

MASTER OF SCIENCE THESIS IN ECOLOGY

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# Environmental determinants of spatio-temporal variation in a scavenger guild on sub-arctic tundra



**Elise Strømseng**

May 29th 2007



Faculty of Science, Department of Biology  
University of Tromsø, N-9037 Tromsø



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Elise Strømseng



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## Abstract

The winter season in the sub-arctic represents a lack of potential prey species for predators in such areas. Most carnivore species are known to be facultative scavengers and carcasses therefore represent an alternative meal during periods of scarce food resources. Carcasses are spatially and temporally pulsed resources in an ecosystem and therefore not a predictable way of obtaining food, but several species are known to utilize- and be more or less dependent on carcasses in winter. In this study, artificial carcasses were used to determine the spatial and temporal distribution of scavenger species in the sub-arctic tundra of eastern-Finmark. Six transects with a total of 48 stations were equipped with a digital camera, logging time-lapses of species activity on the artificial carcasses. A total of 36458 photos of scavenging species were recorded during two winter seasons in 2005 and 2006. Generalized linear models were used to analyse environmental gradients and temporal patterns for 7 of the 10 different species that were recorded by the digital cameras. Regional spatial patterns of distribution, based on distances to forest, coast and altitude were detectable for most species analyzed, except hooded crows (*Corvus corone corax*). The spatial presence of the other species seemed to be dependent on proximity of station to either resource rich areas, preferable habitats according to food preferences or altered by risk sensitivity. Ravens (*Corvus corax*) were by far the most pronounced scavenger showing a generally high presence in all areas independent of environmental variables. Among mammalian scavengers the red fox (*Vulpes vulpes*) was the most abundant species, showing a declining trend with altitude. Temporal patterns of carcass utilization according to diurnal light conditions indicated that avian scavengers were in general dependent on daylight, whereas mammalian species occurred most frequently during the night and morning twilight. All avian scavengers were somehow correlated with each other according to presence at stations. In contrast, mammalian scavengers presented no clear association with either birds or each other.

These results describe for the first time how the avian and mammalian scavengers in sub-arctic tundra areas are distributed according to environmental gradients and their activity pattern during changing light conditions. In addition to competition, this study suggests other factors, which may also be of importance for describing which species are utilising carcasses at a given time or place.

**Keywords:** Scavengers, sub-arctic, winter, carcass, raven (*Corvus corax*), red fox (*Vulpes vulpes*), white-tailed eagle (*Haliaeetus albicilla*), golden eagle (*Aquila chrysaetos*), arctic fox (*Alopex lagopus*), wolverine (*Gulo gulo*).



## 1.0 Introduction

The winter season in cold regions (i.e. alpine and arctic ecosystems) represents a major challenge when it comes to survival for homeotherm animals. Carnivores in such ecosystems often suffer from food scarcity during this period, as winter represents a temporal absence of migrating birds and snow covering possible prey at the ground level (Sonerud 1986; Jędrzejewski and Jędrzejewska 1992; Selva 2004b). However, the winter is also a period that may provide alternative food items due to a higher natural mortality of potential prey species, e.g. large herbivores. Such carcasses are known to be an important resource for carnivores and a common way of obtaining food (Jędrzejewski and Jędrzejewska 1992; Jędrzejewska and Jędrzejewski 1998; DeVault et al. 2003; Selva 2004a; Selva 2004b). Though, obligate scavenging is only known from two lineages of birds (Ruxton and Houston 2004), several carnivore species are known to scavenge frequently, especially during winter (Heinrich 1988; Jędrzejewska and Jędrzejewski 1998; Stahler et al. 2002; Selva 2004a; Selva 2004b; Selva et al. 2005).

The spatial and temporal distribution of carnivore species at high latitudes may be affected by the availability of winter food resources. Even if carcasses represent an alternative meal for facultative scavengers, it is also a spatially aggregated and temporally pulsed resource in an ecosystem (Heinrich 1988; Jędrzejewski and Jędrzejewska 1992; DeVault et al. 2003; Wilmers et al. 2003; Wilmers and Getz 2005), and thus an unpredictable way of obtaining food. Hence, the spatial distribution of facultative scavengers is expected to be only partly determined by the abundance of carcasses, i.e. the distribution of their preferred live prey may be more important. However, in periods of scarcity of live prey, efficiently finding and exploiting alternative prey and carcasses is an advantage (Mullen and Pitelka 1972; Wilmers et al. 2003). The distribution of facultative scavengers may then be determined by other factors such as mobility, sensitivity to competition and predation risk – possibly leading to both a temporal and spatial segregation within a guild of scavengers (Selva 2004b; Selva and Fortuna 2007). Furthermore, also human activity is likely to affect the distribution of scavenging species (Skagen et al. 1991; May et al. 2006), especially since several species has been subject to long-term human persecution (Breitenmoser 1998; Rinden 1998a; Rinden 1998b). It is also noteworthy that subsidies from human settlements has lately led to easier food access for many species (Jędrzejewski and Jędrzejewska 1992; Contesse et al. 2004; Randa and Yunker 2006), thus, indicating that anthropogenic resources also might play a role for the distribution of scavenger species.

The use of carcasses are suggested not to be random, but rather dependent on behavioral adaptations and extrinsic factors (Selva et al. 2005; Selva and Fortuna 2007). Accordingly, since scavenging species differ in their efficiency in locating and exploiting carcasses, asymmetric interspecific competition is likely to occur at such aggregated resources. Competition might thus be a factor that possibly is important for the structure of the scavenger community. Selva (2004b) refers to two general types of competition among guilds of scavengers, which can also be identified as contest- and scramble competition. 1) *Contest competition* is based on interference or direct competition (e.g. aggression). 2) *Scramble competition* can be defined as exploitation- or diffuse competition. Accordingly, in order to be able to control a resource (i.e. carcass) it is therefore important to either be the dominant species, or being the most efficient species in locating and exploiting the carcass. A third type of interspecific interaction that may structure scavenger communities is intraguild predation, which generally also might be seen upon as an extreme form of contest competition (Selva 2004b). Carcasses are focal points of predator activity and thus represent an increased possibility of intraguild predation, affecting especially subordinate scavenger species. Individual body size, dominance, flocking and social foraging techniques are important factors deciding the outcome of negative inter- and intraspecific interactions among scavengers, whereas tolerance or hierarchal positioning may allow different individuals and species to co-exist at a carcass site (Heinrich 1988; Marzluff and Heinrich 1991; Bugnyar and Kotrschal 2002; Selva 2004b; Vucetich et al. 2004). Also, intraguild species may exploit the same resource by differing in their temporal pattern. Such differences in diurnal activity are known to allow subordinate species to exploit carcasses at a lower risk (Selva 2004b).

Arctic and sub-arctic tundra ecosystems are characterized by generally low productivity (Bliss et al. 1973), and the terrestrial food-chain is known to be relatively short (Ims and Fuglei 2005), comprising three main trophic levels. Yet, such areas may be subject to allocthonous subsidies from adjacent ecosystems e.g. nearby forest and ocean (Rose and Polis 1998; Roth 2003), which in turn also may play an important role in structuring the scavenger communities. The process of scavenging is looked upon as a key ecological process in the recycling and redistribution of organic material and nutrients, but also as an important factor influencing the ecosystem diversity and the dynamics of consumers (Rose and Polis 1998; Towne 2000; DeVault et al. 2003; Roth 2003; Melis et al. 2004; Selva 2004b). Unfortunately there are still few systematic studies involving the role of carcasses and scavenging at high latitudes (Selva 2004b; Selva et al. 2005), even though it is most likely an

important factor in determining the trophic structure and the dynamics of alpine and arctic food webs.

The present work took place in sub-arctic tundra in Eastern Finnmark, northern Norway. The aim of this study was to investigate the determinants of temporal and spatial variation in the structure of a scavenger community in sub-arctic tundra during winter. Focus was given to the distribution of species along a spatial resource gradient spanning from the coast to the inland tundra, and the temporal variation in utilization of carcasses by scavengers, during changing light conditions. Data on species distributions were obtained using cameras with time laps functions placed in front of artificial reindeer carcasses. The following predictions were made based on the assumed characteristics of the occurring scavenger species.

1. Competitive dominant species is expected to be most prevalent in the resource rich areas close to the forest and the coast as they may be able to monopolize resources in such areas. Competitive subordinate species may only be able to exploit carcasses in resource rich areas, when more competitive dominant species are absent.

2. Highly mobile species such as birds, which is also likely to possess high carcass detection ability due to diurnal visual detection from air, are expected to have a relatively even distribution across a resource richness gradient. This is because carcass searching incurs relatively little cost (Ruxton and Houston 2004) even in areas with very scattered resources. Moreover competition with other species will be relaxed for such species since they will be able to detect and exploit resources before less mobile species. Therefore, they may even be able to exploit resources in areas with more dominant, but less mobile species.

3. Risk sensitive species will prefer areas with absence of natural enemies and is for this reason expected to be most prevalent in remote inland tundra areas, with fewer dominant predators. Risk sensitive species is also expected to have non-overlapping activity periods with their enemies.

## 2.0 Material and methods

### 2.1 Study area

This study was conducted in eastern Finnmark, northern-Norway during late winter-early spring in 2005 and 2006. The study area includes relatively coast-near tundra areas at approximately 70°N 30°E (Figure 1). Due to the influence of the North Atlantic current, climate is fairly mild in this area. However, permafrost is patchily present (Virtanen et al. 1999a) and the weather is known to be quite harsh during winter periods. The coast-near tundra in eastern Finnmark, which may extend down to the sea-level, is classified as erect shrub-tundra (Walker et al. 2005), whereas the inland and high altitude areas (tree-line approximately at 200-300m) consist of mountain tundra, interspersed with some narrow belts of mountain birch forest (*Betula nana*) in low-land valleys and in the inner parts of the fjords (Oksanen and Virtanen 1995). Thus, the tundra area of interest in this study is bordered by mountain birch forest in some places and coast lines in other.

Beyond the latitudinal and altitudinal forest line the vegetation in the lowland tundra is dominated by shrubs (e.g. *Betula nana*), dwarf shrubs (e.g. *Empetrum nigrum* subsp. *hermaphroditum*, *Vaccinium myrtillus*) interspersed with dicotyledons (e.g. *Bistorta vivipara*) and graminoids (e.g. *Nardus stricta*, *Carex bigelowii*) – while the vegetation cover at higher altitudes (>300-400 m.a.s.l) is very sparse (Virtanen et al. 1999b; Killengreen et al. 2007). Because of generally low productivity in these tundra areas, there are few herbivore species that may constitute a food source for predators and scavengers in winter. The main prey species are tundra voles (*Microtus oeconomus*), grey-sided voles (*Clethrionomys rufocanus*), Norwegian lemmings (*Lemmus lemmus*), rock ptarmigan (*Lagopus muta*), and semi-domestic reindeers (*Rangifer tarandus*). Voles and lemmings exhibit cyclic dynamics with an approximate 5 year period in eastern Finnmark (Yoccoz and Ims 2004). The last population peak was in 2002/2003 and the next peak is therefore expected to be after the present study is conducted, in 2007/2008. An independent trapping study showed that generally, grey-sided voles and tundra voles were present in all parts of the study area in low to moderate numbers (Killengreen et al. 2007). The tundra areas included in this study all harbour rather dense populations of semi-domestic reindeer (Killengreen et al. 2007). However, the coast-near areas is mainly summer pastures for migratory herds. Thus, in the period of the present study the main reindeer herds are located in the continental winter pasture areas in the forest and mountain tundra further south. However, a small, but largely unknown, number of reindeer are still present during the winter in the summer pastures. Because summer and spring/autumn

pastures provide an unstable resource basis for reindeer during winters, a relatively high mortality rate may provide scavengers with carcass resources.

