

**Corvids response to fluctuating abundance of resources in
tundra ecosystems**

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BIO-3950 Master Thesis in Biology, Northern populations and Ecosystems

May 2018



Faculty of Biosciences, Fisheries and Economics Department of Arctic and
Marine Biology

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The cover photo was taken by an automatic camera Reconyx PC85/PC800 (Reconyx Inc., Holmen, WI, USA) at one of the camera sites during winter 2017 in Varanger, Finnmark.

ACKNOWLEDGEMENTS

First, many thanks to my supervisor Dorothee for the great guidance, talks, comments, and discussions that helped me through the past year and for always having her door open for me when I needed it. Thanks also to my other supervisor Rolf for all the comments to improve my thoughts and writing. I would also say thank you to all the technicians that worked on sampling the data during these 13 years and allowed me to realize this thesis. Thanks to Torunn and Eivind for a great time in fieldwork.

I would like to thank my friends for being here when I needed them and my roommates Emily and Vilde for understanding. Finally, a special thanks to Filippo for the statistical help and the interesting and long-lasting chats at the office and Jake for the laughs and good time spent trying to understand how words work...

Merci à ma famille et mon amie Joséphine pour croire en moi et être toujours présents pour moi peu importe les situations.

ABSTRACT

Aim Despite the numerous studies on corvids' behaviour, their dynamics in different ecosystems is unknown. Ravens and hooded crows are opportunistic generalists acting as both predators and scavengers. Ravens are probably the most specialized scavengers on ungulate carcasses and both species are known as efficient hunters of small rodents. Small rodents are a key species in the tundra as they represent the main prey for many terrestrial predators. A study about nest predation using artificial nests, suggested that corvids may respond numerically to the Norwegian lemming in tundra ecosystems. Here I used a 13 year time series to investigate whether two potentially important food resources, small rodents and reindeer carcasses, drive the corvids fluctuations in the ecosystems of Northern Fennoscandia.

Methods To investigate the corvid population dynamics, I used data from camera traps baited with reindeer meat collected in eastern Finnmark during winter between 2005 and 2017, in addition to time series data from small rodent trapping.

Main conclusions This is the first study to assess temporal and spatial variation in corvids dynamics in the tundra of Northern Fennoscandia. The results showed a great deal of temporal and spatial variation in the presence of each species between the time series of three regions. The assumption that the corvids' populations fluctuate with the lemming cycles appears not to be supported here. However, the presence of the ravens was positively correlated with the fluctuations of voles that were in higher density compare to lemming during the study period. The statistical models did not reveal any impact of the relative amount of carcasses in eastern Finnmark on the dynamics of the corvid data. Based on the results, I discuss the different responses of these generalist predators in the arctic tundra.

Keywords

Ravens, spatio-temporal variation, lemming, vole, hooded crow, carcasses, tundra ecosystem, camera traps

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1 INTRODUCTION

Worldwide, corvids are well-known birds due to their long association with humankind. They are present in everyday human life as they are well adapted to our cities and environments (Ratcliffe 1997, Andrén 1992). Except for their behavioural characteristics, not much is known about their activity in the wilderness. In Fennoscandia, only a few studies bring attention to these interesting birds. While they are part of the northern ecosystem, presently, we are not aware of any long time series that have allowed for analyses of the population dynamics of corvids in tundra ecosystems.

Corvids are opportunistic generalist acting both as predators and as scavengers (Ims et al. 2013, Heinrich 1989, Ratcliffe 1997, Combs 1978, Angelstam et al. 1984). They have a great capacity to innovate their foraging behaviour and adapt to changing environments (Careau et al. 2007, Heinrich 1989) which makes them potentially important actors in the arctic tundra. Two species of corvids are present in the arctic tundra, the common raven (*Corvus corax*) and the hooded crow (*Corvus c. cornix*) (Ims et al. 2013, Haftorn 1997). The common raven can be found all year round while some hooded crows migrate to Denmark, Germany or Belgium in October and come back around March (Haftorn 1997, Heinrich 1989). Despite being common nest predators in the Arctic, ravens and crows are also known to feed on small rodents (Andrén 1992, Haftorn 1997).

In the tundra, the plant productivity is low due to low temperature, long winters and a low concentration of nutrients in the soil (Ims and Fuglei 2005). Thus, the number of herbivores and potential prey species is limited. The short snow-free seasons require special adaptations from both predators and prey. The trophic interactions in this ecosystem are ruled by strong seasonal and multi-annual cycles (Ims and Fuglei 2005). In this particular food web, small rodents stand out as the main prey for many terrestrial predators (Ims et al. 2013, Gilg et al. 2003). In fact, the small rodent cycles generate the most marked fluctuations in term of biomass in the arctic tundra (Ims and Fuglei 2005). The small rodent cycles are a unique phenomenon with an interspecific and a geographical synchrony on a regional scale (Krebs et al. 2002). In the Arctic, the different species of lemmings and voles show three to five-year period cycles although the cycles of lemmings

and voles can be very different in terms of amplitude. While most of the interactions between the small rodents and their main predators in the tundra are well documented, there is a lack of information when the focus is on corvids. Generalist predators such as corvids are defined as “predators that have several alternative prey species between which they may ‘switch’, depending on which prey species are currently most abundant” (Hanski et al. 1991). Compared to specialist predators that are suggested to contribute or maintain the multiannual cycles of small rodents in Northern Europe, little is known concerning the role of generalist predators in the dynamic of small rodent population and their impact on the ecosystems in Fennoscandia (Hanski et al. 1991).

The predator-prey dynamics are structured around two interactive processes: the functional and numerical response (Solomon 1949). The functional response is characterized as predator consumption rate in relation to the number of prey (Hellström et al. 2014). On the other hand, the numerical response is defined as the density of predator related to the prey density, which indicates that the predator populations fluctuate depending on the number of prey present in the system at a certain time.

A study of predation on artificial bird nests indicates that corvids may respond numerically to the Norwegian lemming (*Lemmus lemmus*) (Ims et al. 2013). The study focused on predator-prey dynamics in the tundra, and specifically, predation on dummy nest during 4 years (2005-2008). They found out that the corvids and especially the ravens were the ones responsible for most of the predation attempted on the nests. In the tundra, most predators (but in particular generalists) are able to switch their predation to an alternative prey when their main prey is not available or in low quantity (crash phase in rodent cycles). A lemming peak occurred in the study area (eastern Finnmark) in 2007 and the predation rate by the corvids was the highest the year following the peak (crash year). In comparison, vole abundance wasn't able to predict changes in nest predation rates. This suggests that the corvids might respond to lemming density and therefore switch to an alternative prey (eggs) with a distinct time lag of one year after the rodent peak in this region (Ims et al. 2013). Besides the suggestions from this study, little is known about the extent to which corvids respond temporally and spatially to the rodent cycles.

During the winter, the rodents are under a thick layer of snow making them difficult to prey on. During this period, but also during the crash years of small rodents' cycles, most of the predators in the tundra suffer from food scarcity. The exploitation of alternative

food resources such as carcasses is essential to the survival of the population of northern carnivores (Killengreen et al. 2012). In Varanger peninsula, reindeer herds are mostly present in summer but because of limitations in winter pastures and emergent pressures(infrastructures, management) on reindeer ranges, part of the population does not migrate and thus stays year round in the summer habitat (Henden et al. 2014). Furthermore, with the climate changing and the weather-induced winter mortality of ungulates, there is a strong increase in the presence of boreal generalist predators (including ravens and crows) in the mountain and low arctic tundra (Henden et al. 2014, Sokolov et al. 2016). The increasing access to reindeer carrion in late winter might be the reason for the corvids to establish and breed in the tundra (Henden et al. 2014).

Here, I use a 13 year time series of wildlife images from camera traps distributed along three transects to investigate population dynamics of the common raven and the hooded crow in a low-arctic tundra system on Varanger Peninsula in northern Norway. Based on this time series, I explore the temporal and spatial dynamics of the corvids with respect to potential drivers previously unaddressed in the arctic. My main aim will be to examine whether corvids respond numerically to small rodent dynamics in the tundra ecosystems but also to assess other sources of spatial and temporal variation on the Varanger Peninsula. I will especially consider the response to lemming and vole abundances separately, but also examine whether there is any difference between ravens and crows in general temporal and spatial dynamics. Based on the cited literature, my hypothesis is that the corvids respond numerically to small rodent dynamics and that corvids respond stronger to lemming than voles. In addition, knowing that both ravens and crows are opportunistic scavengers I decided to further investigate the impact of the reindeer carcasses on the corvids dynamics (Ratcliffe 1997, Charles 1972).

2 MATERIAL AND METHODS

2.1 Study species

The Raven

The raven nests on high cliffs, trees or buildings (Ratcliffe 1997) with a Holarctic distribution across northern and eastern Europe (Haftorn 1997) as well as North-America, north to Bylot Island (Chevallier et al. 2016). Its breeding season starts at the end of March when there is still snow on the ground (Heinrich 1989). Despite the weather in winter, ravens usually manage to take good care of their offspring, which are able to fly by the end of April. Most of the chicks will not breed until they are 3 years old (Heinrich 1989, Coombs 1978). Ravens usually stay around the nest during the entire breeding season, each of the parents replacing the other in the search for food (Ratcliffe 1997, Heinrich 1989). The nesting place is central in a raven's life, it becomes the focus of its territorial motive and is the roosting location outside the nesting season. It will be fiercely defended year after year against any outsiders. Ravens are opportunistic scavengers and predators (Ims et al. 2013, Heinrich 1989, Ratcliffe 1997). Their diet is omnivorous and varies from grains to ungulate carcasses (Ratcliffe 1997). A large portion of the raven population composed of non-breeders and territorial breeders that do not form flocks that depend mainly on spatiotemporally unpredictable food sources such as carrion (Restani et al. 2001). The distance between the ravens' roost and the potential food resource can be up to a hundred kilometres a day but is mostly around 15 kilometres (Heinrich 1989). Compared to other avian scavengers such as eagles or hooded crows whose distribution in the tundra is influenced by distances to the coast and forest, the ravens show no spatial pattern (Killengreen et al. 2012). In Norway, the population was estimated to be between 20 000 to 50 000 pairs in the late 1970s (Haftorn 1997), but to my knowledge no recent updates are available.

