 1. A map of the study area in Finnmark, Norway. Each point marks one camera location, and each colour represents one peninsula; green = Porsanger, blue = Sværholt, red = Nordkinn, pink = Varanger and ⊗ = stations where failure occurred with the cameras and thus no available data.

Study design and equipment:

The monitoring took place on the four peninsulas in Finnmark; Porsanger peninsula (ca. 70°N 24°E) on three transects (North-, Mid- and South-Porsanger) with five stations each; Sværholt peninsula (ca. 70°N 25°E) also on three transects (North-, Mid- and South-Sværholt) with five stations each; Nordkinn peninsula (ca. 70°N 27°E) on two transects (Nordkinn and Ifjordfjellet) with ten stations each; and Varanger peninsula (ca. 70°N 29°E) on three transects (Nyborg, Komagdalen and Stjernevann) with eight stations on two and five stations on the third, respectively. That gives us in total of 71 stations (fig. 1). These transects cover gradients from coast, starting close to tree line, to highland and therefore altitudinal gradients. By that it is possible to see if there is any difference of occupancy by species or age-groups in relation to those distances. Varanger and Nordkinn have in general lower elevation than in the western areas, Porsanger and Sværholt. Distance between each station for each transect was approximately 5-15 km. All transects are summer-grazing areas for the semi-domesticated reindeer, except for Ifjordfjellet which is spring/autumn grazing area. Reindeer were counted once each winter from an airplane and in the period from late February to early April.

At each station a 20 kg block of frozen reindeer slaughter remains, mainly intestines and fat, were positioned in front of a PC700 Hyperfire™ RECONYX Professional Camera Trap. These digital camera traps use infrared flash instead of normal flash so the animals won't be driven away by the flash. A 4GB memory card was used and the cameras were connected to 6V external battery. The time function was set to take a picture automatically every 5-15 minutes. In Porsanger and Sværholt the picture frequency was set to 15 minutes, while the cameras at Nordkinn and Varanger were set to take pictures every 5 or 10 minutes.

In 2009 the study was conducted for 53 days in total in Varanger and Nordkinn, from 6th of March to 27th of April but only for approximately a month, 34 days, in Porsanger and Sværholt, from 24th of March to 26th of April. At 60 stations, total of 1202 station-days were usable, the average number for each station being 20 days (min=3 days, max= 49 days). That is days where the bait was present and with no snow cover on the camera lens during the day. In Varanger and Nordkinn new bait was put out approximately every 2 weeks. At the same time the memory card was changed. In 2010, only data from Porsanger and Sværholt was available. The period was one month earlier than in the year before, starting the 23rd of February, ending the 25th of March, or 31 days. For the 30 stations, a total of 624 station-days were usable with the average number for each station 20.8 days (min=6, max=28).

Not all cameras worked in Varanger and Nordkinn in 2009 so total number of usable stations dropped from 71 to 60. All cameras in Porsanger worked for both years.

Photo identification

All photographs were analysed in RECONYX Map View Professional, Version: 1.5.1.601. When analysing the pictures, the station the picture was taken at, time and day, species at the bait and number of individuals was noted along with visibility on the pictures, that is whether there was snow accumulation on the camera lens which blocked the view and made the picture unusable and if or when the bait disappeared from the view of the camera.

The distance from coast and altitude were extracted from map data in MapSource 6.16.3 and the following maps: N50 CD20 Kirkenes, N50 CD19 Nordkapp, N50 CD18 Alta, Topo pro CD20 Kirkenes, Topo pro CD19 Nordkapp and Topo pro CD18 Alta.

Individuals of White-tailed Eagles and Golden Eagles were classified into 3 different age groups: 1) juvenile eagles, that is eagles in their second calendar year (cy) that hatched in the spring/summer before, 2) subadult eagles being in their 3rd and 4th calendar year and 3) adults in 5th cy and older. Eagles were aged using methods and photographs described in Helander et al. (1989), Tjernberg and Landgren (1999) and photographs from Leksands Fågelklubb (Lindberg and Gillander 2010).

Statistical methods

Data Analyses

We evaluated the spatial pattern in the observed presence/absence of the different demographic groups of eagles (naïve occupancy estimates) using backward selection on the full additive logistic regression model with year, area, distance from the coast, distance from forest and altitude as predictor variables, and presence at a station as the response variable.

To investigate whether there were similar patterns in the proportion of usable days the baits were used, we used a generalised linear model assuming a poisson error distribution, a log link function, and the number of days the baits at the stations was used as the response variable. The logarithm of the number of usable days was included as an offset variable, and only the stations with at least one observation in a given year were included in the analyses. In the analyses we used backward selection on the full model with year, area, distance from the coast, distance from forest and altitude as predictor variables.

We estimated the time (in hours) individuals of a demographic group spent on a carcass per day as: $\text{time} = np * 60 / \text{pfrec}$, where np is number of pictures with an individual of the demographic group taken on a camera station on a given day and pfrec is the time lapse between pictures taken by the camera (5, 10 or 15 min). The estimated times on the carcasses were analysed using general linear model with a log link function and a gamma

error distribution. All the generalised linear regression models were fitted using the program R, version 2.13.0 (R Development Core Team, 2011)

Site Occupancy and Detection

Program Presence 4.0 (Hines 2006) was used for occupancy and detection probability analyses of the two species of eagles. Data was set up separately for each species and age-group and observations for each day at each station noted. If eagle was observed in a certain day, that day got the encounter history 1, otherwise if not observed it got 0. For example an encounter history like 0011001--0 indicates that an eagle was observed in day 3,4 and 7 but not in the other days, the dashed lines stands for days where data is, for some reason, not available. In our case dashed lines could indicate one out of three events, (1) the camera had not been started or had been ended, (2) snow accumulation on the camera so it was not possible to see if eagle was present or not, or (3) the bait had been eaten up by the scavengers or removed by larger scavengers such as red fox or wolverine.

Single-season, single-species site occupancy models were developed to estimate the proportion of sites occupied (ψ) and detection probabilities (ρ) for each species and age-group for each year, 2009 and 2010. These models account for species with detection probabilities less than 1 which should allow for unbiased estimation of occupancy (MacKenzie et al. 2006).

Occupancy (ψ) and detection probabilities (ρ) can be modelled using covariates. Covariates can be constant over time, like distances from coast and altitude in this case, or vary with time, e.g. day of the year, day one being the first day of the study in the year. But there are several assumptions needed for the models to give unbiased estimators:

1. Occupancy at each site does not change over the survey period.
2. Probability of occupancy is considered constant conditional on the covariates used to account for differences in occupancy probability.
3. Detection probabilities are constant across surveys and sites conditional on covariates; there for there is no unmodeled heterogeneity in detection probabilities.
4. Species detection and detection histories at sites are independent.