Additional prey/carcass resources that can be associated with the nearby forest are mountain hare (*Lepus timidus*), red vole (*Clethrionomys rutilus*), field vole (*Microtus agrestis*), moose (*Alces alces*) and willow ptarmigan (*Lagopus lagopus*). Although these species to some extent also may be found in the lower-most parts of the tundra with well-developed willow thickets, they have their strongholds in the mountain birch forest ecosystem. Yet, other alternative prey located in the low-land areas, can be considered as subsidies from the marine ecosystem. The Barents Sea and the associated fiords are very productive (Dayton et al. 1994; Fogg 1998) and are therefore likely to provide a rich littoral source in the form of marine invertebrates, fish and carcasses of sea mammals for predators and scavengers of the eastern Finnmark tundra.

## 2.2 Study design

The fieldwork was conducted along six study transects (Figure 1) in the period 18<sup>th</sup> of February to 27<sup>th</sup> of April in 2005 and 2006. Three of the study transects were situated at the Varanger peninsula, hereafter named *Komagdalen*, *Vestre Jakobselvdalen* and *Stjernevann*. The other three transects were located at the *Nordkynn* peninsula, *Ifjordfjellet* and in an area in between Bekkarfjord and Hopseide, hereafter named *Bekkarfjord*. All transect areas, except *Ifjordfjellet*, are a summer-grazing pastures for semi-domestic reindeers, whereas *Ifjordfjellet* is an autumn/spring-grazing area.

All study transects were placed as to cover gradients of distances to coast and/or to tree-line, thereby also involving an altitudinal gradient (0-400 m.a.s.l). In addition, an intensive campaign to reduce the population of red fox (*Vulpes vulpes*) on the Varanger peninsula was initiated in April 2005 and continued until the end of the present study. Thus, the three transects at Varanger peninsula (*Komagdalen*, *Vestre Jacobselvdalen* and *Stjernevann*) will be regarded as *experimental transects*, whereas the other tree transects (*Nordkynn*, *Ifjordfjellet* and *Bekkarfjord*) will be regarded as *reference transects*. The red fox reduction campaign was decided by the government (Directorate for Nature Management) in an attempt to relax the competitive pressure on the arctic fox (*Alopex lagopus*) population that for a long time has been endangered in Fennoscandia (Lönnberg 1927; Østbye et al. 1978; Hersteinsson et al. 1989; Hersteinsson and Macdonald 1992; Rinden 1998a; Angerbjörn et al. 2004). The campaign was allowed to exceed the normal hunting period (15<sup>th</sup> of July – 15<sup>th</sup> April) and to use extraordinary means including red fox shooting from snow scooters. The

governments' authority in nature survey, The Norwegian Nature Inspectorate, was in charge of the campaign, but also local hunters were encouraged to shoot red foxes by payment.

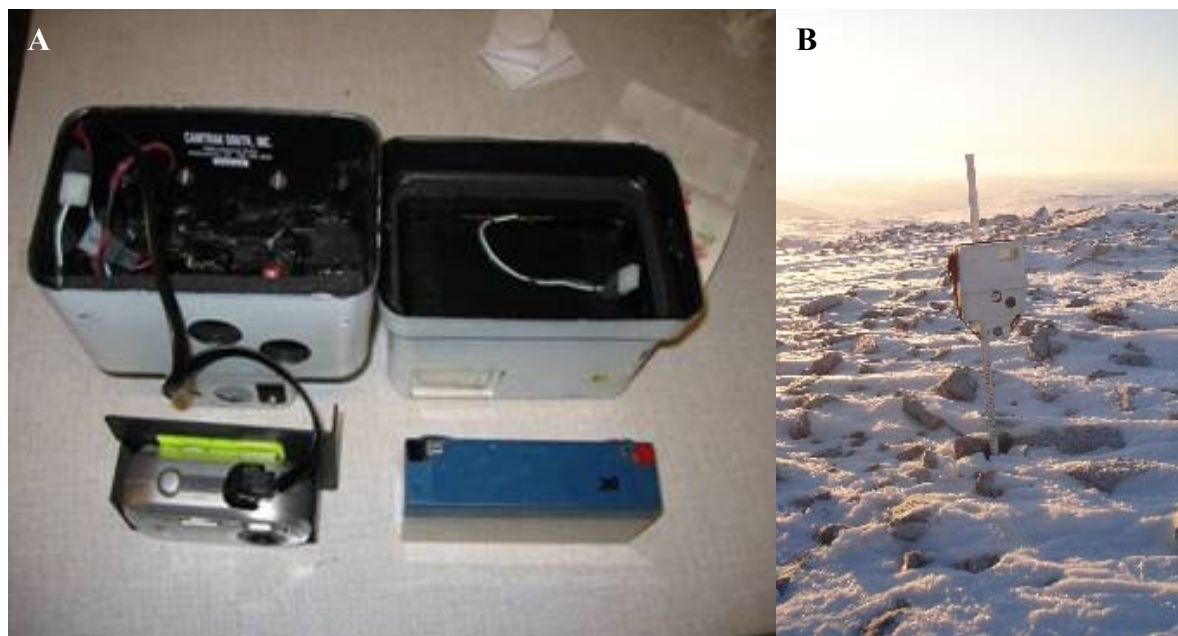
Each of the six study transects consisted of 5-10 carcass stations equipped with one digital camera (more details later), logging time-lapse photos of the immediate area around an artificial carcass. A total of 48 carcass stations were placed out at selected locations with a distance of 5-15 km between the stations. The length of the study transects varied from 40-100 km mainly as a function of the geographic limits of the tundra (decided by coastlines and tree-lines in the study areas). Locally the exact positions of the carcass stations were chosen based on topography, mainly to avoid snow accumulation. The digital camera units were contained in weatherproof boxes that were mounted on iron poles, which were drilled into the ground. Even though, this data logging equipment had not yet been tested during winter in sub-arctic areas, weatherproof photo boxes had been known to work well in recording the species of interest in other areas (Foresman and Pearson 1998; York et al. 2001; Azlan and Lading 2006).

The photo boxes that were used in this study were Sony Digital CamTrakker™ productions and consisted of a SONY digital camera, a 6V internal battery, external and internal flashes and a timer function (Picture 1). The time laps function was set at 10-minutes intervals, and date and time were automatically recorded. This system was favoured instead of infrared sensors which have proven to be temperature dependent (DeVault and Rhodes 2002). Cameras had a 512MB memory stick; and the resolution were put low (640x480 pixels) to avoid data storage limitations, as have been a challenge in earlier studies (York et al. 2001). Both batteries and memory sticks were changed every 14 days, at the same time as new reindeer-carcasses were brought to each of the 48 stations. The artificial carcasses were quadratic frozen blocks (60cm x 40cm x 10cm; 15-20 kg) of slaughterhouse debris of reindeers, consisting of entrails (e.g. kidneys, lungs and fat) and some discarded meat. Only carcasses that had been completely or partly consumed at bi-weekly inspections were renewed.

In the first field season i.e. winter 2005, problems with snow accumulation in the millimetre thick edge of the windows of the photo boxes originated. This happened both in front of the lens and the flash, occasionally making photos blurry. For the 2006 season this was improved by attaching hydrocarbon glasses over the fabric made glass window for the lens, as well as over the external flash on each photo box. The flash system with one internal

and one external flash were necessary in order to get good photos during night-time and in the dark period of February, and partly also March, which are months with little daylight due to the high latitude position of eastern-Finmark. Also the internal batteries caused problems by being emptied too fast during the winter in 2005. New external and insulated 6V batteries were therefore installed in 2006. Further, problems with contacts and flexes and camera malfunctions did occur, as have also been identified as a problem in other studies (Foresman and Pearson 1998). However, this happened mainly at the end of the bi-weekly period, when the carcass was more or less removed by the scavengers and activity in front of the photo boxes was low.

**Picture 1. Photo boxes used in this study were Sony Digital CamTrakker™ Productions. A) A disassembled photo box with internal battery package, Sony digital camera and the weatherproof box. B) A photo box mounted on a pole at one of the transect stations.**



### 2.3 Organizing data and variables

In order to systematize the data, all photos from each separate camera were analyzed in Irfanview graphic viewer version 3.98 for Windows XP and the following details were noted:

- transect
- station
- year
- date
- time of day

- species
- number of individuals present
- photos with no presence of species
- NA – more than 50% of the photo were blurry due to snow accumulation in front of the lense or bad weather conditions.

In order to quantify spatial predictor variables for each of the 48 stations, the *distance to the coast*, the *distance to the nearest road*, and *altitude* (meters above sea level) were measured using Mapsource version. 6.11 (produced by Garmin Ltd). Since the program offered no maps including the treeline, the *distance to the nearest forest* were measured using topographic maps of the series M711, datum WGS84, covering grid zones 35W and 36W. All maps were at a scale of 1:50 000, and the distance was measured manually from each station to the nearest treeline/forest, giving a maximum measurement error of about 100m. Forest was defined as areas with a continuous aggregation of trees, covering more than 1km<sup>2</sup>. When checking for correlations between spatial predictor variables, the distance to coast and distance to road was highly correlated ( $r = 0.65$ ). Due to the confounding between these two variables, only distance to coast was used in the statistical analysis.

The temporal predictor variable, *light*, to be used in the analysis was defined according to diurnal light conditions, and accordingly classified into four categories, morning twilight, day, evening twilight and night. The limit for the two periods of civil twilight is given by the time the sun is geometrically 6 degrees below the horizon, after sunset and before sunrise. All data on light conditions was based on calculations made at the official web-site of U.S. Naval Observatory (Naval Observatory 2006).

## 2.4 Statistical methods

The spatio-temporal variation in presence of each species was analyzed using generalized linear models (GLM) in the R-package, version 2.4.1(Crawley 2005; R Development Core Team 2006)

For the purpose of the statistical analyses the six transects were treated as four separate regions, *Bekkarfjord*, *Ifjordfjellet*, *Nordkynn* and *Varanger* (including Komagdalen, Vestre Jakobselvdalen and Stjernevann). The lumping of transects within the *Varanger* was made due to the close proximity of the transect stations in this region, as well as the fact that the three Varanger transects were all subject to the red fox decimation campaign. The complete datasets consisted of the following predictor variables:



- station (each station within a transect)
- region (*Bekkarfjord, Ifjordfjellet, Nordkynn and Varanger* )
- year (2005 and 2006)
- light (morning twilight, day, evening twilight, night)
- distance to forest
- distance to coast
- altitude.

The number of photos per station with presence of each species in each year was set as the response variable and analyzed using a log-linear model (log link and Poisson distribution; (Venables and Ripley 1999). Only species with a total number of observations  $\geq 60$  were analysed. Herbivore species (reindeer, snow buntings (*Plectrophenax nivalis*) and ptarmigan) which appeared accidentally on the stations in a few cases were not considered further. Though, present in more than 60 photos, magpies (*Pica pica*) were not analysed due to the highly aggregated presence of this species at few stations and mostly in one year.

As photos were taken approximately every 10<sup>th</sup> minute, it was necessary to correct for the proportion of photos that were too blurry or where the species could not be determined. This was done by including a log (photo-no photo) offset term, thus giving a response variable describing the *photo frequency* of a species on a logarithmic scale.