The Hooded Crow

The hooded crows build their nest principally in trees (Charles 1972, Yom-Tov 1974, Andrén 1992). They are distributed across north, east and south east of Europe, and can also be found in the Middle East (Coombs 1978). Their breeding season begins late April beginning of May (Charles 1972) and lasts for about 75 days from the moment they start building the nest to the fledging of young (Coombs 1978). Their offspring usually begin to

fly around their 21st day (Yom-Tov 1974). The breeding pairs are territorial (Yom-Tov 1974) but have difficulties chasing the non-breeder flocks (Stein 2008). In the tundra of northern Fennoscandia, the hooded crow is found close to the tree line and the coast (Killengreen et al. 2012). Hooded crows usually feed close to their nests and their range varies from 16-41 hectares during the breeding season to 36-75 hectares during the non-breeding season (Charles 1972). During winter, the crows will fly to only 2 km away from the nesting site to find food (Charles 1972). Overall, they usually stay in a zone of 0 to 600 meters from the nest (down to 100 meters if there is an intrusion such as a rival individual) (Charles 1972). Crows are also opportunistic generalist that are known to feed on a wide range of food from grain to carrion (Lockie 1955). Similar to the ravens, crows form flocks of non-territorial and non-breeding individuals (Charles 1972). During the breeding season, cannibalism on hooded crows' eggs from neighbouring pairs or non-breeding birds has been observed (Yom-Tov 1974). Today, the number of pairs present in Norway is unknown but there were between 200 000 and 600 000 pairs in the late 1970s (Haftorn 1997).

2.2 Study area

The study was located in the Varanger peninsula (70° - 71° N and 28 - 31 E) in Finnmark county, Northern Norway. The northern and eastern coastal lowlands as well as the interior highlands belong to the arctic bioclimatic subzone E which is mainly low shrub tundra. The southern and western low lands have higher temperatures and are mostly forested by *Betula pubescens* (Ims et al. 2013). Carnivore monitoring by means of time laps cameras has been conducted since 2005 every year through a conservation project targeting the regionally endangered arctic fox *Vulpes lagopus* (Killengreen et al. 2012, www.coat.no). Camera traps were placed in three different regions: Komagdalen, Vestre Jacobselv (Nyborg) and Stjernevann along altitudinal gradients (Fig.1) and refer subsequently as the respective abbreviations: KO, VJ and SV.

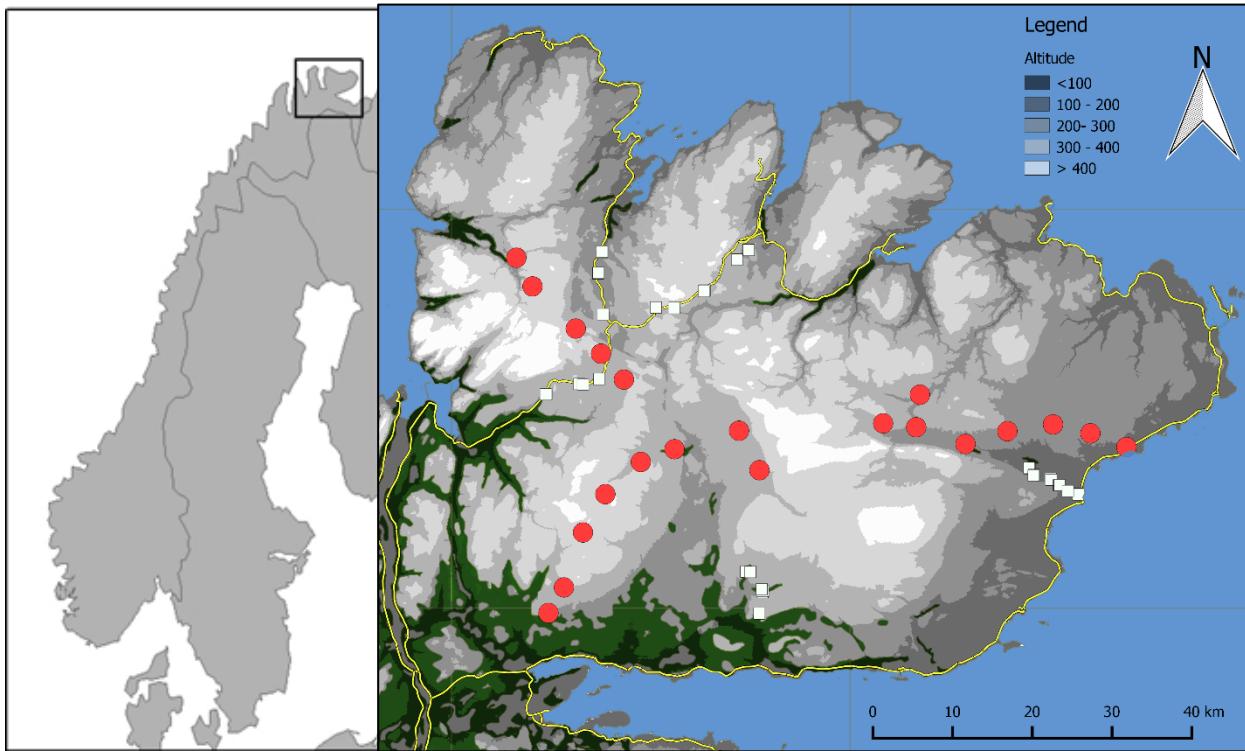


Figure 1. Study area and location of the camera trap sites (in red circles) that were available from 2005 to 2017 in Finnmark, Northern Norway. Roads are shown in yellow, forested areas in green and white squares represent locations of the small rodent trapping sites.

All areas have documented the presence of ravens and hooded crows (Killengreen et al. 2012). The study area includes summer pastures for large populations of semi domestic reindeer (*Rangifer tarandus*) (Hamel et al. 2013). Moose (*Alces alces*) are also present in the peninsula which, in addition to the reindeer, form the main carcass resources for the corvids in winter.

In summer, the main prey species available are different species of small rodents in addition to several species of ground nesting birds such as two species of ptarmigan (rock (*Lagopus muta*) and willow (*Lagopus lagopus*)) (Ims et al. 2013). The three main rodent species present in Varanger peninsula are: the Norwegian lemming, the tundra vole (*Microtus oeconomus*) and the grey-sided vole (*Myodes rufocanus*) (Ims et al. 2013). In recent decades, the outbreaks of the Norwegian lemming have been irregular in the sub- and low-arctic tundra of northern Norway (Ims et al. 2011). Indeed, there have been only two major outbreaks since the 1970s while the vole population in the same region has maintained their 4-5-years population cycles (Ims et al. 2017). Lemmings overwinter in snow beds and rely on mosses as their main winter food. Therefore their access to food is more severely limited by ground icing than it is for voles, which rely mainly on vascular

plants that create more “space” under the snow (Aars & Ims 2002, Korslund & Steen 2006). For that reason, lemmings could be more sensitive to winter climate variation. The two species also have different intrinsic demographic tactics, in particular a winter reproduction for lemmings (Krebs 2010). Indeed, the breeding season of lemmings can last from mid-winter (with snow cover) until the next fall (Ims and Fuglei 2005). The vole breeding season usually starts when the snow melts and lasts until September (Ehrlich unpublished).

2.3 Monitoring design of the corvids

The study was conducted each winter from end of February until the end of April over 13 years (2005-2017). It is important to note that the sampling periods coincide with the period when the ravens start breeding and have established their territories (Henden et al. 2014, Heinrich 1989). The crows breeding season starts at the end of the sampling period (Haftorn 1997). In total, 21 permanent camera sites were distributed in three different regions: KO ($n=8$ sites), VJ ($n=8$ sites) and SV ($n=5$ sites) (Fig.1). The camera sites are placed along four environmental gradients expected to correlate with resource abundance available to corvids: distance to coast, distance to the road, distance to the forest and altitude. The distance to the coast and forest represent the distance to neighbouring ecosystems that can furnish different subsidies to the corvids (Killengreen et al. 2012). Roads are known to attract carrion feeders in search of road kills (Forman & Alexander 1998). Altitude is a determinant of primary productivity in tundra in the sense that it decreases with increasing altitude (Aunapuu et al. 2008). The distance between adjacent camera sites within each region varies from around 5 to 15km.

Each site had a camera trap placed in front of a bait consisting of a 15-20kg frozen block of reindeer slaughter remains, which was positioned around 3m from the camera. The bait was used to attract the local carnivores in order to study the scavenger guild present in the peninsula (Hamel et al. 2013, Killengreen et al. 2012). Each camera (CamTrack, model unknown, USA & Reconyx PC85/PC800; Reconyx Inc., Holmen, WI, USA) was set in time-lapse mode and took photographs of the bait and its surroundings every 10min from 2005 until 2015 and then every 5min for 2016 and 2017. The batteries and memory cards were replaced approximately every 14 days. At that time, the baits were replaced by a new block if it had been entirely or partly consumed.

2.4 Monitoring design and data of the small rodent

Small rodent population data was gathered by snap trapping. There are two snap trapping periods per year, one in spring, shortly after snow melt in late June, and one in the fall, approximately mid-September. There are 109 permanent census sites distributed in the tundra in eastern Finnmark, Fennoscandia. Snap trapping with low sampling intensity were used in order to complete the spatially extensive sampling in 8 days in each season (Ims et al. 2011). In Varanger, the monitoring system encompasses 49 permanent sites (n=11 in Nyborg; n=14 in Komag; n=24 in Stjernevann) (Ims et al. 2011). The sites were distributed equally among two common tundra habitats; dwarf-shrub heaths and riparian meadows including dispersed willow thickets (Ims et al. 2013). At each site a trapping unit corresponding to a 15 m x 15 m small quadrat is deployed with 12 snap traps (Ims et al. 2011). The trapping showed that the study period included the increases (2005 – 2006 and 2010), two peaks (2007 and 2011) and two crash phases (2008 and 2012) of two cycles of the lemming population. There were three vole peaks; the two first coincided with the lemming peak, while the last in 2015 occurred when there was no lemming peak evident. Thus the lemming peaks, whenever present, appear synchronously with the vole peaks (Fig.2). However, the cycle amplitude exhibited variability between the species and areas (Krebs et al. 2002).