If these assumptions are violated the model can be biased and the factors influencing occupancy or detection may give unreal results.

Models were ranked using Akaike's Information Criterion (AIC) and models with ΔAIC values ≤ 2 were considered to best explain the data and the one we present here (Burnham and Anderson 2002). The variance inflation factor, \hat{c} , of the global models were used for assessing the fit of the models, the best fit being $\hat{c}=1$. If $\hat{c} > 1$ then there is overdispersion but $\hat{c} < 1$ gives an underdispersion (Burnham and Anderson 2002). If the overdispersion

parameter exceeds 4 than it is likely that there is some structural lack of fit in the model. When overdispersion occurred, $\hat{c} > 1$, we corrected AIC and standard errors using Quasi-likelihood methods (QAIC). To see how well the top models are favoured to the others, Akaike weights were used, a high value compared to other models suggesting that a model stands out as much better than the other, while similar values suggest that several models are equally plausible.

The global models, or the most complex model with all covariates included (Burnham and Anderson 2002), were different between years. Altitude and distance from coast were highly correlated for the areas Porsanger and Sværholt ($r=0,93$ and $0,6$ respectively, fig. 2). Since we only had data from these two areas in 2010, only distance from coast was used in the analyses of the 2010 data. However both altitude and distance from coast was used in 2009 since Varanger and Nordkinn did not show the same level of correlation between altitude and distance from the coast ($r=0,47$ and $-0,06$ respectively) (fig. 2). In 2009 the global model was: $\psi(\text{coast+alti+area}),\rho(\text{coast+alti+area+day})$ while in 2010 it was $\psi(\text{coast+area}),\rho(\text{coast+area+day})$, area being the four different peninsulas and day being number of days from the start of the study in the year. The day covariate was used to see if there would be any changes with time in detection probabilities, e.g. increase in carcass use as the year progresses. The covariates distance from coast and altitude were normalized before entered as covariates in the analyses.

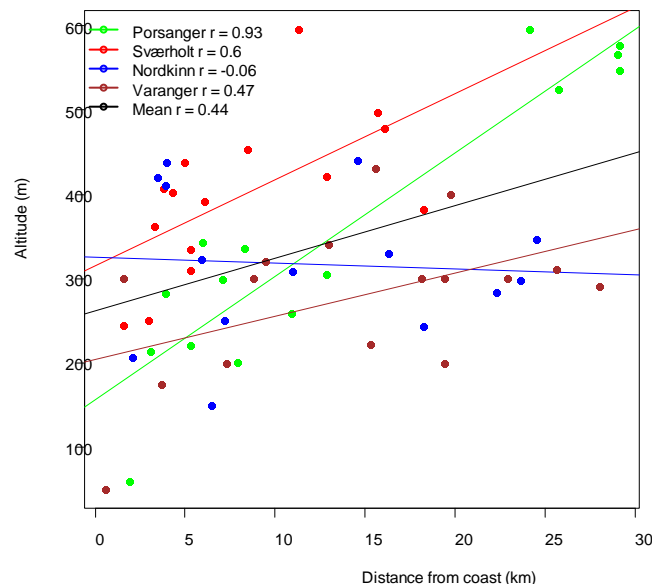


Figure 2. The relationship between altitude (m) and distance from coast (km) for the different camera locations within study areas and the pearson correlation coefficient.

Results

General patterns

Juvenile Golden Eagles (GE) were very rare. None were observed in 2009 and only once were one seen in 2010 (table 1). Subadult GE (2-4cy) were more common and occurred at a similar proportion of stations and at a similar number of station days as adult GE (table 1 and 2). Juvenile White-tailed Eagles (WTE) and subadult WTE were also relatively rare (table 1 and 2) while adult WTE were fairly common on the carcasses. However, the proportion of stations and the number of station days with observations of adult WTE was similar to what observed for subadult and adult GE (table 1 and 2).

There were no differences between years in the proportion of stations observed with eagles of the different species and demographic groups (Fisher exact test $P > 0.30$ for all tests, table 1). In logistic regression analyses we found that the main predictor for spatial variability in the observed presence/absence of adult GE, subadult WTE and adult WTE was area ($p < 0.01$ for all tests). More stations were observed with these demographic groups on the peninsulas Sværholt and Nordkinn, than at Porsanger and Varanger (fig. 2). In addition to an effect of area, we found some evidence for a negative effect of distance from the coast on observed presence on a station, both for adult GE (est. regression coefficient = -0.068 , SE = 0.039) and adult WTE (est. regression coefficient = -0.092 , SE = 0.041). The presence of subadult GE showed a decreasing trend with altitude (estimated regression coefficient = -0.0043 , SE = 0.0019). The number of observations of juvenile eagles was too low to support detailed analyses (table 1).

In general, Sværholt peninsula seems to be the most important area for the eagles in relation to proportion of days they are present at carcass each year (Table 2). However, subadult GE were fairly evenly distributed between the areas. The proportions of station-days used by the different demographic groups of eagles was generally low, the most frequent use of the carcasses was seen on Sværholt where 9.24% of the station-days was used by adult Golden Eagles.

For subadult GE and subadult WTE there was no clear spatial pattern in the proportion of station days used. However, for adult WTE there was a negative effect of distance from the coast on the proportion of station days used (est. regression coefficient = -0.056 , SE = 0.024). For adult GE there also was a tendency for such a pattern (est. regression coefficient = -0.067 , SE = 0.040), and a negative effect of distance from forest on the proportion of station days used (est. regression coefficient = -0.123 , SE = 0.037). In addition, there were differences between areas in the proportion of station days used. The main pattern was that there was a higher proportion of station days used by adult GE on Varanger peninsula than in the other areas (est. regression coefficient = 1.50 , SE = 0.32), and a higher proportion of station days used by adult WTE on Nordkinn peninsula than in the other areas (est.

regression coefficient = 0.49, SE = 0.23), when the effects of distance to the coast and forest were controlled for.