The most complex models fitted for **each species** were:

$$\textit{Photo frequency} = \textit{Region*Year} + \textit{Light * Distance to coast} + \textit{Light*Distance to forest} + \textit{Light*Altitude} + \textit{Region*Distance to coast} + \textit{Region*Distance to forest} + \textit{Region*Altitude}.$$

For some species this model had a high residual deviance (i.e. showed overdispersion, a larger deviance than what is expected under the Poisson distribution assumption), and an approach based on quaslikelihood was used (quasipoisson family in the R-function glm). Model selection was based on the information criterion QAIC<sub>c</sub> which is a corrected version of AIC<sub>c</sub> (Burnham and Anderson 2004), taking into account the overdispersion factor,  $\hat{c}$ , calculated from the most complex model in the analysis. The overdispersion factor,  $\hat{c}$ , is defined as the squared Pearson residuals divided by the residual number of degrees of freedom (McCullagh and Nelder 1989). Differences in QAIC<sub>c</sub> were then used to calculate AIC weights, which were used to rank models in terms of statistical support. Finally, the

squared correlation between predicted and observed values ( $R^2_{adj}$ ) was used to give a measurement of the predictive power of the most supported models (Zheng and Agresti 2000; Mittlböck 2002). All estimated coefficients from the selected models are presented with  $2*SE$ , and the model selection for all species including AIC weights values and  $R^2_{adj}$  values are given in Appendix I.

It was necessary to adjust the full model for some species due to lack of presence in certain transects or absence during some light conditions. Such levels were therefore removed from the full model. “Night” was excluded from the full model for golden eagles (*Aquila chrysaetos*) and white-tailed eagles (*Haliaeetus albicilla*), although one photo of a white-tailed eagle was taken during night. “Komagdalen” transect was excluded in the full model of wolverines (*Gulo gulo*) due to lack of presence in this area. Further, both “Stjernevann” transect and “night” was excluded from the full model of hooded crow (*Corvus corone corax*) analysis, although one photo of crows was taken when the light conditions were by definition “night”. Arctic foxes were analysed only in Varanger region, and solely for 2006, since there were no observations of this species during 2005. “Evening twilight” was also excluded from analysis of arctic foxes, due to lack of presence during this light condition.

In order to test for inter-specific relations at carcass stations, the observed photo frequencies of each species in total or in each region were obtained from one of the two models listed under, depending on matter of investigation:

$$Photo\ frequency = Total / (photo-nophoto)$$

$$Photo\ frequency = Region / (photo-nophoto)$$

These estimates were subject to pairwise correlation analyses on an overall or a regional scale, to test for negative or positive relations of the appearance of species at stations. The correlation analysis was performed using Spearman correlation in order to account for outliers and non-linearity. A correlation test was also performed and P-values were adjusted for multiple testing, using the Holm sequential procedure which is much more powerful than the Bonferroni correction (Wright 1992). As in the former analysis, the photo-nophoto term was included to correct for the number of photos taken, although this time not on a logarithmic scale.

## 3.0 Results

### 3.1 Overall species occurrences

A total of 10 carnivore species were photographed while scavenging on the artificial carcasses during the winters of 2005/2006 (Table 1, Picture2). This species assembly included 6 bird and 4 mammal species, where raven (*Corvus corax*) was by far the most commonly recorded species in terms of number of photos, followed by red fox, hooded crow and golden eagle. All species, except stoat (*Mustela erminea*), gulls (*Larus* spp.) and magpies, had sample sizes suitable for statistical analyses. Most species appeared both as solitary individuals and in pairs or flocks, but only in the case of ravens and hooded crows there were frequently more than one individual per photo. Analysis for ravens and hooded crows was only performed for number of photos as this measure was highly correlated with the number of individuals of ravens or hooded crows present in each photo ( $r = 0.91$  and  $0.94$ , respectively). Ravens and red foxes were the only species found to be present at all 48 stations. White-tailed eagles and golden eagles were present in all transects, but only at approximately half of the stations. Other avian scavengers as hooded crows and gull species were not present at Stjernevann transect, additionally gulls were also lacking at Ifjordfjellet. Magpies were not present at all in Varanger region, and their presence was highly aggregated at Nordkynn. Among the other mammalian scavengers, wolverines were found in all transects except Komagdalen, and one stoat was observed at four occasions at one station in 2006 in the Bekkarfjord. Arctic foxes were only present in 2006, in two of the three transects incorporated in Varanger region (i.e. the experimental transects, Vestre Jakobselvdalen and Komagdalen).

Picture 2. A selection of some of the photos from eastern-Finmark 2005 and 2006.  
A) White-tailed eagle B) Ravens C) Hooded crows D) Two golden eagles  
E) Black-backed gull F) Two red foxes G) Wolverine H) Arctic fox.



## 3.2 Spatial and temporal determinants of species occurrences

### 3.2.1. Raven

A fairly complex, and still much overdispersed, model for raven was selected (Appendix 1). This model included the interaction between region and the three spatial environmental gradient variables (i.e. altitude, distance to coast and distance to forest), and the interaction between year and region. The most statistically significant effects (see Table 2) were light conditions, interactions year\*region and distance to forest\*region. The latter interaction was due to the significant decrease in the frequency of ravens with distance to forest at Ifjordfjellet, whereas for the other regions this effect was less clear or partly opposite. Also the region-specific coefficients of the other environmental gradient variables were erratic and uncertain, and taken together there were no clear spatial trend of raven presence. There was an increase in the frequencies of ravens from 2005 to 2006 at Bekkarfjord, and although such a year difference also was apparent for the other regions, it was not as clear, presenting solely a significant difference between Bekkarfjord and Ifjordfjellet. Ravens appeared at the carcasses clearly most frequently in daylight, followed by mornings, evening and very rarely during nights (Figure 6). Despite the large overdispersion in the selected model of ravens, the predictive power of the model was quite high ( $R^2_{\text{adj}} = 0.86$ ).

### 3.2.2. Golden eagle

The chosen model for golden eagles was an overdispersed model that included interactions between region and all the environmental variables (see Table 2; Appendix 1). Ifjordfjellet and Bekkarfjord had by far the largest amount of golden eagle recordings, and statistically significant differences were detectable among regions, as Bekkarfjord had a higher presence of golden eagles than Nordkynn and each of the transects included in Varanger region (Figure 2). The overall frequency of golden eagles increased with altitude (Figure 3), and this effect was statistically significant in Varanger region. Further, the interaction between region and the environmental variables also presented a positive effect of distance to forest at Nordkynn region. However, the regional distribution of golden eagles, with most photos taken at Ifjordfjellet and Bekkarfjord, revealed an overall highest frequency in the distance zone close to the forest (Figure 5). A year effect due to more golden eagles being present in 2006 than in 2005 was almost significant at Bekkarfjord, whereas in Varanger region there was a significant decline from 2005 to 2006. Further, daylight was the best predictor of golden eagle frequency, followed by morning twilight and evening twilight

(Figure 6). Although being somewhat overdispersed, the selected model of golden eagles had a relatively high predictive power ( $R^2_{\text{adj}} = 0.70$ ).

### **3.2.3. White-tailed eagle**

The temporal and spatial variation in white-tailed eagle was best predicted with a model containing the same terms as for the golden eagle (Appendix 1), however, the model was less overdispersed and had clearer effects (Table 2). The frequencies of presence were highest at Nordkynn and Bekkarfjord (Figure 2), while in Varanger they were significantly lower. The interaction between the environmental variables and region showed some clear effects in all regions except Ifjordfjellet. The latter region had however only 25 observations of white-tailed eagles yielding unreliable estimates. The observed overall frequencies, revealed a declining trend with altitude (Figure 3). However, the effect of altitude was opposite at Bekkarfjord and Varanger region, with a significant negative trend in Bekkarfjord (Table 2). Distance to coast had significant negative effects in Nordkynn and Varanger, whereas in Bekkarfjord this effect was positive. The overall pattern revealed however a high frequency of white-tailed eagles in the closest distance zone to the coast (Figure 4), resulting from most white-tailed eagles photos coming from the coastal regions Bekkarfjord and Nordkynn. Distance to forest was also a significant predictor for Bekkarfjord revealing a negative trend, which was also evident in the overall pattern (Figure 5). On a temporal scale, the frequency of white-tailed eagles increased from 2005 till 2006 in Bekkarfjord, whereas the opposite was true in Varanger. Daylight was the best predictor of white-tailed eagle presence, followed by evening twilight and then morning twilight (Figure 6). Even if the selected model for white-tailed eagles was less overdispersed, the predictive power were not as high ( $R^2_{\text{adj}} = 0.52$ ).

### **3.2.4. Hooded crows**

For the hooded crows the model selection resulted in a much overdispersed model with one interaction term (i.e. year\*region; Appendix 1). Even if the predictive power of the model were high ( $R^2_{\text{adj}} = 0.94$ ), still the confidence intervals of the model coefficients were too wide to warrant any definitive conclusions about effects of environmental variables (Table 2).

### **3.2.5. Red fox**

Red foxes were analysed using a quite overdispersed, but simple model including only one interaction term (i.e. year\*region; see Table 2; Appendix 1). The interaction was due to a declining presence of red fox in Varanger, which resulted in lower frequency in Varanger compared with the three other regions in 2006. Effects of environmental variables revealed that red fox presence declined generally with altitude (Figure 3). Also the effects of light conditions were significant, morning twilight being the period with highest frequencies, followed by night, evening twilight and finally daylight (Figure 6). Although there were clear effects revealed by the analysis, the selected model for red foxes had a relatively low predictive power ( $R^2_{\text{adj}} = 0.40$ ).

### **3.2.6. Wolverine**

For wolverines a fairly complex and barely overdispersed model resulted from the model selection (Appendix 1). This model included the two temporal variables and the interaction terms between regions and the three environmental variables. A clear interpretation of the coefficients could only be done in the case of light conditions and the region\*altitude interaction (Table 2). The latter term was due to increasing frequency of wolverine records with increasing altitude in Varanger region, which was an effect that were not present within other regions. However, the overall pattern for all regions combined was that wolverines occurred at the highest altitudes (Figure 3). With respect to the effect of light condition, morning twilight was the period with the highest frequency of wolverine presence (Figure 6). Despite quite little overdispersion the best model of wolverines had a low predictive power ( $R^2_{\text{adj}} = 0.37$ ).