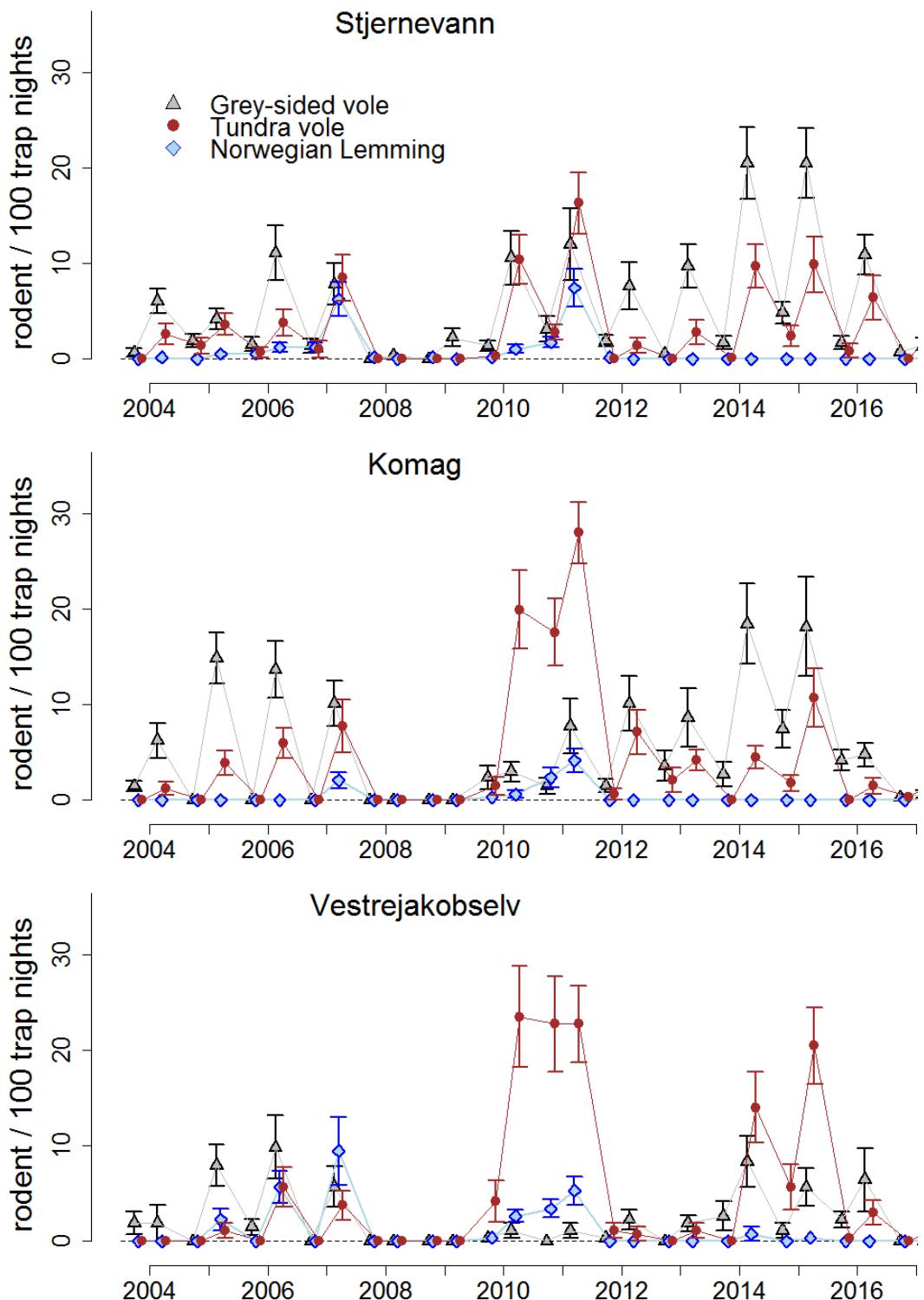


Figure 2. Population time series of the three most common rodent species in Varanger Peninsula (Stjernevann, Komag and Vestre Jacobselv) the Norwegian lemmings, Grey-sided voles and Tundra voles. Note that although the species are synchronized their cycles have different amplitudes, shapes and regularity (i.e. the lemming is missing in the last peak in 2015)(www.coat.no).

2.5 Analysis

2.5.1 Response variables

Determining relative abundance for unmarked animals using camera traps is relatively new in ecology. Thus, the best method and sampling design are still discussed (Hamel et al. 2013, Denes et al. 2015). Usually, camera trap data is used to record presence/absence of a given species on trapping stations which is suitable for occupancy estimation (probability of presence corrected for detection probability). However, here occupancy may be saturated due to the omnipresence of the ravens at the camera sites. But photos of corvids on baited trap stations carry more information, for instance, as there are often several individuals (i.e. flocks) and even species (i.e. both ravens and hooded crows) present on each photo. However, a lot of the data obtained from camera traps are zeros due to the number of pictures without individuals on it (or not seen by the observer) (Denes et al. 2015). Thus, the resulting counts might reflect a disproportionate number of absences, which is called “zero inflation” (Martin et al. 2005). This can lead to important estimation error and hide important ecological patterns (Martin et al. 2005, Zuur et al. 2009). For this study it was necessary to determine a relative abundance index using the pictures from the cameras.

I used response variables that are assumed to reflect the relative abundance of ravens:

- *Relative presence*: The proportion of pictures per day with ravens present at each camera sites. I subtracted the number of obscured, bad quality photographs from the number of photographs taken.
- *Maximum number*: the maximum number of individuals counted in a picture per day at each camera site.

The hooded crows generally were less present than the ravens on the baited camera stations (Fig 2). Therefore, I decided to use a different response variable than the ones used for the ravens:

- *Annual presence*: Crows recorded (i.e. presence) or not (absence) on a camera site in given year.

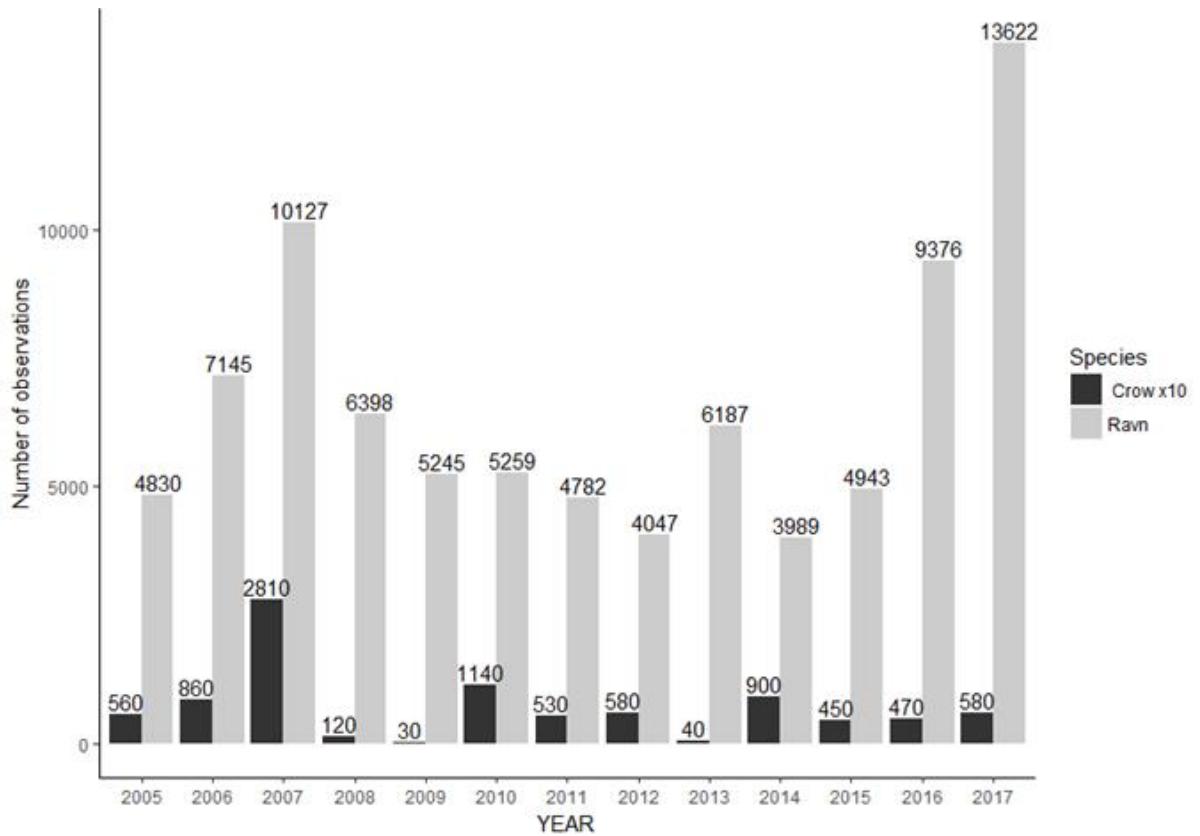


Figure 3. Bar plot representing the number of observations (pictures) with ravens (grey) and crow (black) taken by all the cameras from 2005 until 2017 in Varanger peninsula, Finnmark. Note that for the crows the number of observations has been multiplied time 10 in order to make bars visible. Also that the time lapse settings of the cameras were change from 10 min to 5 min after 2015.

2.5.2 Predictor variables

All predictor variables considered in the analysis are presented in Table 1 with a description of their spatial and temporal scaling. For the distance variables, forest was defined as areas of at least 1km² with continuous tree aggregation while roads were defined as asphalt covered roads (to distinguish from the gravel roads) and the distance varied from 0.4-21km. Distance from coast and forest to the 21 camera sites varied 0.6-30.6km, 0.1-24km, respectively. The altitude varied between 50 to 430m above sea level. The number of reindeer carcasses found per year is used to reflect the winter conditions for reindeers (Henden et al. 2014). I used data from eastern Finnmark from November until May (official statistics for reported reindeer carcasses; www.rovbase.no) including the municipalities of Båtsfjord, Berlevåk, Gamvik, Sør. Varanger, Tana, Nesseby, Vadsø and Vardoe. The data covers the study period from 2005 until 2016. The proportion of pictures with bait was also integrated in the models, as a

covariate to correct for the fact that there was a smaller probability to observe ravens after the bait was gone. Finally, because the sampling period also correspond to the breeding season of ravens, it was important to include Julian days.

Corvids are expected to respond numerically to small rodent with a 1 year time lag, so I used the rodents abundance indices from the autumn before (year t-1) as predictors of change in corvids dynamics in year t (Ims et al. 2013). Moreover, the autumn catch of lemmings may be a better descriptor of the abundance of lemming in following late winter and early spring (i.e. when corvids were monitored) than the subsequent summer catches; because lemming crashes may take place in late spring.

Table 1: Description of the spatial and temporal scaling of predictor variables considered to be included in the statistical models.

Covariates available	Covariate description
<i>Distance to the forest</i> <i>Distance to the coast</i> <i>Distance to the road</i> <i>Altitude</i>	Spatial: camera site Temporal: invariant
<i>Abundance of lemmings</i> <i>Abundance of voles</i>	Spatial: study regions Temporal: year
<i>Abundance of carrions</i>	Spatial: study area Temporal: year
<i>Date in Julian days</i>	Spatial: camera site Temporal: day
<i>Number of day with bait</i> <i>Proportion of pictures with bait</i>	Spatial: camera site Temporal: day

Both the data from the camera traps and the small rodent trapping were analysed using the software R version 0.99.933 (R Development Core Team 2009). Due to the different scale for each of the covariates, I had to rescale all the covariates (by subtracting the mean and dividing by the standard deviation for each covariate) by means of the scale function in R.