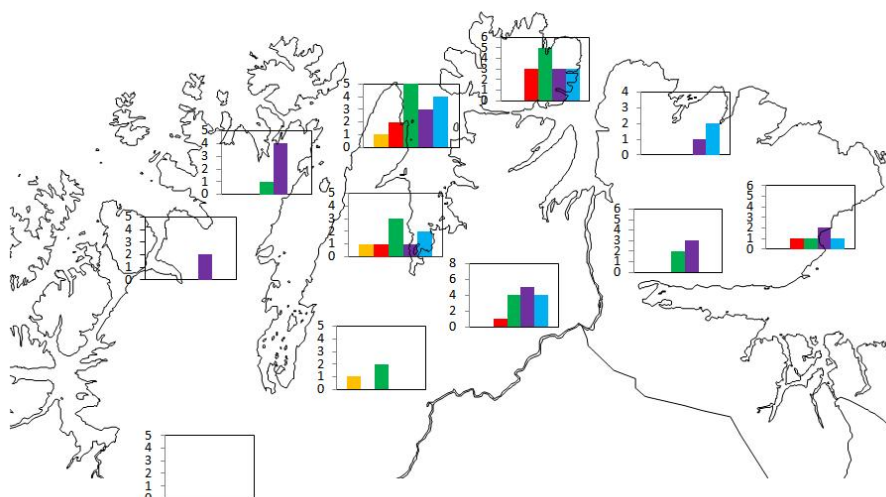
Table 1. Number of days with eagles, number of stations with eagles present and proportion of stations with eagles present on carcass in the winters 2009 and 2010

species	2009			2010		
	n days w/birds	no. stations	prop. of stations	n days w/birds	no. stations	prop. of stations
Juv GE	0	0	0	1	1	0.03
Sub. GE	45	24	0.40	23	10	0.33
Ad GE	55	16	0.27	19	9	0.3
Juv WTE	7	3	0.05	0	0	0
Sub. WTE	9	8	0.13	3	3	0.10
Ad WTE	55	23	0.38	27	10	0.33
Total	128	60		63	30	

Table 2. Proportion of total station-days with eagles present on carcass in the winters 2009 and 2010 for each peninsula." All areas" gives an estimate of the proportion of all station-days in the year. Pors = Porsanger, Svær = Sværholt, Nord = Nordkinn and Var = Varanger area

species	2009					2010				
	Pors	Svær	Nord	Var	All areas	Pors	Svær	Nord	Var	All areas
Juv GE	0 %	0 %	0 %	0 %	0 %	0 %	0,31 %	NA	NA	0,16 %
Sub. GE	3,49 %	3,78 %	4,10 %	3,53 %	3,74 %	5,03 %	2,45 %	NA	NA	3,69 %
Ad GE	0 %	7,56 %	3,28 %	7,35 %	4,58 %	1,34 %	4,60 %	NA	NA	3,04 %
Juv WTE	0 %	2,94 %	0 %	0 %	0,58 %	0 %	0 %	NA	NA	0 %
Sub. WTE	0 %	1,26 %	1,09 %	0,59 %	0,75 %	0 %	0,92 %	NA	NA	0,48 %
Ad WTE	0,39 %	9,24 %	7,92 %	0,88 %	4,58 %	1,34 %	7,06 %	NA	NA	4,33 %

2009



2010

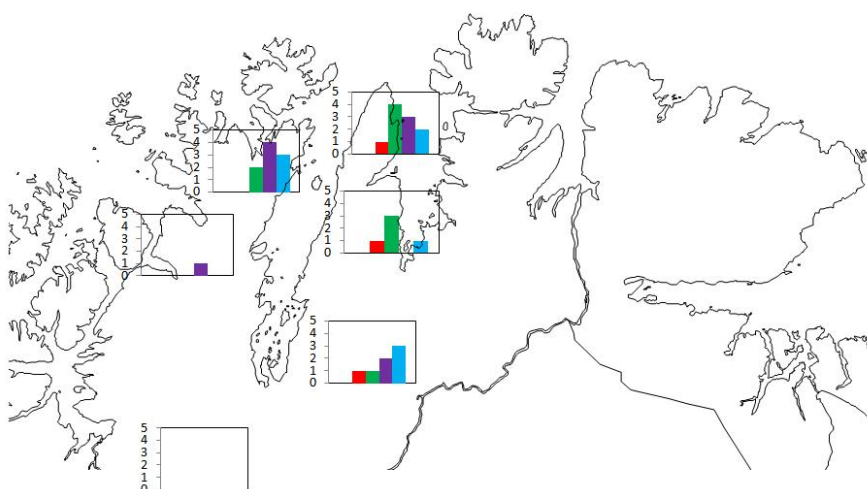


Figure 2. Number of stations for each transect with eagles present. Yellow: first year White-tailed Eagles, red: subadult White-tailed Eagles, green: adult White-tailed Eagles, purple: subadult Golden Eagles and blue: adult Golden Eagles