### **3.2.7. Arctic fox**

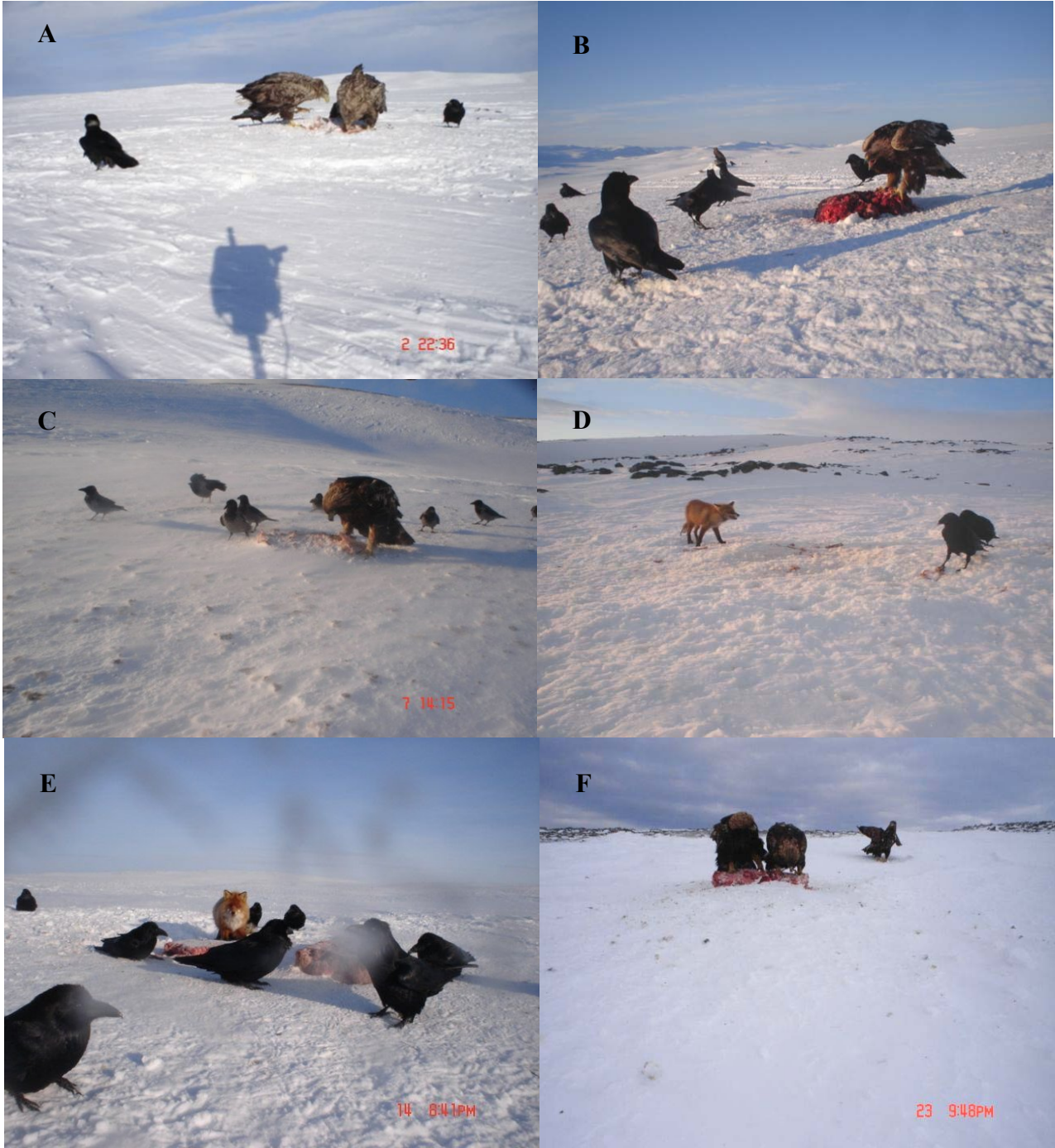
For the arctic fox in Varanger region a heavily overdispersed model with few parameters was chosen (Appendix 1), and this model revealed that arctic fox frequency increased with distance from the coast (Table 2; Figure 4). Most photos were taken during night and morning twilight, and a few photos were also taken at day light conditions (Figure 6). However, the effects of light conditions were not significant, probably due to the large overdispersion. All in all the prediction power of the best model for arctic foxes was very low ( $R^2_{\text{adj}} = 0.26$ ).

### **3.3 Interspecific relations and multispecies occurrences**

Investigating the association between species by conducting correlation analyses based on station-specific frequencies revealed that avian scavenger species were in general positively correlated with each other, while mammalian species did not reveal any clear association with either avian or other mammalian species (Table 3: see also Appendix 2 for region specific correlations). The positive association among the two eagle species were the strongest ( $r=0.44$ ), but also the associations between ravens and the two eagle species, golden eagles ( $r =0.34$ ) and white-tailed eagles ( $r =0.33$ ) were strong. Further, hooded crows correlated the most with white-tailed eagles ( $r =0.40$ ). Among the mammalian scavengers, red fox and wolverine yielded a low ( $r=0.16$ ), but still a statistically significant association. Finally, photos with multispecies occurrences at the carcass were also taken (Picture 3).



**Picture 3. Multispecies occurrences at the artificial carcass. A) Two white-tailed eagles feeding at the presence of a couple of ravens, B) Golden eagle and a small group of ravens, C) Golden eagle and hooded crows, D) Red fox at the presence of a couple of eagles, E) Red fox together with a group of ravens, F) White-tailed eagle on the side of two golden eagles.**



## 4.0 Discussion

### 4.1 Spatial determinants of species occurrences

Determinants of spatial and temporal distribution of species have been a long term subject for ecologists. However, little attention has been given to composition of terrestrial scavenger communities, and the present study is one of the first investigating the distribution of a scavenger guild in a sub-arctic tundra ecosystem.

Among the avian scavengers the raven was the only species that was present at all 48 carcass stations. Except for the negative effect of distance to forest at Ifjordfjellet, there were no clear spatial patterns detectable. Thus, the overall result was that ravens were present in large numbers in the study area and that they were just as common near the coast and the forest, as in the remote inland tundra. As described in other studies, ravens are able to fly over large distances in search of food and they are also known to be the first and most pronounced species at carcasses (Heinrich 1988; Stahler et al. 2002; Selva et al. 2003; Selva 2004a; Selva 2004b; Selva et al. 2005). Possibly, an aggregation of this species at a resource might be caused by ravens' efficiency in locating carcasses, but it might however also come as a result of communicative means. It has been suggested that non-kin group assemblages of ravens fly in formation to cover even larger areas, and thereafter vocalize to their con-specifics when finding a carcass (Heinrich 1988). The flocking behaviour of ravens might accordingly not only be beneficial in the locating of carcasses, but also valuable for spotting danger at sites of focal predator activity, i.e. at carcasses. Finally, ravens are able to perform quick take-offs when exposed to threats or disturbance, explaining why feeding in open and exposed areas not seem to be too risky. Factors as mobility, vision, vocalization and flocking behaviour might thus enlighten why ravens can be found in large numbers at all locations in this study, independent of environmental variables.

Eagles were expected to be efficient in locating and monopolizing carcasses, as they are a predator species with advantages both in mobility and vision. Although the two species of eagles were quite correlated according to presence at stations, they presented a clear preference of regions due to their appearance in the photos. This spatial segregation between golden eagles and white-tailed eagles may be altered by their primary food preference. Golden eagles have broad food-niches and preferably eat prey that can be obtained in relation to inland tundra and forest, e.g. ptarmigans, rodent species, mountain hares and reindeers (Tjernberg 1981; Nyström et al. 2006). In contrast, white-tailed eagles in Fennoscandia are

known to primarily feed on fish and waterfowls, although their diet are also known to contain a certain amount of terrestrial mammals and carcasses (Sulkava et al. 1997). Ifjordfjellet most likely offers a high quantity of terrestrial food resources for golden eagles, due to the large amount of forest in this area. Opposite, waterfowls and fish are easily obtained at coast-near areas as Nordkynn, and might therefore explain the high amount of white-tailed eagle presence in the photos from this area. Interestingly, the presence of the two eagle species overlapped at Bekkarfjord which is an intermediate area between the two distinct regions Nordkynn and Ifjordfjellet. Bekkarfjord offers both a high amount of forest and a close distance to the coast, indicating that this area would be suitable for both species, and accordingly that food preference is likely to influence habitat choice more than inter-specific competition. This is in line with other studies that also have found an overlapping presence of the two eagle species in other areas (Halley and Gjershaug 1998). Among the other environmental variables both eagles were positively associated with high altitude in Varanger region, possibly reflecting that food searching and locating carcasses are easier and less disturbed in open glands at higher altitudes than e.g. in the forest (Selva et al. 2003; Selva 2004a; Selva 2004b).

Both species of eagles were persecuted in Norway for almost 100 years until protection in 1968, and are accordingly known to take off when exposed to human disturbance (Skagen et al. 1991). However, I suggest that since eagles have no other enemies than each other (Halley and Gjershaug 1998) in this area, they should be able to cover large distances when performing food searches and monopolize resources when found. Hence, both species could be found at most locations sporadically, especially in open glands where visual detection of carcasses and potential danger are high.

Gulls, hooded crows and magpies are known to be present at carcasses (Platt and Sherrod 1974; Skagen et al. 1991; Halley and Gjershaug 1998; Selva 2004a; Selva 2004b). In this study, these species were present at few stations which were in close relation to either the forest or the coast. Although the number of observations for gull species was not high enough for analysis, the distribution of this species is likely to be a result of food preferences, since they preferably eat fish and utilise other marine resources. Magpies and hooded crows utilise everything from human waste (Vuorisalo et al. 2003) to invertebrates and carcasses, but despite a high number of photos, analysis of hooded crows did not bring out a clear trend in the spatial distribution, probably due to the extremely aggregated presence in few stations.

Possibly, subordinate species as hooded crows, magpies and gulls benefit from feeding on left-overs from larger predators, rather than putting effort into food search over large areas themselves. Hence, following the movement or associate directly with larger predators and con-specifics, might be of importance for such species in order to detect carcasses (Wilmers et al. 2003; Selva 2004b). Finally, feeding in smaller groups or flocks (Picture 3), as observed in this study, is most likely beneficial for these subordinate species, due to the possible risk of intraguild predation.

Wolverines occurred very scattered and a clear overall pattern of spatial presence was not detectable by analysis. Wolverines was however limited to high altitude areas in Varanger region. This is in consistence with earlier findings that wolverines in Fennoscandia are known to have large home ranges and accordingly, occur scattered in alpine and forested areas at higher altitudes (Rinden 1998b). Undoubtedly, wolverines and can travel large distances in search for food, and reindeers and carcasses are known to be an important winter food resource (Myhre and Myrberget 1975). Wolverines are a top-predator of the sub-arctic tundra with an excellent nose, but with limited visual abilities (Brainerd et al. 2006), accordingly indicating that it might be a risk sensitive species. Lately, increased human activity and infrastructure in once remote areas, has been suggested to have large impacts on the distribution of wolverines (May et al. 2006), due to risk sensitivity. Clearly, the apprehension of humans and human activity might affect the spatial distribution of wolverines, but this study could not verify such statements, as no measurement on human activity was performed. Finally, wolverines has been protected in the northern part of Norway since 1982, however, there are still licence killing and possibly some illegal killing of this species (Rinden 1998b).

Red foxes are believed to utilise carcasses as a secondary resource, and found to be the most prominent mammalian scavenger in temperate forest during winter (Jędrzejewska and Jędrzejewski 1998; Selva 2004a). Red foxes were the most prominent mammalian scavenger species in this study as well, but since there have been no recordings of red fox activity in summer and autumn periods it is difficult to say whether this activity is significantly higher in winter. For a longer period researchers have agreed that the red fox population has increased and expanded its range geographically, further north and higher up in the mountains (Østbye et al. 1978; Hersteinsson and Macdonald 1992; Kaikusalo and Angerbjörn 1995; Elmhagen et al. 2002; Tannerfeldt et al. 2002). Explanations for this have been related to climate change, and the fact that during the last century, the average air temperature has been increasing

(Hersteinsson and Macdonald 1992), giving a trend of altitudinal increase and a northward expansion of the treeline (Moen et al. 2004). Also in Finnmark the average temperature has been increasing during the last century (Hanssen-Bauer 1999), and the present study found that red fox presence is negatively associated with altitude in eastern-Finnmark. This might indicate that being close to the forest and the coast is preferable for this species, something that might be related to food access, shelter or protection for potential predators as eagles, which were positively associated with altitude in this study.