2.5.3 Statistical models

2.5.3.1 *Models for raven*

The variable *relative presence of ravens* was analysed by fitting a quasibinomial generalised linear mixed model specifying the camera site as random intercepts (R package MASS and the function glmmPQL).

Different elements can cause real overdispersion such as many zeros, covariates not accounted for and clustering of observations (Zuur et al. 2009, Hilbe 2011). Here, pre-analysis showed overdispersion. Thus, I chose a quasi-likelihood approach to avoid any problems with the models (Wolfinger & O'connell , 1993). Oversdispersion is here modelled as quasi-binomial distribution (Zuur et al. 2009) implemented with the glmmPQL function in R (Breslow & Clayton 1993).

The variable *maximum number of raven* was overdispersed compared to a Poisson distribution as could be expected due to flocking behaviour. I therefore chose to analyse this variable by means of a negative binomial generalised linear mixed model specifying the camera site as random intercepts. The negative binomial model was implemented in R by means of the function glmer.nb (R package lme4).

Before modelling the effect predictor variables on the two raven response variables, I first investigated the overall spatial and temporal variation in raven *presence* and *maximum numbers*. This was done by estimating annual means for the two variables at the spatial scale of regions and sites. These estimates were then checked for the presence of overall temporal trends across the 13-year time series by means of a quasibinomial generalized linear model for the *presence* and a negative binomial generalized linear model for the *maximum numbers*. Degree of synchrony between time series was computed by Spearman rank cross-correlation coefficients. As a measure of temporal variance in the regional time series coefficient of variation (CV) as computed and the degree of temporal auto-covariance were computed by means of AR1-coefficients.

For both of the raven response variables

The two main fixed predictor variables in the models were the rodent density indices (lemming and vole abundance indices; $r=0.276$). The spatial environmental gradients were

also included in the models as covariates. We never included both “distance to the road” and “distance to the coast” in the same model as these two variables were highly correlated ($r=0.666$). Also, because “distance to the coast” was more correlated to “altitude” ($r=0.499$) compared to “distance to the road” ($r=0.338$) we chose to include “distance to the road” in the different models. The abundance of reindeer carriions was also used as a covariate to assess any effect it might have on the presence of the ravens in the study area.

The selection of the negative binomial model of maximum number of raven was based on the AIC criterion. The models were ranked according to their AIC scores and weights (Zuur et al. 2009). Because of the numerous covariates included in the study, we used the dredge function of the MuMin library to realise model selection (Zuur et al. 2009). I specified the function to always keep the two main predictors variables (lemming and vole density indices). The goodness of fit was assessed by visualizing the different residuals vs fitted values plots. For the quasi-binomial model of relative presence of raven, reliable AIC values cannot be calculated using glmmPQL in the R-package MASS because it maximises a penalised quasi-likelihood, rather than the full likelihood (Zuur et al. 2009). Thus, for the model selection I used the estimates and confidence intervals of the fixed effects to decide whether or not to include them in the model.

2.5.3.2 *Model for hooded crow*

The response variable *presence of crow* was modelled by a binomial generalized mixed model (R function glmer in package lme4) specifying camera sites as random intercepts.

I obtained annual mean estimates for each region and plotted these estimates against time to check for trends and eventual synchrony between regions.

I used the same rodent and gradient predictor variables as for raven. Since the crow data was at an annual time scale, proportion of pictures with the bait was replaced by number of days with bait present per year and the Julian day in season was not used.

The model selection was realized using the dredge function from the package MuMin and was based on their AIC scores and weight. The goodness of fit of the model was assessed using Hosmer-Lemeshow goodness of fit test and a Chi squared test with 8 degree of freedom was used to assess the fit of the observed versus fitted values.

3 RESULTS

3.1 Ravens

3.1.1 Relative presence

Figure 4 illustrates the time series of the estimated annual relative presence of ravens across the 13-year time series for the three study regions. There was a great deal of temporal variability in these time series (CV values in table 2), in particular for KO and SV. However, these temporal fluctuations in relative presence of ravens were not significantly auto-correlated within the series ($p>0.05$ for all AR1 coefficients in table 2) or significantly synchronous between series ($p>0.05$ for all Spearman rank correlation coefficients in table 2). However, it should be noticed that the correlations are positive between KO and VJ (0.483) but negative between KO and SV (-0.428) and VJ and SV (-0.307). The regression of relative presence indicates a declining trend (negative regression coefficients) for regions KO and SV, while there was a slight positive trend for VJ that also had the highest mean relative presence across the 13-year time series.

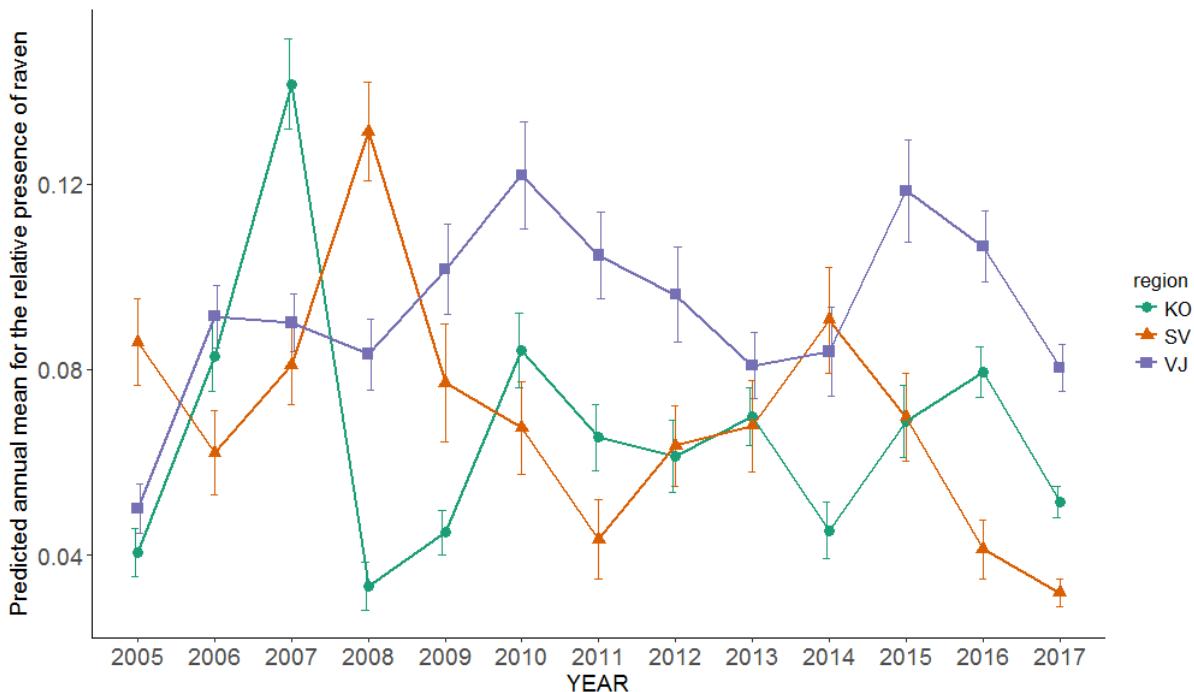


Figure 4. Time series of annual relative presence of ravens in Finnmark, northern Norway for the three region of the study area (KO=Komag, SV=Stjernevann and VJ=Vestre Jacobselv). The annual estimates (with standard error bars) were obtained from the generalized linear model described in the Material and Methods.

Table 2. Statistics on spatial and temporal variation in the *relative presence of ravens* variable at the regional level. (**Mean**: mean value across years; **Trend**: Linear trend estimate (logit scale); **CV**: Coefficient of variation represented by the standard deviation divided by the mean; **AR1**:First order auto-correlation; **Spearman Cross Correlation**: temporal correlation between region)

Variable	Region	Mean	Trend	CV	AR1	Cross corr
<i>Relative presence</i>	VJ	0.091 (SE= 0.002)	0.014 (SE= 0.006)	0.201	0.190	KO: 0.483 SV:-0.307
	KO	0.065 (SE= 0.001)	-0.014 (SE= 0.006)	0.417	-0.285	VJ: 0.483 SV: -0.428
	SV	0.064 (SE= 0.002)	-0.077 (SE= 0.008)	0.361	0.355	VJ:-0.307 KO: -0.428

Comparing the estimates of the different models shows that some of the estimates were relatively constant despite the different variables included in the models (Appendix B). The covariate representing the total number of carcasses in the region from November until May of each of the sampling period (except 2017) was added to the most complex model (Model (1), Appendix B). However, it wasn't statistically significant (estimate (variables scaled): -0.020+/- 0.019; p_value : 0.295) and thus the other models tested didn't included it and used the full dataset including year 2017.

For the two main predictor variables, the estimates were stable in all the models tested and the confidence intervals show a clear and significant effect (Fig.5, Appendix B). The predicted proportion of pictures with ravens appears to be increasing when the number of voles the year before was high. However, the predicted proportions of pictures with ravens seems to decrease as the number of lemmings the year before was high. Translating these results in odds ratios:

- For an increase of the number of voles the year before of one standard deviation or 9.69 voles, the odds of having ravens on the pictures increases by 13% (OR= $\exp(0.123)=1.130$).

- On the other hand, for an increase in the number of lemming the year before of one standard deviation or 2.30 lemmings, the odds of having ravens in the pictures decreases by 7% ($OR=\exp(-0.065)=0.937$; $(1-0.937)*100=7\%$)

In term of environmental gradient, the covariates “distance to the forest” and “distance to the road” didn’t seem to have a significant effect on the proportion of pictures with ravens, also the confidence intervals included zero which demonstrates very low support for these effects on the relative presence of ravens (Fig.5, Appendix B). Although the confidence intervals for the effect of altitude on the predicted proportion of pictures with ravens were quite large, the effects clearly show that ravens are more present at the bait station when the camera is positioned at higher altitudes (Fig.5).

The near absence of ravens in the pictures when the proportion of pictures with bait is near zero and the significant increase in the predicted proportion of pictures with ravens when the bait can be seen in the pictures, show the importance of the effect of daily presence of the bait (reported as the proportion of pictures with bait). The predicted proportion of pictures with ravens is almost zero at the beginning of the sampling period and slowly increases as closer to the end of the sampling period (corresponding to end of April) (Fig.5).