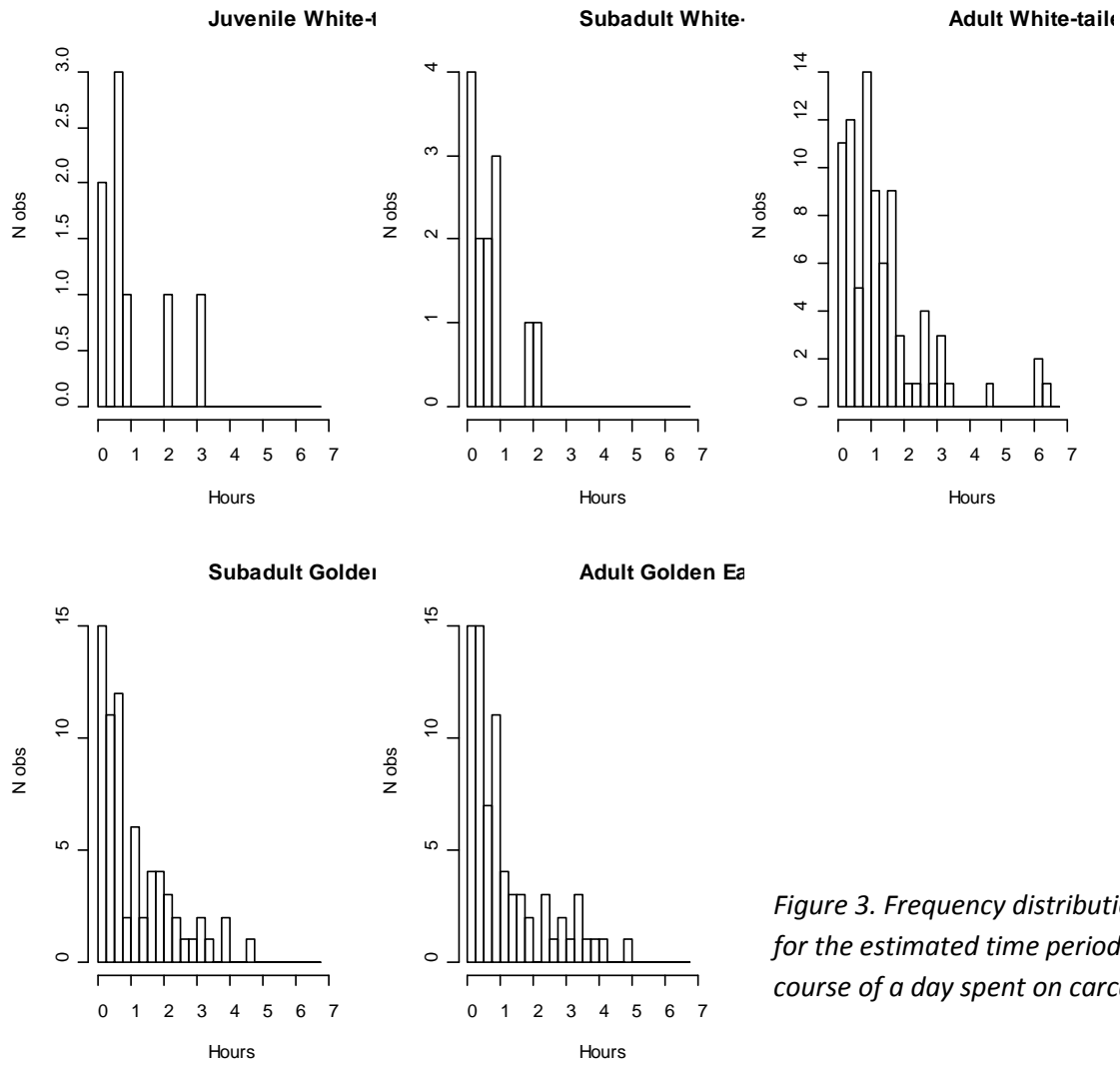


Figure 3. Frequency distributions for the estimated time period in the course of a day spent on carcasses

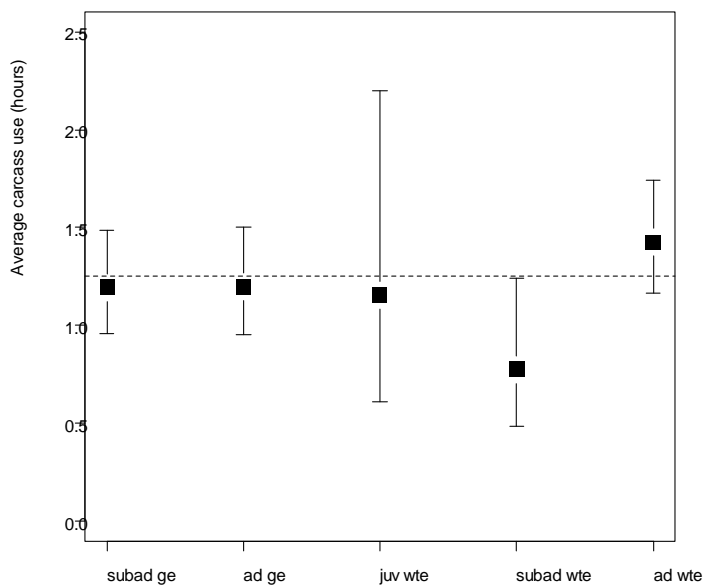


Figure 4. Average time spent on carcass each day for the different demographic groups with 95% confident intervals. Dashed line represents the overall average 1.25 hours

Carcass use

On days when they were present, eagles of a given demographic group were in general observed for one hour or less on the carcasses (fig. 3). At most they spent six and half hours (fig. 3). These numbers do not distinguish individuals of the same demographic group, since it's very hard to recognise individuals on carcasses. It is therefore likely that more than one individual used the carcass on the days with long periods of use. On average the demographic groups spent 1 hour and 15 minutes on days they were present, and there were little difference in the average time spent between demographic groups (fig. 4). Subadult White-tailed Eagles tended though to spend a bit less time than the other groups and adult White-tailed Eagles somewhat more time, but not significantly so ($p > 0.1$).

Only four observations included both a Golden Eagle and a White-tailed Eagle at a carcass at same time. Out of a total of 191 station-days with observations of eagles, both Golden Eagles and White-tailed Eagles were observed at the same day in only 16% of them. There was no significant effect of the presence of the other species or another demographic group at the same day, on the time period the different demographic groups spend on carcass ($p \geq 0.10$). However, there was a tendency for adult Golden Eagles to spend less time on the carcass in days when White-tailed Eagles were also present (effect = -0.42, se=0.26, $p=0.1$).

Occupancy and detection modelling

Due to small sample sizes for juvenile eagles and subadult White-tailed Eagles, occupancy models were only fitted to the data on subadult and adult Golden Eagles, and adult White-tailed Eagles. The best occupancy models for the 2009 data suggested that occupancy decreased with distance from coast for both species and age groups (table 3, 4, fig. 5-7). For subadult Golden Eagles and adult White-tailed Eagles occupancy also differed between areas. For subadult Golden Eagles, occupancy was estimated to be highest on Varanger and Nordkinn and lower at Porsanger and Sværholt (fig. 7). A similar pattern was estimated for adult White-tailed Eagles, occupancy was estimated to be highest on Varanger, slightly lower at Nordkinn and Sværholt and low at Porsanger peninsula (fig. 5). In general, the detection probability also varied with distance from coast and between areas. For subadult Golden Eagles detection probabilities tended to increase with distance from the coast (table 4, appendix), while detection probabilities for adult eagles decreased with distance from the coast (table 4, appendix). The estimated detection probability was very low for subadult Golden Eagles and adult White-tailed Eagles on Varanger, an area with estimated occupancy close to 1 (fig. 5 and 7, appendix). Furthermore, the detection probability varied with altitude and day in the season for adult eagles of both species. Adult Golden Eagles showed

a trend towards an increase in the detection probability with increasing altitude, while adult White-tailed Eagles showed a trend towards a decrease in the detection probability with increasing altitude (table 4). Adults of both species showed an increasing trend in the detection probability as the winter season progressed (table 4). Several models for adult Golden Eagles showed similar AIC weight, so there was no single best model. The covariates seemed to affect detection probabilities more than occupancy probabilities, and the evidence for an effect of distance to the coast on occupancy was weak (table 3).

For 2010 the sample sizes was smaller. Overdispersion occurred for both subadult Golden Eagles and adult White-tailed Eagles ($\hat{c}=5,7$ and $2,9$ respectively) which was accounted for by re-ranking the models using quasi-AIC (QAIC, table 3). Occupancy in the best models was constant for both species and both demographic groups of Golden Eagles (table 3) and variability in the data was only explained by variation in detection probabilities. The detection probability of subadult Golden Eagles was higher at Porsanger peninsula than at Sværholt, and increased through the study period (table 4, appendix). Detection probabilities for adult Golden Eagles decreased with distance from the coast, was lower at Porsanger peninsula than at Sværholt, and increased through the study period (table 4, appendix). Also the detection probability of adult White-tailed Eagles with distance from the coast, was lower at Porsanger peninsula than at Sværholt (table 4, appendix).

Table 3. The best models of site occupancy (ψ) and detection probabilities (ρ) of the 3 different demographic groups with sufficient data to be modelled, in 2009 and 2010.