Both red foxes and arctic foxes are known to feed primarily on small rodents and carcasses (Elmhagen et al. 2002). In addition red foxes today are known to utilize human waste and subsidies from urban settlements (Contesse et al. 2004), and both red- and arctic foxes are known to utilize subsidies from the coast (Roth 2003). Taken together, the two fox species strongly overlap in their diets (Frafjord 2000; Elmhagen et al. 2002), indicating a potential for inter-specific competition. This study predicted opposite patterns of presence or temporal segregation between possibly competing species where one is clearly subordinate. As the red fox is superior to the arctic fox in both body size and weight it is also able to inhibit the arctic foxes access to resources as food and denning areas (Østbye et al. 1978; Rudzinski et al. 1982; Frafjord et al. 1989; Korhonen et al. 1997; Linnell et al. 1999). It is likely, however, that arctic foxes in eastern Finnmark, at least nowadays, are typical inland-foxes (Tannerfeldt and Angerbjörn 1998), and that there is a spatial segregation (Hersteinsson and Macdonald 1992; Elmhagen et al. 2002; Tannerfeldt et al. 2002; Roth 2003) between the two fox species, since this study found that arctic fox presence increased with distance to coast. Additionally, there was a weak negative correlation between the two fox species in our study transects where arctic foxes were present. The spatial pattern of arctic fox presence might also be influenced by risk sensitivity, especially since humans performed an extensive persecution on this fur specie throughout the whole of Scandinavia during the late 1800's and early 1900's (Lönnberg 1927). Little is known about the arctic fox population in eastern-Finnmark, but the overall population numbers in Scandinavia today are critically low (Dalén et al. 2006; Nystrøm et al. 2006), even if the arctic fox has been protected in Norway since 1930 (Hersteinsson et al. 1989). However, one should keep in mind that the analysis of arctic foxes in this study was based on a limited number of data, and solely for 2006.

## **4.2 Temporal determinants of species occurrences**

As found in other studies there was clearly a temporal segregation between avian and mammalian scavengers on the carcass (Selva 2004b). Avian scavengers arrived in the morning twilight, and were more or less present during the whole day until the evening set in, whereas mammalian scavengers preferably used the night and the morning twilight as primary feeding time. The risk of approaching a carcass when a dominant species is present may have led to the pattern of night-time and twilight feeding among mammalian scavengers, especially since eagles are possible predators of most of the mammalian species in this study.

Additionally, risk sensitivity might also affect the feeding pattern of mammalian species as these are less mobile in order to perform quick take-offs. During evening twilight and during night, avian scavengers were either present in small numbers or not present at all, possibly because they would then suffer from poor visibility and thereby also expose themselves to risk.

Year effects were detectable for eagles, ravens and red foxes. For the avian species an increasing effect over the years might have been caused by either a behavioral effect e.g. learning, or reproductive success, thus altering an increase in population numbers. On the other hand, negative year effects might come as a result of changes in the abundance and distribution of different preferred prey species, or possibly from declining population numbers. However, since no data was available on population numbers, this potential cause can not be verified. For red foxes there was a clear decrease in abundance from 2005 till 2006 at Varanger region, something that was expected due to the decimation of the red fox population in this region. A total of 181 (2005) and 105 (2006) red foxes were shot until May 2006, and the effects of this removal was most pronounced in Komagdalen where the presence of red foxes in photos declined radically from 303 photos of red foxes in 2005 to only 20 in 2006. Further, the winter of 2005 did not give one single photo of arctic foxes, but interestingly they appeared in photos taken during night and morning twilight in Varanger during 2006, when the decimation of red foxes had been ongoing for almost one year. In this case it is possible that the decimation of the red fox population might have loosened the stress for the arctic fox, which thereby could perform food searching during night and visit the artificial carcasses at lower risk.

## **4.3 Interspecific relations and multispecies occurrences**

Flight has been suggested to be an advantage in locating a resource, since it allows an area to be searched more rapidly for food (Houston 1979; Heinrich 1988; DeVault et al. 2003;

Ruxton and Houston 2004), and this might explain why all avian species were somewhat positively correlated to each other when it came to visiting the same carcass stations. Ravens and both eagle species correlated the most with each other, indicating that mobility, vision and their ability to use information passed by other species or con-specifics might have been an aid in locating carcasses (Heinrich 1988; Stahler et al. 2002; Selva 2004a). As found in other studies hooded crows associated with white-tailed eagles (Skagen et al. 1991), something that in this study might be a result of crows being aggregated at few stations, close to the coast and the forest, which is also the primary habitat of white-tailed eagles. All mammalian species presented consequently a weak negative or no association with all other species at all stations, indicating that the mammalian species preferred feeding at stations less visited by eagles and at times when avian species were not present. Interestingly, there was a weak association observed between red foxes and wolverines in the overall analysis. However, this pattern most likely resulted from a high overlap in the use of some of the carcass stations, at Varanger region (Appendix 2).

Multispecies occurrences were photographed at the carcass at some occasions. Ravens were able to feed at the presence of eagles, hooded crows, gulls and red foxes, indicating that they were either tolerated by the other species or they were exposing themselves to a risk. However, factors like hierarchal positioning, tolerance and social foraging techniques as scrounging, have been suggested as factors of importance when it comes to such non-violent interactions at food resources (Bugnyar and Kotrschal 2002). Additionally, several other studies have also described subordinate species foraging or waiting patiently, in close relation to by definition larger and dominant predator species (Kruuk 1967; Platt and Sherrod 1974; Skagen et al. 1991; Wilmers et al. 2003; Vucetich et al. 2004). Also, both corvid species in this study often fed in larger groups of maximum 20 individuals. Clearly, such behaviour would favor an increased vigilance to detect predators or aggressiveness by a dominant species at a feeding site, and at the same time reduce each individual's chance of being predated or killed.

Red foxes were the only mammalian scavenger to interact with other species at the carcass, and were at a few occasions photographed while feeding at the presence of eagles. It is noteworthy that the foxes in these photos often were at a larger distance from the carcass than were the eagles. However, other avian scavengers did not seem to bother the red fox, which were photographed several times while feeding at the carcass together with ravens and

hooded crows. This behavior might possibly be due to its dominance over corvids, or as suggested by Selva (2004b), the possible cost of energy and loss of food it would suffer from trying to chase away numbers of corvids during the cold winter temperatures.

Finally, in competition for a resource mammalian scavengers would clearly suffer from slower mobility and for not having the same kind of visual overview that avian scavengers benefit from. Mammalian scavengers were therefore not expected to be as efficient in locating carcasses, and accordingly not as likely to be present in the stations in this study. One should however, also bear in mind that the number of mammalian scavenger individuals is low compared to the number of avian individuals, something that clearly also is of importance when it comes to the frequencies of photos taken at the carcass stations.

#### **4.4 Methodological considerations**

Large predators typically leave remains of their kills available for scavengers (Selva 2004a), and in eastern-Finnmark natural mortality probably also accounts for a large amount of the available carcasses in the study area. However, some artefacts may have resulted from the use of artificial carcasses. As the artificial carcass was made up of slaughter debris there was no need for having a certain species to open the carcass, as have been known to be an important factor for the presence of species in other studies (Selva et al. 2003). With respect to statistical issues, using short-interval time-laps recording resulted in the same individuals becoming recorded repeatedly, which certainly contributed to autocorrelation and aggregated data. Clearly the frequency of presence in photos by species is not transferable to number of individuals present in the study area, but rather measures the intensities of species-specific use of different locations. Due to aggregated presence of species at certain stations, all selected models in this study were overdispersed, and had more or less predictive power according to  $R^2_{\text{adjusted}}$ . This measure of prediction power was probably quite affected by single outliers, thus explaining why models with low overdispersion had a low predictive power and vice versa.



## 5.0 Conclusion

- In contrast to scavenging guilds in Africa and in temperate forest (Houston 1979; Wilmers et al. 2003; Selva 2004b), the scavenging guild in eastern-Finnmark during the present study, only consisted of 10 different avian and mammalian species, where ravens and red foxes were the most frequent visitors of carcasses.
- Temporal patterns in utilization of carcasses were clearly the most evident predictor structuring the scavenger community in eastern-Finnmark. A clear temporal segregation was found between mammalian scavengers, which were most active during the night and morning twilight, and avian scavengers which were most present in daylight conditions. However, temporal overlaps in activity during morning twilight, and partly also daylight, existed.
- As predicted in this study the distribution of highly mobile species was relatively even and their overall appearance did not show any clear significant trend for any of the environmental variables, although regional trends were clearly detectable for the eagle species. Making use of calls or the movement of con-specifics and other species probably also explain why all avian scavengers were associated with each other, and why avian scavengers can be found at most locations, independent of environmental variables.
- Among the mammalian scavengers results of spatial patterns were only found for red- and arctic foxes. Past or present interspecific competition with the red fox, may have affected the spatial pattern of the arctic foxes, especially since the first photos of arctic foxes were taken after a year of red fox decimation at Varanger region. Wolverines occurred scattered and a clear overall trend of spatial distribution was not detectable.
- The scavenger community of eastern-Finnmark does not seem to be structured by contest competition, and scramble competition is probably of a greater matter for this scavenging guild. However, mobility, sensory abilities, innate behaviour related to food searching and risk sensitivity to intraguild predators, seem to be more important factors in the determination of spatio-temporal patterns of distribution among scavengers in eastern-Finnmark.