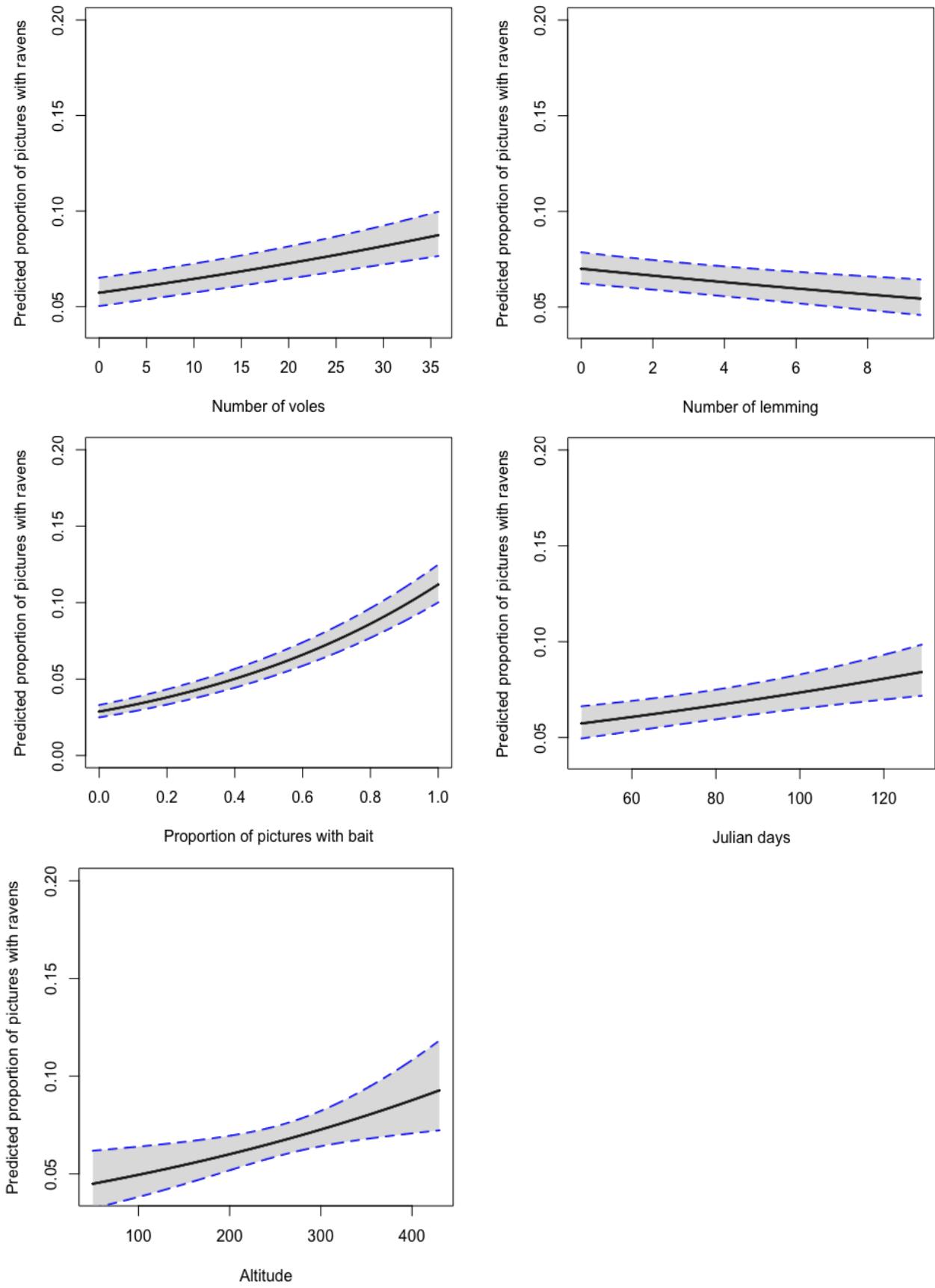


Figure 5. Predicted proportion of pictures (95% CI) with ravens between 2005 and 2017 in Finnmark, Northern Norway, according to the abundance of voles and the abundance of lemmings **the fall before** (i.e. number of lemming/100 traps nights), the proportion of pictures with the bait, the progression in the study period (i.e. Julian days) and the Altitude.

3.1.2 Maximum number of ravens counted

The time series of the estimated annual maximum number of ravens across the 13-year time series for the three study regions is illustrated in Figure 6. There was considerable temporal variability between years, in particular for KO (CV values in table 3). These temporal fluctuations were not significantly auto-correlated within the series ($p>0.05$ for all AR1 coefficients in table 3) or significantly synchronous between series ($p>0.05$ for all Spearman rank correlation coefficients in table 3). However, similar to the relative presence of ravens, the correlations are positive between KO and VJ (0.445) but negative between KO and SV (-0.170). The regression of the maximum number indicates a significant declining trend (negative regression coefficient) for SV, while there was no significant trend for VJ and KO.

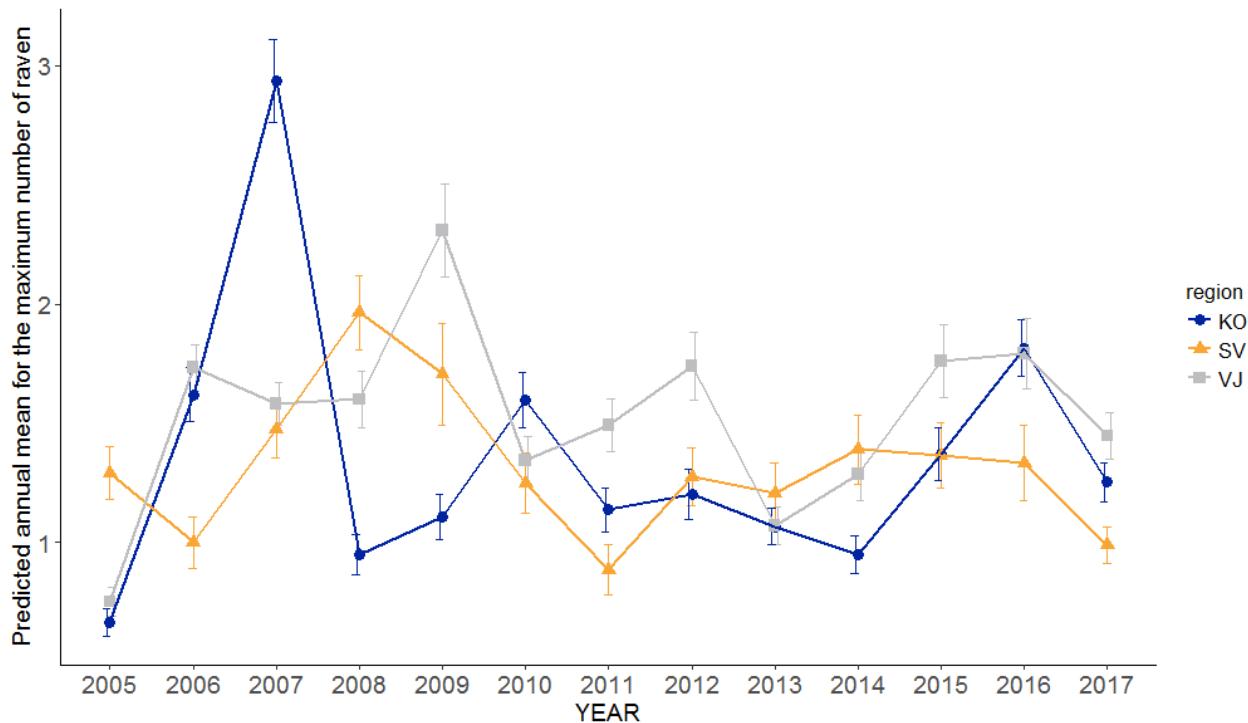


Figure 6. Time series of the maximum number of ravens counted in a picture in Finnmark, northern Norway for the three region of the study area (KO=Komag, SV=Stjernevann and VJ=Vestre Jacobslev). The annual estimates (with standard error bars) were obtained from the generalized linear model described in the Material and Methods.

Table 3. Statistics on spatial and temporal variation in the *maximum number of ravens* variable at the regional level. (**Mean**: mean value across years; **Trend**: Linear trend estimate (log scale); **CV**: Coefficient of variation; **AR1**:First order correlation; **Spearman Cross Correlation**: temporal correlation between region)

Variable	Region	Mean	Trend	CV	AR1	Cross corr
Maximum number	VJ	1.474 (SE= 0.031)	0.009 (SE= 0.005)	0.248	-0.162	KO: 0.445 SV: 0.346
	KO	1.354 (SE= 0.028)	-0.005 (SE= 0.005)	0.417	-0.102	VJ: 0.445 SV:-0.170
	SV	1.298 (SE= 0.036)	-0.018 (SE= 0.007)	0.220	0.477	VJ: 0.346 KO: :-0.170

To visualize the spatiotemporal features *within* the three regions (KO, VJ and SV), I displayed the annual maximum number of ravens counted in a picture at each camera site (Fig.7). The variation between camera sites in the same transect can be quite dramatic with, for example, a maximum of between two to three ravens seen at the camera site s3 in Stjernevann from 2006 until 2014 compared to more than 10 ravens counted two years in a row (2006, 2007) at the camera site s1.