Model	Δ AIC	AIC wgt	no.Par.
Subadult Golden Eagles 2009			
$\psi(\text{coast+area}),\rho(\text{coast+area})$	0	0,34	10
$\psi(\text{coast+area}),\rho(\text{area})$	0,11	0,33	9
$\psi(\text{coast+area}),\rho(\text{area+day})$	1,36	0,17	10
$\psi(\text{coast+area}),\rho(\text{coast+area+day})$	1,58	0,16	11
Subadult Golden Eagles 2010			
$\psi(.),\rho(\text{area+day})$	Δ QAIC	AIC wgt	no.Par.
$\psi(.),\rho(\text{area+day})$	0	0,30	4
$\psi(\text{coast+area}),\rho(.)$	0,54	0,23	4
$\psi(\text{coast}),\rho(\text{area+day})$	1,05	0,18	5
$\psi(.),\rho(\text{coast+area+day})$	1,13	0,17	5
$\psi(\text{area}),\rho(\text{area+day})$	1,91	0,12	5
Adult Golden Eagles 2009			
$\psi(\text{coast}),\rho(\text{coast+alti+area+day})$	Δ AIC	AIC wgt	no.Par.
$\psi(\text{coast}),\rho(\text{coast+alti+area+day})$	0	0,18	9
$\psi(.),\rho(\text{coast+alti+area+day})$	0,2	0,16	8
$\psi(.),\rho(\text{coast+area+day})$	0,38	0,15	7
$\psi(\text{alti+area}),\rho(\text{coast+alti+area+day})$	0,94	0,11	12
$\psi(\text{area}),\rho(\text{coast+alti+area+day})$	1,07	0,11	11
$\psi(\text{alti+area}),\rho(\text{coast+alti+area})$	1,11	0,10	11
$\psi(\text{area}),\rho(\text{coast+area+day})$	1,22	0,10	10
$\psi(\text{area}),\rho(\text{coast+area})$	1,54	0,08	9
Adult Golden Eagles 2010			
$\psi(.),\rho(\text{coast+area+day})$	Δ AIC	AIC wgt	no.Par.
$\psi(.),\rho(\text{coast+area+day})$	0	0,34	5
$\psi(\text{area}),\rho(\text{coast+area+day})$	1,02	0,20	6
$\psi(\text{coast}),\rho(\text{coast+area+day})$	1,56	0,15	6
$\psi(\text{coast}),\rho(\text{area+day})$	1,56	0,15	6
$\psi(\text{coast+area}),\rho(\text{coast+area+day})$	1,60	0,15	7
Adult White-tailed Eagles 2009			
$\psi(\text{coast+area}),\rho(\text{coast+alti+area+day})$	Δ AIC	AIC wgt	no.Par.
$\psi(\text{coast+area}),\rho(\text{coast+alti+area+day})$	0	0,73	12
$\psi(\text{area}),\rho(\text{coast+alti+day})$	1,95	0,27	8
Adult White-tailed eagles 2010			
$\psi(.),\rho(\text{coast+area})$	Δ QAIC	AIC wgt	no.Par.
$\psi(.),\rho(\text{coast+area})$	0	0,46	4
$\psi(.),\rho(\text{coast+area+day})$	1,73	0,19	5
$\psi(\text{area}),\rho(\text{coast+area})$	1,92	0,18	5
$\psi(\text{coast}),\rho(\text{coast+area})$	2	0,17	5

Table 4. Parameter estimates and their standard errors for the best occupancy models, for each demographic group and year. Covariates which are not included in the best models are marked with dashed line and NA where altitude and areas were not included in the modelling, in 2010. Sværholt was used as intercept in the models.

	Sub. GE 2009	Sub. GE 2010	Ad. GE 2009	Ad. GE 2010	Ad. WTE 2009	Ad. WTE 2010
ψ Intercept	-10,34 (5,05)	-0,38 (0,44)	-0,51 (0,35)	-0,004 (0,52)	0,17 (0,81)	0,65 (0,67)
Coast	-11,36 (5,61)	-	-0,66 (0,45)	-	-2,29 (1,13)	-
Altitude	-	NA	-	NA	-	NA
Var	30,71 (14,84)	NA	-	NA	25,84 (103113,12)	NA
Nord	51,38 (167674,65)	NA	-	NA	3,10 (2,45)	NA
Pors	10,46 (5,26)	-	-	-	-3,36 (2,03)	-
ρ Intercept	-0,76 (0,46)	-3,57 (0,67)	-2,72 (0,78)	-3,77 (0,74)	-3,52 (0,73)	-3,18 (0,56)
Coast	0,32 (0,22)	-	-0,80 (0,59)	-1,21 (0,63)	-0,55 (0,26)	-1,86 (0,65)
Altitude	-	NA	0,71 (0,35)	NA	-0,58 (0,22)	NA
Var	-2,64 (0,60)	NA	1,65 (0,65)	NA	-2,68 (0,74)	NA
Nord	-2,46 (0,57)	NA	-0,31 (0,49)	NA	-0,10 (0,41)	NA
Pors	-1,48 (0,54)	1,26 (0,53)	-27,10 (170775,81)	-1,42 (0,64)	-1,78 (1,97)	-1,33 (0,63)
day	-	0,04 (0,03)	0,04 (0,02)	0,08 (0,03)	0,06 (0,02)	-

Adult White-tailed Eagles

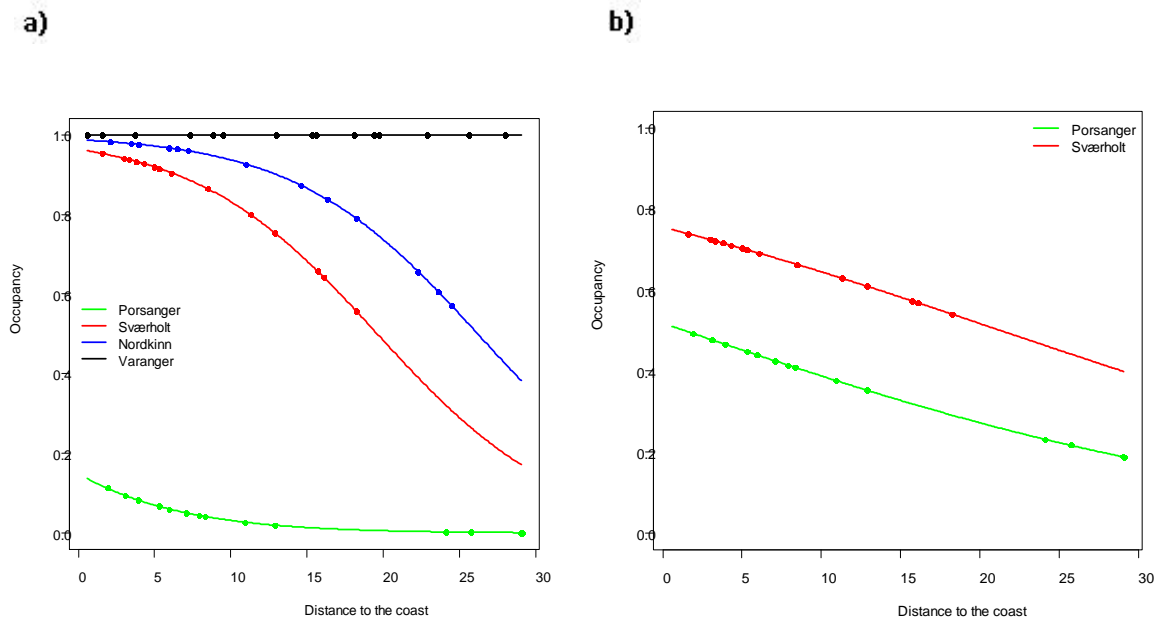


Figure 5. Estimates of occupancy probabilities of adult White-tailed Eagles in relation to distance from coast (km) in the years a) 2009 and b) 2010, calculated from the global occupancy models.