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## 7.0 Figures

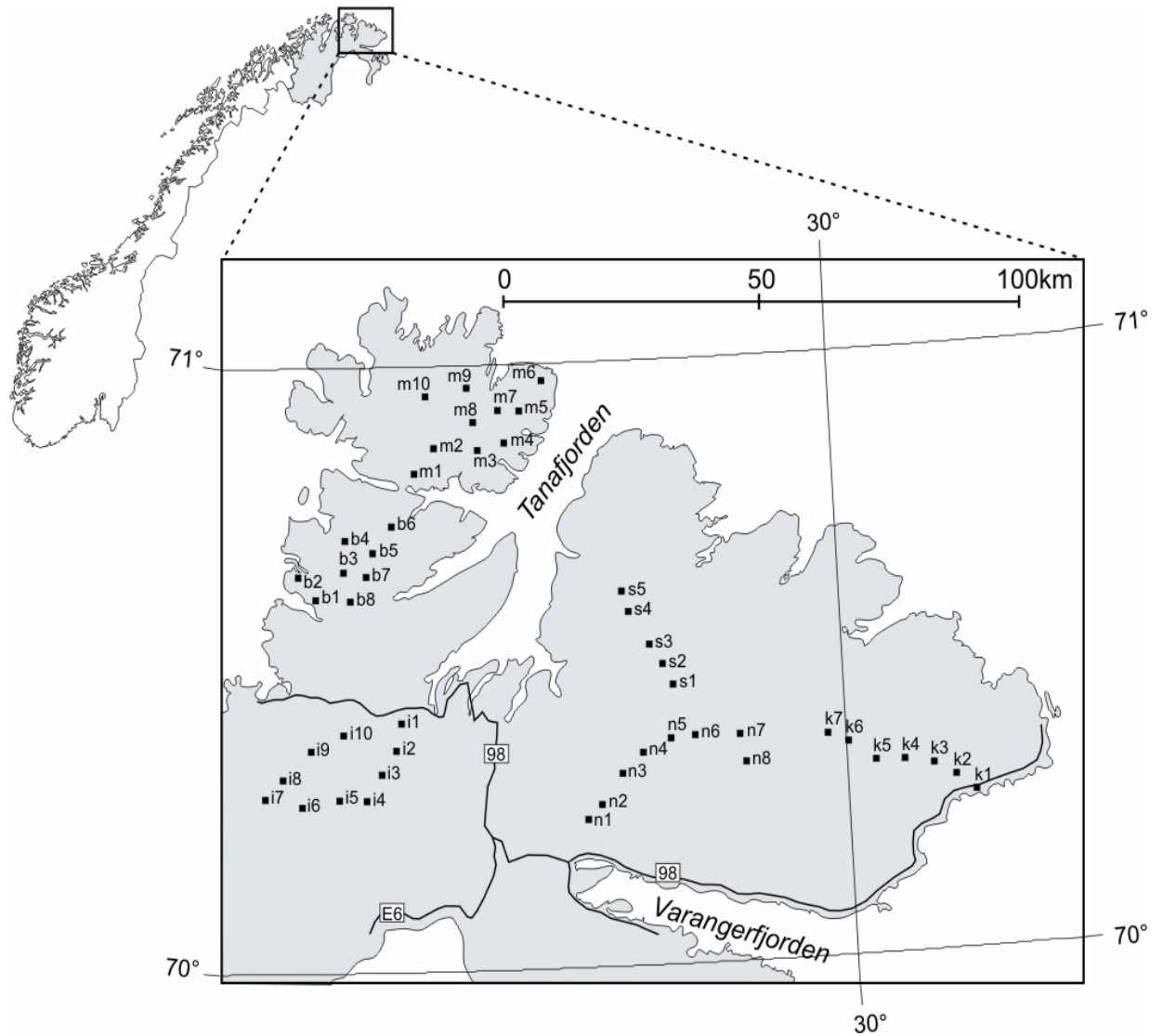
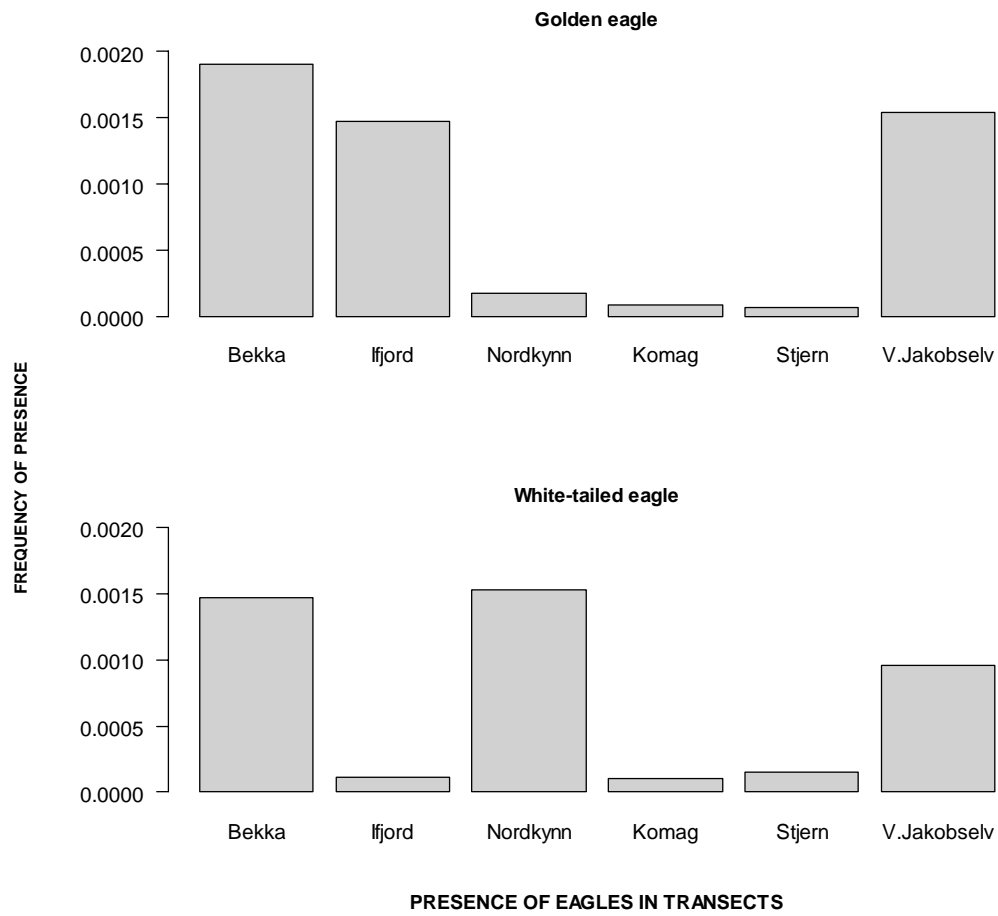
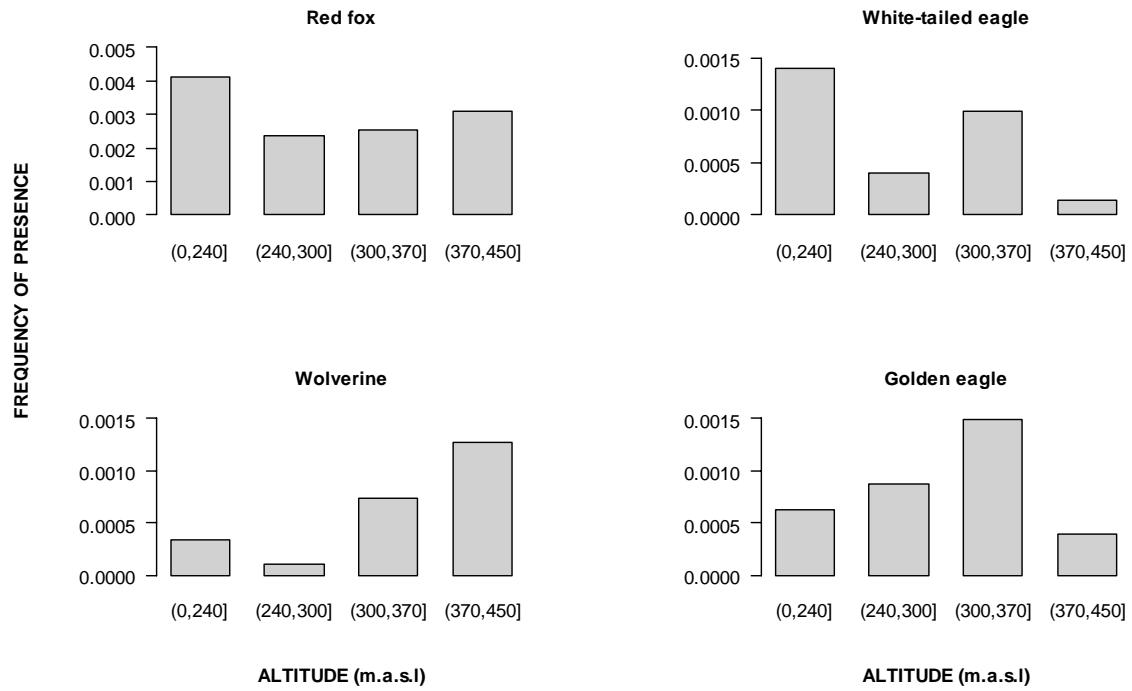


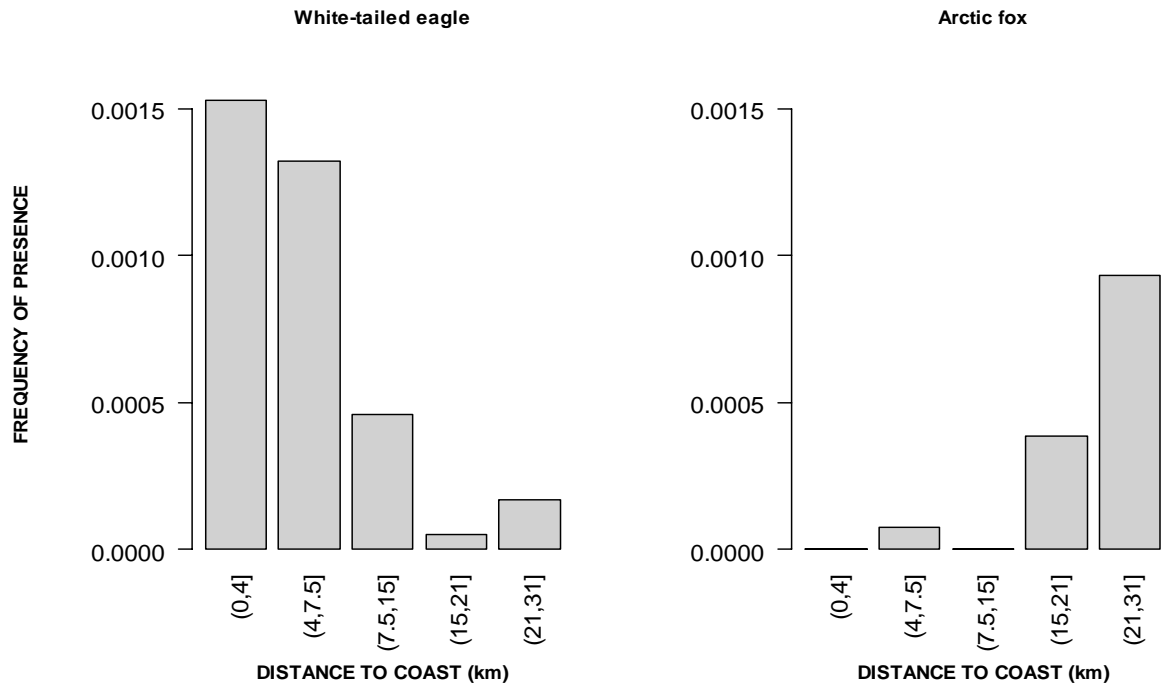
Figure 1. Map over the study area in eastern-Finnmark, northern-Norway, including the localities of the 48 carcass stations that were equipped with digital cameras. The six study transects are marked: m= Nordkynn (10 stations), i= Ifjordfjellet (10 stations), b= Bekkarfjord (8 stations), k= Komagdalen (7 stations), n= Vestre Jakobselvdalen (8 stations), s= Stjernevann (5 stations). Varanger region in analysis is comprised from the photo boxes in the three latter transects. Line= main roads.