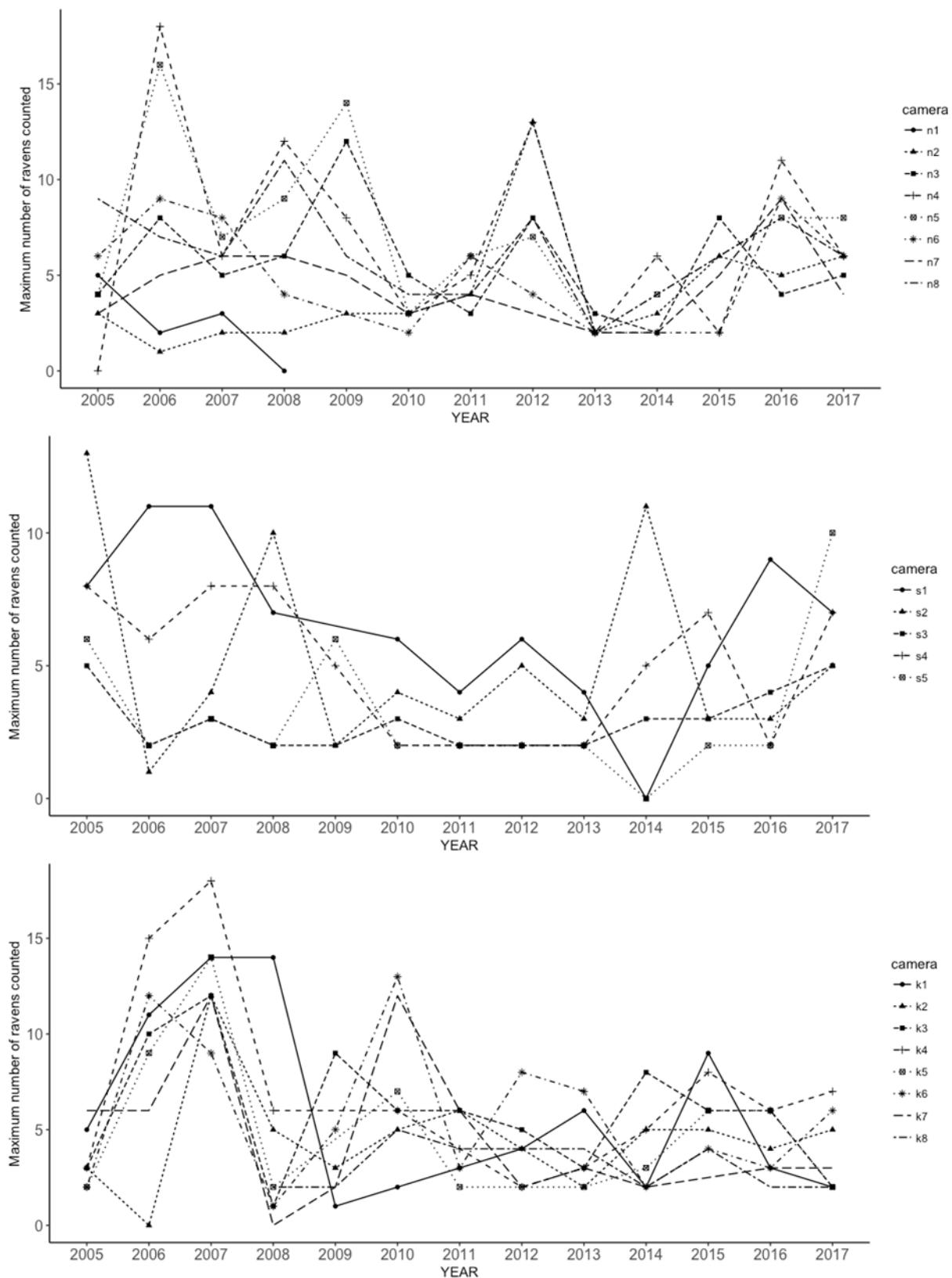


Figure 7. Times series of ravens in Finnmark, Northern Norway, based on the maximum number seen on a picture during the entire study period. Each graph illustrate a region, Nyborg (top), Stjernevann (middle) and Komag (bottom). Each lines represent a camera site within the region. Note that in Nyborg the camera n1 was removed after 2008.

Based on the results for the AIC, the most appropriate model for investigating the effects of the small rodents and the environmental gradients on the maximum number of ravens counted per day contained the covariates: altitude, julian day, proportion of pictures with bait and the rodent densities ($\Delta\text{AICc}=0.48$)(Appendix A, Table A.1). Similarly to the first response variable, the covariate representing the total carcasses wasn't included in the best model after AIC selection, thus we used the full dataset including year 2017 for the selected model.

The confidence intervals for the lemming abundance estimates included 0, which demonstrate low support for the lemming abundance the fall before on the predicted maximum number of ravens counted (Fig.8; Appendix A, Table A.2). However, the importance of the vole abundance the fall before on the predicted maximum number of ravens counted was statistically significant (Appendix A, Table A.2). If the number of voles the year before was to increase by one standard deviation, or 9.69 voles, the maximum number of ravens counted would be expected to increase by 1.107 [95%CI - 1.074 ; 1.138].

The altitude was not statistically significant as having an effect on the maximum number of ravens counted (Appendix A, Table A.2). The effect of the bait on the number seems to be the strongest one with an expected increase in the number of ravens counted of 1.481 [95%CI - 1.437 ; 1.528] if the proportion of pictures with the bait increase by one standard deviation (47%). There is supportive evidence that Julian days have an effect on the maximum number of ravens counted. That is, if the Julian day increases by 13 days (one standard deviation) in the season, the maximum number of ravens counted should increase by 1.058 [95% CI – 1.027 ; 1.089] (Appendix A, Table A.2).

The variance of the random intercepts indicates that the variation among the camera sites for the maximum number of ravens counted is quite small (0.0278).

Thus, the model selected was compared with the corresponding GLS model (generalized least squares model fit without the random intercept) and the AIC values suggested that the mixed model with the random camera site component was better despite that the effect is small.

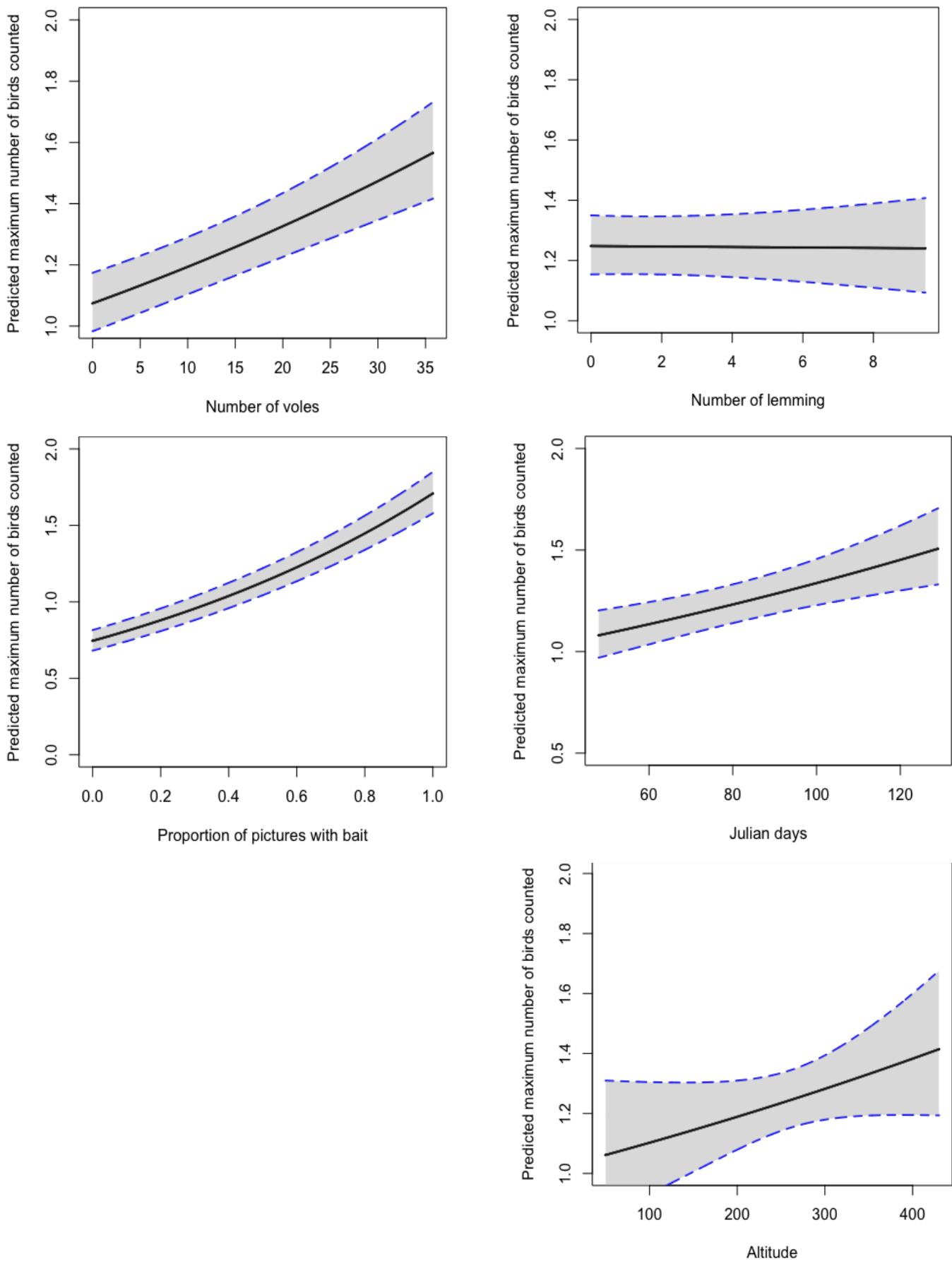


Figure 8. Predicted maximum number of ravens counted (95% CI) between 2005 and 2017 in Finnmark, Northern Norway, according to the abundance of voles and the abundance of lemmings **the fall before** (i.e. number of lemming/100 traps nights), the proportion of pictures with the bait, the progression in the study period (i.e. Julian days) and the Altitude.

3.2 Hooded crows

Figure 9 illustrates the time series of the estimated annual presence of hooded crows across the 13-year time series for the three study regions. There is temporal variation in these time series. The high values of the coefficient of variation reflect the elevated number of zeros (CV values in table 4; Fig. 9). These temporal fluctuations were not significantly auto-correlated within the series ($p>0.05$ for all AR1 coefficients in table 4) or significantly synchronous between series ($p>0.05$ for all Spearman rank correlation coefficients in table 4). The regression of the annual presence of hooded crows indicates no significant trend for the three region of the study area.

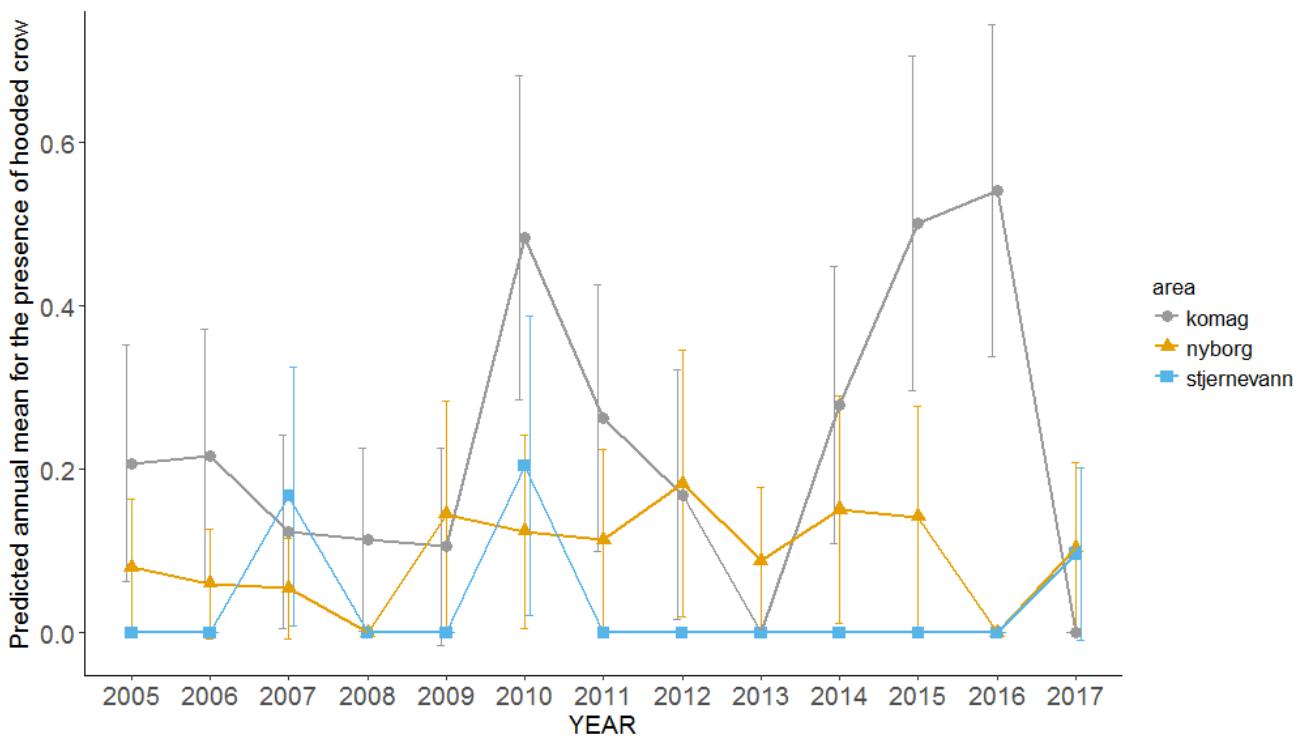


Figure 9. Time series of the annual presence of hooded crow in Finnmark, northern Norway for the three region of the study area (KO=Komag, SV=Stjernevann and VJ=Vestre Jacobselv).). The annual estimates (with standard error bars) were obtained from the generalized linear model described in the Material and Methods.