Adult Golden Eagles

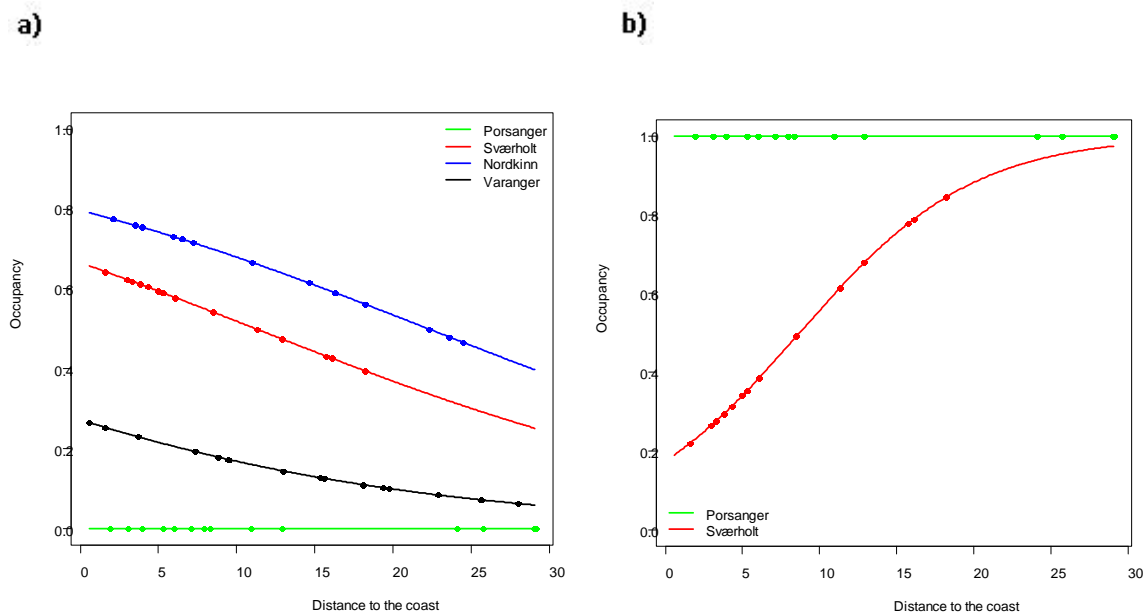


Figure 6. Estimates of occupancy probabilities of adult Golden Eagles in relation to distance from coast (km) in the years a) 2009 and b) 2010, calculated from the global occupancy models.

Subadult Golden Eagles

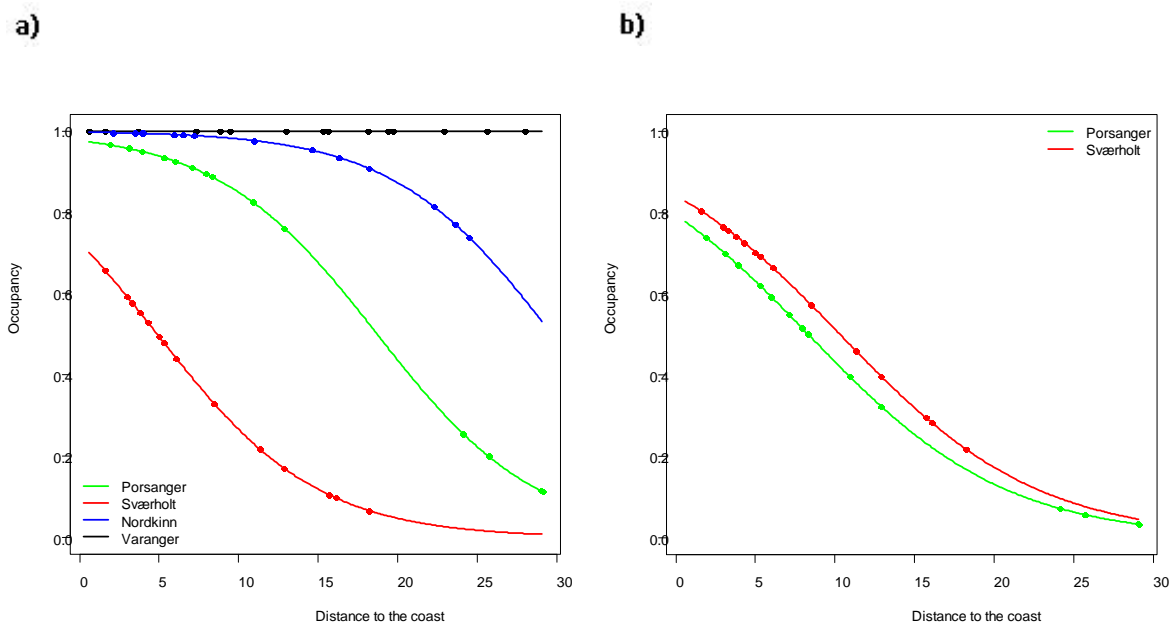


Figure 7. Estimates of occupancy probabilities of subadult Golden Eagles in relation to distance from coast (km) in the years a) 2009 and b) 2010, calculated from the global occupancy models.