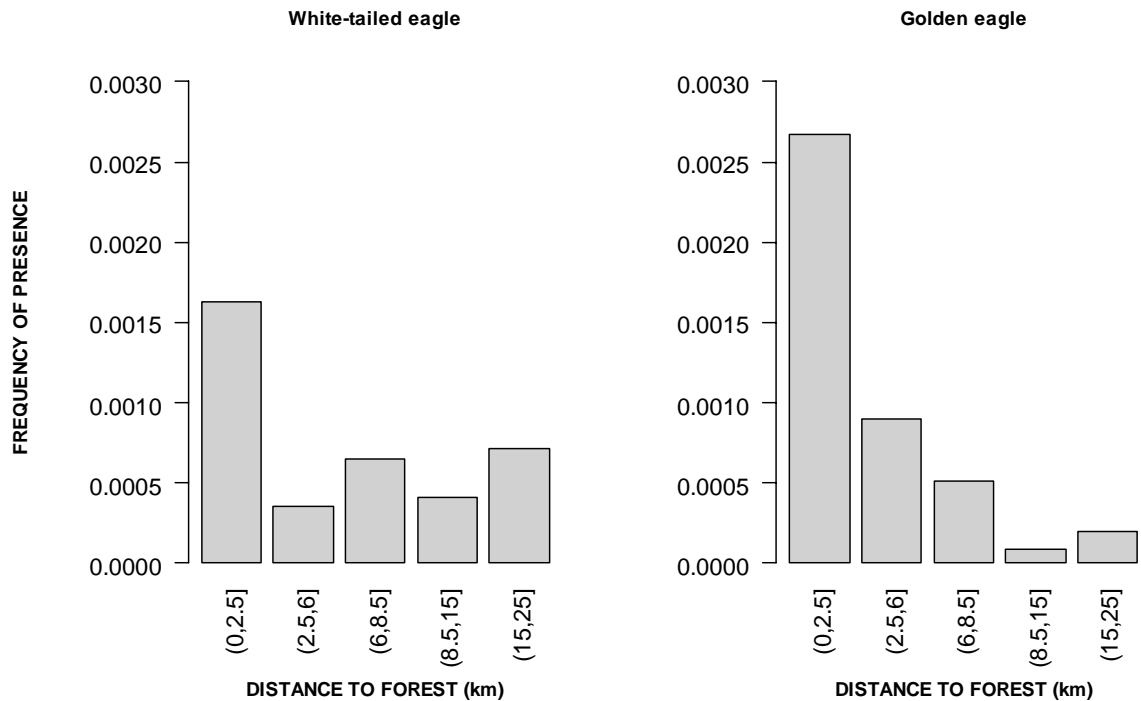
**Figure 2. Spatial pattern of overall presence of white-tailed eagles and golden eagle among the six transects in eastern-Finnmark. Bekka = Bekkarfjord, Ifjord = Ifjordfjellet, Nordk = Nordkynn, Komag = Komagdalen, Stjern = Stjernevann and V. Jakobselv = Vestre Jakobselvdalen.**



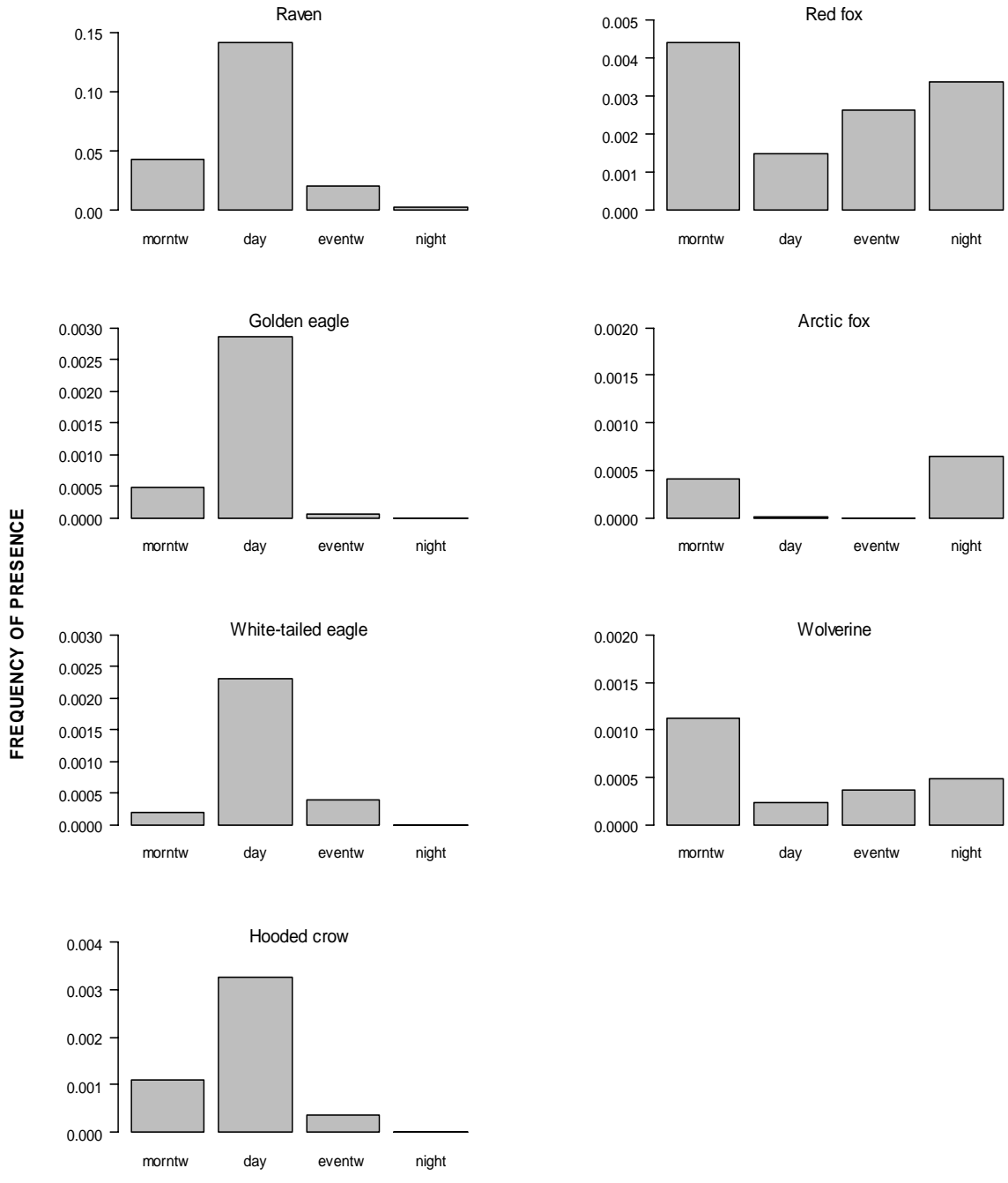
**Figure 3. Spatial patterns of presence of scavenger species according to altitude (*in* meters above sea level) for all study transects combined. Only data for species with overall or regional statistically significant effects of altitude in the statistical analysis are shown.**



**Figure 4. Spatial patterns of presence of scavenger species according to distance to coast (*in* km) for all study transects combined. Only data for species with overall or regional statistically significant effects of distance to coast in the statistical analysis are shown.**



**Figure 5. Spatial patterns of presence of scavenger species according to distance to forest (*in* km) for all study transects combined. Only data for species with overall or regional statistically significant effects of distance to forest in the statistical analysis are shown.**



ACTIVITY PATTERN OF SPECIES DURING LIGHT CONDITIONS

**Figure 6. Temporal activity pattern of avian and mammalian scavenger species during changing light conditions, morning twilight, daylight, evening twilight and night.**

## 8.0 Tables

**Table 1** The 10 scavenger species recorded at the artificial carcasses during February – April 2005/2006 (\* only in 2006), and their frequencies according to the number of transects, stations and photos they were present. Number of individuals is the sum of the number of individuals over all photos, and thus the ratio *No. of individuals/No. photos* gives the mean number of individuals per photo. Maximum number of individuals in a photo for each species is also given.

<b>Scavenger</b>	<b>No. transect</b>	<b>No. stations</b>	<b>No. photos</b>	<b>No. individuals</b>	<b>Max. no individuals</b>
<b>Avian species</b>					
Raven	6	48	32891	69258	20
Hooded crow	5	11	770	2050	20
Golden eagle	6	25	730	827	4
White-tailed eagle	6	26	540	610	4
Magpies	3	5	188	343	9
Gulls ( <i>Larus</i> spp.)	4	7	60	82	3
<b>Mammalian species</b>					
Red fox	6	48	1059	1078	2
Wolverine	5	18	122	122	1
Arctic fox *	2	4	94	94	1
Stoat *	1	1	4	4	1

**Table 2: Coefficients  $\pm 2*St.E$  obtained from the selected model for of each species. Significant results ( $p \leq 0.05$ ) are denoted with bold font. Region Bekkarfjord, year 2005 and daylight are the reference level for all models ; i.e. the intercept is:  $\beta = \text{Region Bekkarfjord} + \text{year 2005} + \text{daylight} + [\text{environmental gradients} = 0]$ . The regions are denoted as: I: Ifjordfjellet, M: Nordkynn, V: Varanger (Komagdalen, Stjernevann, Vestre Jakobselvdalen). The levels of the temporal variable light are denoted as: m: morning twilight, e: evening twilight, n: night. The interaction coefficients for the spatial environmental gradient variables are denoted as F: distance to forest (increment: 1000m), C: distance to coast (increment: 1000m), A: Altitude (increment: 100m), Y=year in interaction terms.**

Avian species	Alti (in100m)	Forest (1000m)	Coast (1000m)	Year	Light	Region	Interactions Nordkynn (M)	Interactions Ifjordfjellet (I)	Interactions Varanger (V)	R <sup>2</sup> adj.
<i>Raven</i>	0.20 $\pm$ 0.28	0.07 $\pm$ 0.08	0.07 $\pm$ 0.08	<b>0.57 <math>\pm</math> 0.29</b>	m: <b>-1.21 <math>\pm</math> 0.43</b> e: <b>-2.03 <math>\pm</math> 0.54</b> n: <b>-4.28 <math>\pm</math> 0.65</b>	I: 1.51 $\pm$ 1.56 M: 0.20 $\pm$ 1.18 V: 0.82 $\pm$ 1.10	F: -0.05 $\pm$ 0.08 C: 0.04 $\pm$ 0.10 A: -0.02 $\pm$ 0.31 Y: -0.21 $\pm$ 0.40	<b>F: -0.13 <math>\pm</math> 0.12</b> C: -0.05 $\pm$ 0.09 A: -0.11 $\pm$ 0.44 <b>Y: -0.46 <math>\pm</math> 0.38</b>	F: -0.07 $\pm$ 0.08 C: -0.06 $\pm$ 0.09 A: -0.08 $\pm$ 0.32 Y: -0.16 $\pm$ 0.36	0.86
<i>Golden eagle</i>	-0.28 $\pm$ 0.48	-0.22 $\pm$ 0.25	-0.06 $\pm$ 0.12	0.51 $\pm$ 0.54	m: <b>-1.63 <math>\pm</math> 1.40</b> e: <b>-3.54 <math>\pm</math> 3.12</b>	I: 0.58 $\pm$ 5.14 <b>M -5.62 <math>\pm</math> 4.70</b> <b>V: -2.99 <math>\pm</math> 2.10</b>	<b>F: 0.33 <math>\pm</math> 0.32</b> C: 0.007 $\pm$ 0.44 A: 0.07 $\pm$ 0.84 Y: 1.49 $\pm$ 2.77	F: 0.13 $\pm$ 0.25 C: -0.12 $\pm$ 0.24 A: 0.46 $\pm$ 1.57 Y: 0.35 $\pm$ 0.81	F: 0.06 $\pm$ 0.27 C: -0.05 $\pm$ 0.14 <b>A: 0.01 <math>\pm</math> 0.007</b> <b>Y: -1.18 <math>\pm</math> 0.88</b>	0.70
<i>White-tailed eagle</i>	<b>-0.76 <math>\pm</math> 0.58</b>	<b>-0.33 <math>\pm</math> 0.30</b>	<b>0.13 <math>\pm</math> 0.12</b>	<b>1.27 <math>\pm</math> 0.66</b>	m: <b>-2.17 <math>\pm</math> 1.76</b> e: <b>-1.69 <math>\pm</math> 1.18</b>	I: 91.5 $\pm$ 1077 M: 0.71 $\pm$ 2.02 V: -2.29 $\pm$ 2.36	F: 0.21 $\pm$ 0.30 <b>C: -0.26 <math>\pm</math> 0.16</b> A: 0.34 $\pm$ 0.62 Y: 0.48 $\pm$ 0.88	F: 8.09 $\pm$ 1460 C: -6.02 $\pm$ 1000 A: -26.8 $\pm$ 5816 Y: 17.5 $\pm$ 4784	F: 0.25 $\pm$ 0.31 <b>C: -0.19 <math>\pm</math> 0.13</b> <b>A: 1.15 <math>\pm</math> 0.82</b> <b>Y: -1.31 <math>\pm</math> 1.00</b>	0.52
<i>Hooded Crow</i>	-1.72 $\pm$ 2.46	-0.23 $\pm$ 0.32	-0.11 $\pm$ 0.32	3.40 $\pm$ 5.98	m: -1.07 $\pm$ 6.36 e: -2.41 $\pm$ 11.22	I: 1.55 $\pm$ 9.02 M: 1.83 $\pm$ 7.88 V: 1.50 $\pm$ 7.50	Y: -5.18 $\pm$ 12.06	Y: -1.48 $\pm$ 9.17	Y: -2.24 $\pm$ 7.65	0.94

Table 2 continue: Coefficients  $\pm 2 \cdot \text{St.E}$  obtained from the selected model for of each species. Significant results ( $p \leq 0.05$ ) are denoted with bold font. Region Bekkarfjord, year 2005 and daylight are the reference level for all models ; i.e. the intercept is:  $\beta = \text{Region Bekkarfjord} + \text{year 2005} + \text{daylight} + [\text{environmental gradients} = 0]$ . The regions are denoted as: I: Ifjordfjellet, M: Nordkynn, V: Varanger (Komagdalen, Stjernevann, Vestre Jakobselvdalen). The levels of the temporal variable light are denoted as: m: morning twilight, e: evening twilight, n: night. The interaction coefficients for the spatial environmental gradient variables are denoted as F: distance to forest (increment: 1000m), C: distance to coast (increment: 1000m), A: Altitude (increment: 100m), Y=year in interaction terms.