Table 4. Statistics on spatial and temporal variation in the *annual presence of hooded crow* variable at the regional level. (**Mean**: mean value across years; **Trend**: Linear trend estimate (logit scale); **CV**: Coefficient of variation; **AR1**:First order correlation; **Spearman Cross Correlation**: temporal correlation between region)

Variable	Region	Mean	Trend	CV	AR1	Cross corr
<i>Annual presence of crow</i>	VJ	0.104 (SE= 0.032)	0.029 (SE= 0.085)	0.587	0.022	KO: 0.087 SV:0.049
	KO	0.232 (SE= 0.046)	0.009 (SE= 0.066)	0.778	0.114	VJ: 0.087 SV: -0.032
	SV	0.044 (SE= 0.025)	0.022 (SE= 0.152)	1.998	-0.314	VJ:0.049 KO: -0.032

Similar to the ravens, the covariate representing the total carcasses wasn't selected in the best model after the AIC criteria selection. We used the full dataset including year 2017 for the model selected.

The model selected describing the probability of presence of hooded crows included altitude, number of days with bait, lemming abundance and vole abundance (Appendix C, Table C.1), but variation in the probability of presence of hooded crow in the peninsula resulted mainly from the variation in altitude (Appendix C, Table C.2). The probability of presence of crows is high at low altitudes (between 50 to 150 meters) and low at high altitudes (< 150 meters) (Fig.10). The effects of the number of days with bait, the abundance of voles and the abundance of lemmings were not statistically significant with 0 included in the confidence intervals, demonstrating low support for these effects on the probability of presence of hooded crows (Appendix C, Table C.2).

The variance of the random intercepts is quite large 2.993 telling us that variation among the camera sites is quite large for the hooded crow data.

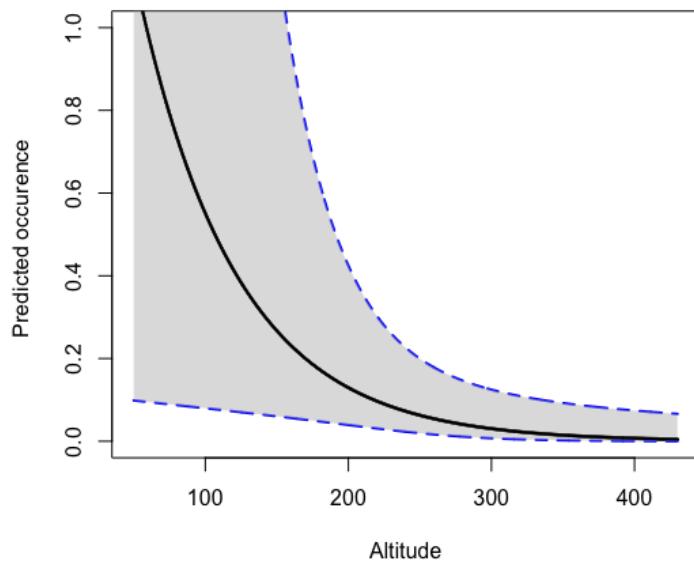


Figure 10. Probability of presence of hooded crow (95% CI) between 2005 and 2017 in Finnmark, Northern Norway, according to the altitude.

4 DISCUSSION

Spatial and temporal variation

This study is the first to assess the temporal and spatial dynamics of corvids in tundra ecosystems and the potential drivers, which might affect them. The 13-year time series shows that there is a great deal of temporal variation in the regional time series in Varanger peninsula. However, the temporal fluctuations for both species were not significantly auto-correlated within the series and there is no evidence of synchrony between the three areas. The estimated values showed a declining trend in the presence of ravens in Stjernevann. In addition, there was also a small declining trend in Komag and a slight increasing trend in Vestre Jacobselv. The hooded crow temporal fluctuations did not indicate any particular trend for the study area.

The influences of environmental gradients, likely to reflect the availability of potential resources from nearby ecosystems on the corvids distribution were analyzed in a similar way as in the paper from Killengreen et al. (2012). Here, the results for the ravens were the same with no spatial pattern related to the distance to the forest and coast. However, there was a small positive effect of altitude on the presence of ravens. In contrast with the results from Killengreen et al. (2012), I did not find any effects of forest on the presence of hooded crows. The coast did not seem to influence their distribution either but the range of altitudes examined had an effect on their presence at the camera sites. Hooded crows are tree nesters (Charles 1972, Yom-Tov 1974, Andrén 1992), and it is thus expected that they are present at lower altitudes where trees are present. Considering this, the absence of effect of forest on the presence of hooded crow could be due to the smaller amount of forested areas here compare to the study by Killengreen et al. (2012).

Different factors determine temporal fluctuations in abundance. There are “intrinsic” factors such as demographic strategies, density dependence or physiological characteristics that are specific to the species and there are “extrinsic” factors. The latter include food availability, weather, diseases and predator-prey interactions (Begon et al. 2006). In the Arctic, very few studies focused on the intrinsic processes and the effects of climate, diseases and predators on corvids population (Ratcliffe 1997). Most of the knowledge acquired on corvids is related to food (availability and identification) and behaviour (Heinrich 1989). Here, I investigated

whether two potentially important food resources, small rodents and reindeer carcasses, drive the corvids fluctuations in the ecosystems of Northern Fennoscandia.

Small rodents

The results for the lemming predictor variable were different for the two raven response variables. On the one hand, the maximum number of ravens seen in the pictures does not seem to be affected by the lemming dynamics. On the other hand, the results suggest that there is a weak negative relationship between the lemming dynamics and the relative presence of ravens. After a peak year, before the lemming population crashes, it is common to observe lemmings on the surface of the snow (Ims et al. 2017). I suggest that ravens might spend some time predating on them and thus spend less time at the bait which could explain the negative relationship with the presence of ravens.

Contrary to the main hypothesis based on the paper by Ims et al. (2013), the camera data indicated that the spatio-temporal dynamics of lemmings did not affect the corvids fluctuations on Varanger peninsula. However, the 13-year time series showed an increase in the presence of ravens in the entire study area after high vole densities in the fall. Ims et al. (2013) based their assumptions about corvids response to lemming dynamics specifically on the fact that they were the most prevalent nest predators during the rodent crash year in 2008, and that lemming abundance predicted nest predation rates the subsequent summer, whereas vole abundance did not. The discrepancy between their results and the results obtained here may be due to the difference in season. Ims et al. (2013) consider the nest predation rates in summer whereas here the corvids fluctuations were analysed in winter. I suggest that the summer following a lemming peak, the corvids come back to the areas that they remember to be abundant resources areas, but in the absence of high densities in small rodents, they predate on other preys such as eggs. Ims et al. (2013) based their conclusions on one lemming peak in 2007 that was also associated with a peak in tundra and grey-sided voles. Another study realized in the same system and same period as Ims et al. (2013), also found out a positive correlation of proportions of ravens on pictures with lemmings but suggested that it could be due to other factors as well (see below) (Killengreen et al. 2012). In this 13 year-time series, there were three vole peaks; the two first coincided with lemming peaks, while the last one occurred when there was no lemming peak evident. In addition, voles were more abundant than lemmings in the three regions. This shows that, here, ravens react to the availability of the most common small rodent as it is expected considering their opportunistic generalist

lifestyles. As for the hooded crows, their presence in the peninsula was not affected by the small rodent fluctuations. Thus, the assumption that the corvids' populations, as for specialized predators in this ecosystem such as the arctic fox (Ims et al. 2017), fluctuate specifically with the lemming cycles appears not to be supported here.

The response of corvids to small rodents in tundra ecosystems may be affected by the presence of mustelids and stoats. A study by Steen et al. (1997) focused on the cause of death of lemmings in late August in the mountainous area in Norway. They found out that most of the carcasses found had the skull crushed, which either mustelids, stoats or corvids can do. However, the mustelids usually leave a tooth mark on the skull of the rodent and eat the carcasses in a different way than the corvids. Most of the carcasses they found had tooth holes but were eviscerated and the heart and lung were eaten (which reflect ravens way of feeding). Thus, they propose that it could be that the mustelids kill the rodent first and then the ravens scavenge on it. They also found that the mustelids were killing more than their daily usual demand so they suggest that the corvids might scare the mustelid away and feed on the carcasses. Relating this to our study, not much is known about the impact of the mustelids and stoat in the tundra. Corvids are opportunistic generalists that were observed stealing food items such as lemmings or eggs from arctic fox caches or other birds nest (Careau et al. 2007, Erikstad et al. 1982). This and evidence from Steen et al. (1997) shows that corvids can adopt different foraging behaviour and feed on the resources that take the least energy and time to acquire.