Discussion

Demographic structure

I found that both juvenile Golden Eagles and juvenile and subadult White-tailed Eagles were rare sights at the monitored carcasses. This finding is consistent with data on satellite tagged juvenile Golden Eagles and recovery of ringed immature White-tailed Eagles, which suggest that they disperse south, out of Finnmark in the wintertime (Strann et al. 2007, Jacobsen et al. 2011). Studies in Alaska also show evidence for a seasonal north – south migration in immature Golden Eagles (McIntyre et al. 2008). The data from satellite tagged juvenile and subadult Golden Eagles suggest that they return to Finnmark in March-April, although the time varies and some may stay in Finnmark throughout the winter (Jacobsen et al. 2011). In contrast, data from further south in Norway, (Smøla, Møre and Romsdals county, ca 63°N), have shown that juvenile White-tailed Eagles stayed the whole winter near their natal site, not migrating until next spring (in their second calendar year) and then mostly north. This northward migration had a similar timing to when most local birds return to Finnmark from their wintering grounds. The southern eagles returned south the next autumn, and stayed there over the winter before they repeated this behaviour again the next spring (Bevanger et al. 2011). This may suggest that most juvenile and subadult eagles, whether they hatch at high latitudes in Finnmark or in the lower latitudes at Smøla, are using more northern latitudes in summer and southern latitudes during the winter. The observed frequency of subadult Golden Eagles seems, however, to deviate from this pattern. Subadult Golden Eagles were seen relatively often on the carcasses in the winter, and at a similar number of days and proportion of stations as adult Golden and White-tailed Eagles (table 2 and 3). Furthermore, as suggested by changes in the estimated detection probabilities, there was only a weak tendency towards an increase in carcass use by subadult Golden Eagles over the study period and the temporal change in detection probabilities was more pronounced for the adult eagles than the subadult Golden Eagles (table 4). These results suggest that subadult Golden Eagles are present in Finnmark at substantial numbers in the latter half of the winter with only weak evidence for an increase in numbers in March-April. It also seems, by data on satellite tagged Golden Eagles (Jacobsen et al. 2011), that immature Golden Eagles move less as they become older. It may also be that some of these subadult Golden Eagles have started to settle in a breeding territory, as they are known to do at some point as subadults (Steenhof et al. 1983, Whitfield et al. 2004).

Intensity of carrion use and inter-specific interactions

The period the carcasses were used by a demographic group of eagles was on average 1.25 hours, with most estimates being less than an hour. Similar short periods of carcass use has previously been reported by Stalmaster and Gessman (1984). I found no difference between species and demographic groups in the average period the carcasses were used during a day. This contrast to the findings of Halley and Gjershaug (1998) and Stalmaster and Gessaman (1984) whom found that immature eagles spent longer time feeding, when undisturbed, than adults. Furthermore, I found no evidence for interference between individuals of different species or demographic groups. This finding is consistent with the results of Kolodziejczyk et al. (2005) on wintering White-tailed Eagles, but is in contrast to the results of Stalmaster and Gessaman (1984) which found that juvenile and subadult Bald Eagles (*Haliaeetus leucocephalus*) spent less time feeding and more time waiting than adults when at carcass at same time. A problem with my study is that I don't have data on individual birds, as they are difficult to distinguish based on the pictures. This is likely to reduce the ability to detect differences between demographic groups in carcass use and interactions. However, the dominance of relatively short time periods spent scavenging leaves plenty of time during the day for other individuals to exploit the same carcass without causing substantial interference. Furthermore, Golden Eagles and White-tailed Eagles were seen at the same carcass on the same day in 16% of the station days. In most days there were no eagles at the carcasses at all. This suggests that interference at the carcass may be of little importance in this study system. Continuous focal watches are probably needed to evaluate this hypothesis properly. However, the low frequency of carcass use observed suggest that a considerable effort will have to be invested in such a study to obtain the necessary sample sizes.

Spatial and temporal patterns of carrion exploitation

The abundance of eagles seemed in general to be affected by distance from coast, that is, their presence on carcasses increased to some extent the closer to the coast the stations were. This was more evident for adult eagles than for immature. A reason for this pattern is likely to be that food availability is higher along the coast. This is in particular likely to be true for White-tailed Eagles which often feed on fish and seabirds (Willgohs 1961). The abundance of Golden Eagles in Finnmark have previously been suggested to be more affected by distance from forest than coast (Killengreen et al. 2011) while in my analyses, the distance from coast was the best predictor of whether a station had at least one observation of an adult Golden Eagle, while the frequency of observations of adult Golden Eagles was more related to the distance from the forest. My results are therefore at least partly consistent with the findings of (Killengreen et al. 2011). Many of the prey species used by Golden Eagles, such as ptarmigans and hares (Watson 2010), are found inland and

may be more abundant close to forests than far into the tundra. The main determinant of the abundance of subadult Golden Eagles was less clear. The logistic regression models for presence/absence on a station suggested that altitude was more important than distance from coast or forest, with stations more likely to be visited at least once at lower altitudes than higher. However, in the occupancy models, altitude was not included in the best models.

There was significant spatial variation in the abundance of eagles in the study region. With the exception of subadult Golden Eagles, Porsanger peninsula seemed not to be used to any greater extent by the eagles (fig. 2). White-tailed Eagles seemed to prefer the Sværholt and Nordkinn peninsulas while adult Golden Eagles preferred the Varanger and Nordkinn peninsulas. In contrast, Killengreen et al. (2011) found both species more often on Nordkinn than on Varanger peninsula. The most likely reason for such spatial patterns is that they are associated with variation in food availability. For White-tailed Eagles the spatial variation may be associated with the distribution of sea bird colonies, and suitable hunting grounds for fish (Willgoos 1961, Lorentsen 2011). For Golden Eagles the spatial variation may be associated differences in the abundance of ptarmigans and hares (Watson 2010). In addition, for both species the spatial variability may be associated with the spatial distribution of reindeer, and reindeer carcasses. The study region cover only summer pastures for semi-domesticated reindeer, however, in some years a significant number of reindeer are left to overwinter on the peninsulas (Audun Stien, pers. com.). It is well known that Golden Eagles predate reindeer calves (e.g. Johnsen et al. 2007, Norberg et al. 2006, Tjernberg 1981). Golden Eagles are also known to predate on adult reindeers (Nybakk et al. 1999), and eagles in general feed on reindeer carcasses. Since reindeer mortality rates are elevated in the winter, especially when winters are harsh (Tveraa et al. 2003), high reindeer densities may supply a substantial amount of food for both species of eagles. The spatial distribution of eagles may therefore potentially vary between years, if the spatial distribution of overwintering reindeer and associated carcasses varies between years.