Mammalian species	Alti (in100m)	Forest (1000m)	Coast (1000m)	Year	Light	Region	Interactions Nordkynn (M)	Interactions Ifjordfjellet (I)	Interactions Varanger (V)	R <sup>2</sup> adj.
<i>Red fox</i>	<b>-0.45</b> $\pm$ 0.22	0.005 $\pm$ 0.032	-0.02 $\pm$ 0.03	0.39 $\pm$ 0.78	<b>m: 1.12</b> $\pm$ <b>0.68</b> e: 0.70 $\pm$ 0.72 <b>n: 0.92</b> $\pm$ <b>0.36</b>	I: 0.03 $\pm$ 0.92 M: -0.16 $\pm$ 0.82 V: 0.50 $\pm$ 0.76	Y: -0.24 $\pm$ 1.08	Y: -0.07 $\pm$ 1.14	<b>Y: -1.26</b> $\pm$ <b>0.96</b>	0.40
<i>Wolverine</i>	0.61 $\pm$ 2.80	-0.97 $\pm$ 2.68	0.31 $\pm$ 0.63	0.26 $\pm$ 0.62	<b>m: 1.41</b> $\pm$ <b>1.06</b> e: 0.42 $\pm$ 1.36 n: 0.61 $\pm$ 0.66	I: -0.33 $\pm$ 108 M: 3.33 $\pm$ 9.98 V: -15.95 $\pm$ 17.8	F: 1.10 $\pm$ 2.68 C: -0.80 $\pm$ 0.92 A: -0.61 $\pm$ 3.02	F: 0.90 $\pm$ 2.71 C: -0.23 $\pm$ 0.66 A: 0.32 $\pm$ 3.27	F: -0.95 $\pm$ 3.00 C: -0.23 $\pm$ 0.64 <b>A: 6.47</b> $\pm$ <b>5.64</b>	0.37
<i>Arctic fox</i>			<b>0.18</b> $\pm$ <b>0.12</b>		m: -0.39 $\pm$ 2.60 d: -4.77 $\pm$ 10.20					0.26



**Table 3: Correlation matrix for overall trends of association among the 7 scavenger species photographed during this study. P-values are given in the second half of the matrix. Significant results, due to Holm correction for multiple testing, are marked with bold font. Correlation analysis made on a regional scale can be viewed in Appendix 2.**

Species	Raven	Golden eagle	White-tailed eagle	Hooded crows	Red fox	Wolverine	Arctic fox
<b>Raven</b>		0.34	0.33	0.23	0.01	-0.008	-0.07
<b>Golden eagle</b>	<b>0.000</b>		0.44	0.33	0.14	0.004	-0.04
<b>White-tailed eagle</b>	<b>0.000</b>	<b>0.000</b>		0.40	0.10	-0.009	-0.05
<b>Hooded crows</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		0.05	0.01	-0.03
<b>Red fox</b>	1.000	0.056	0.572	1.000		0.16	-0.07
<b>Wolverine</b>	1.000	1.000	1.000	1.000	<b>0.012</b>		-0.04
<b>Arctic fox</b>	1.000	1.000	1.000	1.000	1.000	1.000	

# Appendix 1

Total 2005/2006: Region = Varanger, Komag, Vestre Jakobselv, Ifjordfjellet, Bekkarfjord and Nordkynn, Coast = Distance to coast, Forest = Distance to forest, Alti = altitude,  $\hat{c}$  = overdispersion-factor. Model selection based on AIC weights,  $R^2 = R^2_{\text{adjusted}}$ . The selected models are shown in bold.

Species	Measure	Year	Light	Region	Region: Year	Coast	Forest	Alti	Light: Coast	Light: Forest	Light: Alti	Region: Coast	Region: Forest	Region: Alti	Np	AIC weights	$R^2_{\text{adj}}$	
<b>Raven</b> 32891 obs - #69258	Quasi- poisson $\hat{c} = 30.93$				X				X	X	X	X	X	X	32	0.00	<b>0.86</b>	
					<b>X</b>				<b>X</b>	<b>X</b>	<b>X</b>				<b>23</b>	<b>0.99</b>		
			X		X	X	X	X							14	0.00		
<b>Golden eagle</b> 730 obs - #827	Quasi- poisson $\hat{c} = 4.86$		<b>X</b>		X				X	X	X	X	X	X	28	0.00	<b>0.69</b>	
					<b>X</b>								<b>X</b>	<b>X</b>	<b>X</b>	<b>22</b>		<b>0.97</b>
					X	X	X	X	X							19		0.02
		X	X	X		X	X	X	X							13		0.00
						X	X							9	0.00			
<b>White- tailed eagle</b> 540 obs - #610	Quasi- poisson $\hat{c} = 2.92$		<b>X</b>		X				X	X	X	X	X	X	28	0.00	<b>0.52</b>	
					<b>X</b>								<b>X</b>	<b>X</b>	<b>X</b>	<b>22</b>		<b>0.99</b>
		X	X	X	X	X	X	X	X				X	X	X	19		0.00
						X	X							13	0.00			
		X	X	X			X	X						9	0.00			
<b>Hooded Crow</b> 770 obs - #2050	Quasi- poisson $\hat{c} = 14.13$				X				X	X	X	X	X	X	28	0.00	<b>0.94</b>	
					<b>X</b>								<b>X</b>	<b>X</b>	<b>X</b>	<b>22</b>		<b>0.04</b>
					X	X	X	X	X				X	X	X	19		0.00
					<b>X</b>		<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>						19		0.00
		X	X	X	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>							<b>13</b>		<b>0.94</b>
			X	X		X	X	X						10	0.00			

Species	Measure	Year	Light	Region	Region: Year	Coast	Forest	Alti	Light: Coast	Light: Forest	Light: Alti	Region: Coast	Region: Forest	Region: Alti	Np	AIC weights	R <sup>2</sup> adj.	
<b>Red fox</b> 1059 obs - #1078	Quasi- poisson $\hat{c} = 7.57$				X				X	X	X	X	X	X	32	0.00	<b>0.40</b>	
					X				X	X	X				23	0.04		
		X	X	X	X	X	X	X	X							14		<b>0.51</b>
		X	X	X			X	X	X							11		0.07
		X	X	X			X		X							10		0.20
														9	0.09			
<b>Wolverine</b> 122 obs	Quasi- poisson $\hat{c} = 2.20$				X				X	X	X	X	X	X	32	0.00	<b>0.36</b>	
					X				X	X	X				23	0.00		
		X	X	X	X	X				X	X	X	X	X	23	0.08		
		X	X	X			X	X	X	X	X	X	X	X		20		0.00
		X	X	X	X	X	X	X	X	X	X	X	X	X		14		0.00
														11	0.00			
<b>Arctic fox</b> 94 obs	Quasi- poisson $\hat{c} = 34.76$		X				X	X	X						6	0.09	<b>0.26</b>	
			X				X	X							5	0.33		
			X				X		X						5	0.11		
			X				X								4	<b>0.36</b>		
			X					X							4	0.00		

## Appendix 2

Correlation matrix for presence of species at stations. A) Bekkarfjord transect, B) Ifjordfjellet transect, C) Nordkynn transect, D) Varanger region (including Komagdalen transect, Vestre Jakobselvdalen transect and Stjernevann transect). Significant results due to Holm correction for multiple testing are marked with bold font.

### A. Bekkarfjord transect

Species	Raven	Golden eagle	White-tailed eagle	Hooded crows	Red fox	Wolverine
<b>Raven</b>		0.58	0.56	0.39	0.06	-0.15
<b>Golden eagle</b>	<b>0.000</b>		0.64	0.52	0.35	0.01
<b>White-tailed eagle</b>	<b>0.000</b>	<b>0.000</b>		0.55	0.17	0.009
<b>Hooded crows</b>	<b>0.009</b>	<b>0.000</b>	<b>0.000</b>		0.11	0.20
<b>Red fox</b>	1.000	<b>0.032</b>	0.800	1.000		0.22
<b>Wolverine</b>	1.000	1.000	1.000	0.588	0.525	

### B. Ifjordfjellet transect

Species	Raven	Golden eagle	White-tailed eagle	Hooded crows	Red fox	Wolverine
<b>Raven</b>		0.43	0.19	0.22	0.03	0.10
<b>Golden eagle</b>	<b>0.000</b>		0.39	0.42	0.16	-0.08
<b>White-tailed eagle</b>	0.830	<b>0.000</b>		0.50	0.08	-0.07
<b>Hooded crows</b>	0.517	<b>0.000</b>	<b>0.000</b>		-0.03	-0.07
<b>Red fox</b>	1.000	1.000	1.000	1.000		0.06
<b>Wolverine</b>	1.000	1.000	1.000	1.000	1.000	

### C. Nordkynn transect

Species	Raven	Golden eagle	White-tailed eagle	Hooded crows	Red fox	Wolverine
<b>Raven</b>		0.29	0.39	0.17	0.07	0.02
<b>Golden eagle</b>	0.009		0.29	-0.03	0.08	0.07
<b>White-tailed eagle</b>	<b>0.000</b>	0.009		0.35	0.18	-0.02
<b>Hooded crows</b>	1.000	1.000	<b>0.000</b>		0.16	0.21
<b>Red fox</b>	1.000	1.000	0.920	1.000		0.14
<b>Wolverine</b>	1.000	1.000	1.000	0.550	1.000	

### D. Varanger region

Species	Raven	Golden eagle	White-tailed eagle	Hooded crows	Red fox	Wolverine	Arctic fox
<b>Raven</b>		0.29	0.34	0.27	0.02	-0.009	-0.07
<b>Golden eagle</b>	<b>0.000</b>		0.58	0.28	0.14	0.11	-0.05
<b>White-tailed eagle</b>	<b>0.000</b>	<b>0.000</b>		0.32	0.10	0.07	-0.07
<b>Hooded crows</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		0.02	-0.07	-0.05
<b>Red fox</b>	1.000	1.000	1.000	1.000		0.31	-0.07
<b>Wolverine</b>	1.000	1.000	1.000	1.000	<b>0.000</b>		-0.06
<b>Arctic fox</b>	1.000	1.000	1.000	1.000	1.000	1.000	