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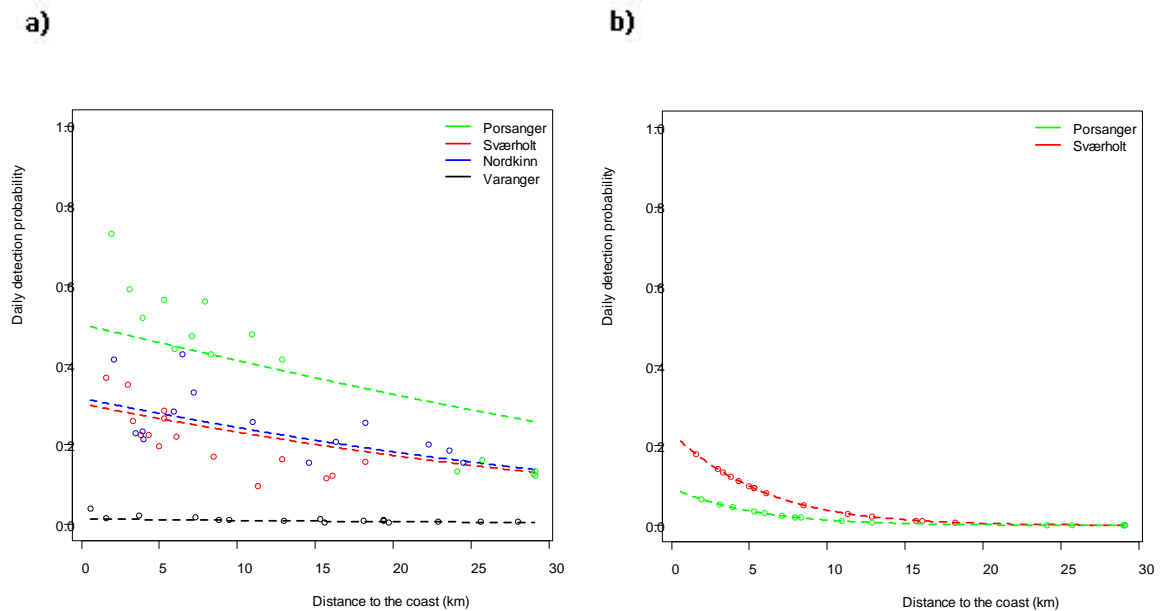
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Appendix

1.

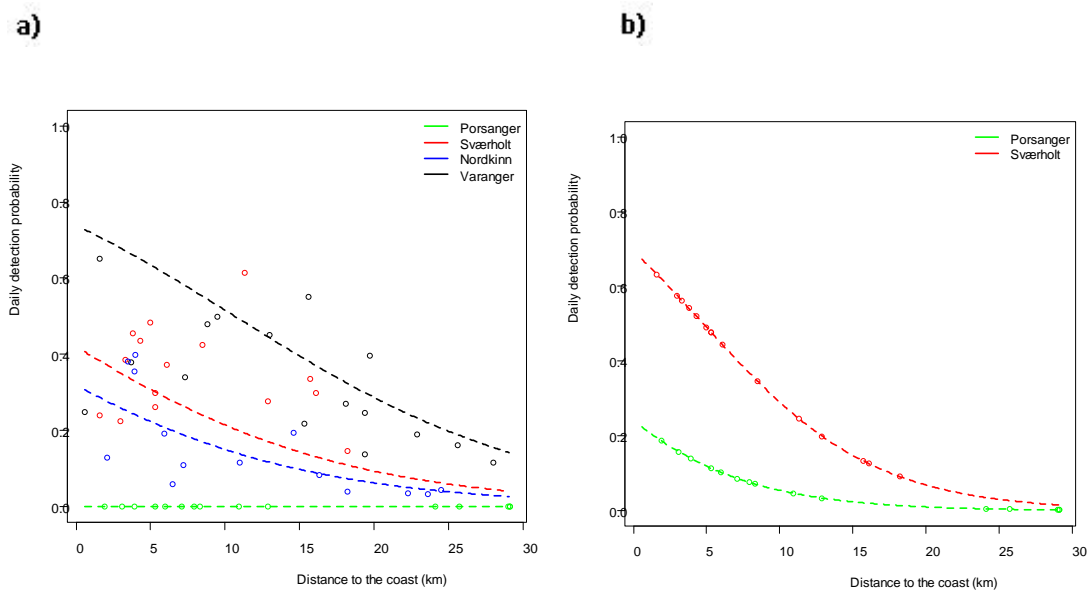
Adult White-tailed Eagles



Daily detection probabilities of adult White-tailed Eagles in relation to distance from coast (km) in the years a) 2009 and b) 2010, calculated from the global occupancy models. Detection probabilities in the years 2009 include altitude as a covariate making a scatter of estimated detection probabilities around the regression line.

2.

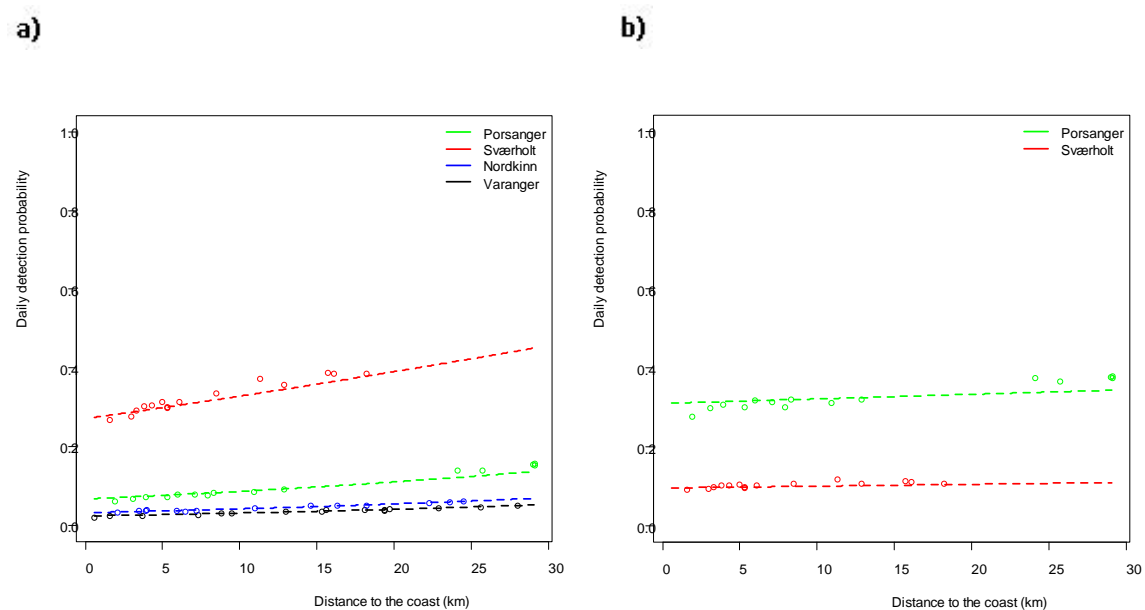
Adult Golden Eagles



Daily detection probabilities of adult Golden Eagles in relation to distance from coast (km) in the years a) 2009 and b) 2010, calculated from the global occupancy models. Detection probabilities in the years 2009 include altitude as a covariate making a scatter of estimated detection probabilities around the regression line.

3.

Subadult Golden Eagles



Daily detection probabilities of subadult Golden Eagles in relation to distance from coast (km) in the years a) 2009 and b) 2010, calculated from the global occupancy models. Detection probabilities in the years 2009 include altitude as a covariate making a scatter of estimated detection probabilities around the regression line.