Reindeer Carcasses

The statistical models did not reveal any impact of the relative amount of carcasses in eastern Finnmark on the dynamics of the corvid data. As ravens are probably the most specialized scavengers on ungulate carcasses (Heinrich 1989), a positive response of raven presence to carcass availability was expected. A previous study carried out in the same system reported an increase of the proportion of pictures with ravens with a peak in lemming density (Killengreen et al. 2012, Ims et al. 2011) and an increase in reindeer mortality over the first three years of the study (Anonymous 2008). Taking in account what I found, if the lemming abundance does not affect the ravens' dynamics significantly, it can be hypothesized that the reindeer mortality reflected as the number of carcasses in eastern Finnmark play a more important role in the dynamics of the ravens than acknowledge before. Here, it might be that the baits and the behavioural reaction of the ravens to them hide a clear positive effect of

carcasses on ravens' presence in the peninsula. As for the hooded crow, a more extensive examination of their dynamics will be necessary to reinforce the inferences made here. As done for another generalist in the same system, the red foxes, in the study by Killengreen et al. 2011, a diet analysis through pellets could be a good way of assessing the amount of carriions present in the diet of the two corvids species.

What responses of the corvids are reflected by the camera traps?

Camera traps give different information on the corvids such as the presence, number and behaviour of the birds. Here the dataset covers 13 years of camera trapping and reflects possible responses of the corvids. Considering the numerical response to small rodents, the trapping is done during the fall before the camera trap sampling period. Thus, a rodent peak represents an increase in food availability in the tundra before winter. This should lead to an increase in survival rates for both adults and the juveniles born the year before, and it can be seen on the cameras the spring after. The breeding success of the ravens could not be assessed here due to a mismatch between the time juveniles start flying and the actual period used for the camera traps sampling. Thus the sampling period should be moved to the late summer to determine if the breeding of the birds was successful (more juvenile will be seen around the carcasses). A study by Temple (1974) in Alaska, showed that the composition of ravens aggregating at a landfill change over the season with the juveniles arriving at the landfill to feed in the summer. The increase in the presence of raven the year following high rodent densities can also reflect an aggregative response. Thus, they should aggregate in patches with high prey densities (Yu & Englund 2010). Here, I suggest that they could aggregate in the fall during the high rodent densities and settle in the areas for the rest of the year.

An important challenge when studying birds such as corvids is that they are mobile animals inhabiting large home ranges. Non-breeding ravens are highly vagrant and well known for their large search radius (Ratcliffe 1997). However, they may gather at food sources and roosts at night for a varying amount of time (Heinrich 1989). Here, ravens are observed at baited camera traps. The fact that ravens are at the bait and the time they spend at the bait reflect a behavioural response. Two factor can affect this, learning (i.e. the bait were positioned at the same location each year) or the availability of other resources in the tundra (Killengreen et al. 2012). In this 13-year time series, the great deal of fluctuation in the maximum number of ravens seen between the camera sites and the declining trend in Komag

and Stjernevann give low support to the possibility of a learning behaviour. If learning was the main driver of the presence of raven, one would expect more stability through the years. Mostly, the corvids were seen in pairs on the pictures and despite the absence of identification, it is probably the same pairs seen through the years. Knowing that corvids' pairs are territorial, the presence of the camera site in one of the pairs' territory could explain their omnipresence at the bait. However, the camera data presented in this study does not allow to distinguish between numerical, aggregative or behavioural responses, all of which could also co-occur.

The low number of observations with hooded crows suggest that the distribution of the camera sites was not the most appropriate to assess their fluctuations. An expansion of the study area including areas at a lower altitude or close to the forest edge could be suggested for further study of hooded crow dynamics in the tundra of Northern Fennoscandia. Another factor is that their breeding season starts in late April. This may have an impact on the presence of crows at the camera sites since it has been found that crows travel less in search of food, and spend more time in the forest building their nest during this time (Charles 1972). Also, some of the hooded crow living in the tundra migrate to the south for the winter and come back around March (Haftorn 1997, Heinrich 1989) which coincide with the beginning of the sampling season of this study.

The estimates used in this study are assumed to reflect the relative abundance of corvids but are not true estimates of the corvids abundance. The likelihood that an individual is photographed depends on the number of corvids present at the camera site on this particular day and the lengths of time spend on or around the bait. It is likely that the same individual is recorded multiple times during the sampling season. In the absence of identifications of the individuals, the detection of an animal reflects both the number and the behaviour of the birds (Burton et al. 2015). In other studies occupancy analysis has been used to analyze camera trap data to take into account imperfect detection and repeated observations of the same individual (e.g. Hamel et al. 2013). Occupancy estimates the proportion of sites occupied by a species taking into account the probability of detection and assuming closed populations at each sampling site (Mackenzie et al. 2006). However, for long surveys and when working with highly mobile species the closure assumptions is likely to be violated (Hamel et al. 2013). Occupancy reflects then habitat use, but the relationship of this estimate to abundance is also unclear, as for the response variables used here. In addition, because ravens were observed at

nearly all cameras in all years, occupancy estimates would have been saturated for this species.

Here, different response variables were used as proxies of abundance. For the ravens, the relative presence represented as the proportion of pictures per day with ravens present at each camera site, and the maximum number of individuals counted in a picture per day at each camera site, were assumed to reflect the relative abundance. For the hooded crow, the annual presence was estimated. The maximum number of individuals counted seems to be quite reliable as a proxy of abundance as it reflects the number of individuals present at a particular time and site. However, it has its own limitations, counting birds on a picture is easy when there are one or two, but as soon as flocks of ravens appear, it gets much harder to distinguish each individuals. Moreover, because the birds are not marked it might be the same flocks of ravens moving around the peninsula at different time and sites. The relative presence of the ravens and hooded crows is a useful indication of habitat use. Habitat use reflects the availability of resources and is also closely related to population abundance. Here, I studied the corvids response to fluctuating abundance of resources in Varanger peninsula and the relative presence of corvids in the pictures combine with the maximum numbers provide a reasonable proxy for overall abundance. Except for the lemmings, the overall results for the ravens were congruent.

Further studies might want to include the time the picture was taken when looking at the maximum numbers of ravens counted. It is then possible to compare if the pictures were taken at the same time but at a different site and thus reflect relative abundance or if they were taken at different sites and at different times that does not allow distinguishing between different flocks or same one.

5 CONCLUSION

The study of the 13-year time series reveals that there are considerable temporal and spatial variations in corvids' dynamics in Varanger. The time series show that the ravens respond to vole density fluctuations but not to lemmings. For hooded crows, on the contrary, there is no evidence that small rodents play a role in their population dynamics. Despite the major role that small rodents, and in particular lemmings, play in the ecosystem of northern Fennoscandia, it seems that they are not the only driver of corvids' fluctuations. Corvids are well-known for their scavenging and opportunistic behavior, thus it is difficult to assess what exactly is driving their temporal variations across the different regions. Their behavior and demography in the tundra of northern Fennoscandia remain unstudied. This is the first study to assess temporal and spatial fluctuations in the corvids dynamics. The growing presence of these generalist predators has a negative impact on nesting birds, such as ptarmigans living in these areas. It's been shown that ptarmigans' nests have higher chances of being predated when close to hooded crow's nests, and that territorial hooded crows and ravens were the most important predators on ptarmigans' nests. Knowing that there is a great deal of temporal and spatial variation in corvids' dynamics, future studies should further investigate the causes of these fluctuations and the impact it has on the entire ecosystem of northern Fennoscandia.

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7 APPENDIX

Appendix A

Table A.1 Model selection for analysis of the maximum number of ravens seen. For each model the number of parameters (K), AICc and the difference in AICc to the best model (Δ AICc) are presented. The selected model is shown in bold and correspond to the one with the lowest Δ AICc and the highest weight.

Models	K	AICc	Δ AICc	weight
altitude + julianday + lem + prop_pict_bait + vole	8	23796.03	0.00	0.15
julianday + lem + prop_pict_bait+ vole	7	23796.51	0.48	0.12
distroad+ julianday + lem + prop_pict_bait + vole	8	23796.99	0.96	0.09
altitude + julianday + lem + prop_pict_bait + totalcarc + vole	9	23797.05	1.02	0.09
altitude + distforest + julianday + lem + prop_pict_bait + vole	9	23797.38	1.35	0.08
julianday + lem +prop_pict_bait+ totalcarc + vole	8	23797.49	1.46	0.07
altitude + distroad+ julianday + lem + prop_pict_bait +vole	9	23797.70	1.67	0.07
distroad+ julianday + lem + prop_pict_bait + totalcarc + vole	9	23797.99	1.96	0.06

Table A.2 Summary of the estimates describing variation in the predicted maximum number of ravens seen between 2005 and 2017 in Varanger peninsula, Northern Norway.

Fixed Effects				
Variable	Estimate	P.value	95% CI	
(Intercept)	0.220	<0.001	[0.144 ; 0.297]	
Altitude	0.065	0.104	[-0.013 ; 0.144]	
Julian day	0.057	<0.001	[0.027 ; 0.086]	
Lemming	-0.001	0.917	[-0.029 ; 0.026]	
Proportion of pictures with bait	0.393	<0.001	[0.363 ; 0.424]	
Vole	0.102	<0.001	[0.072; 0.131]	

Random Effect		
	Variance	Std.Dev.
camera (Intercept)	0.02788	0.167

Appendix B

Table B. Parameters estimates of different models for the analysis of the proportion of pictures with ravens. The analysis was realised using GLMMQL and the covariates for the small rodents abundance indices and the different environmental gradients were included. No model selection was realised but the different estimates and their confidence intervals were calculated (95% CI). Note that the covariates altitude, julian day, proportion of pictures with bait and the small rodents area mostly stable through all the 9 models tested.

Variables	Models								
	(1) A + DF + DR + JD + L + PB + V	(2) DF + DR + JD + L + PB + V	(3) DR + JD + L + PB + V	(4) DB + L + PB + V	(5) L + PB + V	(6) A + L + PB + V	(7) A + JD + L + PB + V	(8) A + DR + JD + L + PB + V	(9) A + DF + JD + L + PB + V
Altitude (A)	0.160 (-0.013;0.333)	-	-	-	0.182 (0.050;0.314)	0.176 (0.041;0.311)	0.171 (0.029;0.314)	0.172 (0.020;0.324)	
Distance to forest (DF)	-0.018 (-0.178;0.140)	-0.102 (-0.244;0.039)	-	-	-	-	-	-0.008 (-0.151;0.134)	
Distance to road (DR)	0.023 (-0.129;0.175)	0.090 (-0.054;0.235)	0.066 (-0.081;0.214)	-	-	-	0.015 (-0.121;0.151)	-	
Julian Day (JD)	0.071 (0.034;0.107)	0.072 (0.035;0.109)	0.072 (0.036;0.109)	0.072 (0.035;0.109)	-	0.070 (0.034;0.107)	0.071 (0.034;0.107)	0.070 (0.034;0.107)	
Lemming (L)	-0.065 (-0.101;-0.029)	-0.065 (-0.101;-0.029)	-0.063 (-0.099;-0.027)	-0.063 (-0.099;-0.027)	-0.062 (-0.098;-0.026)	-0.064 (-0.100;-0.028)	-0.065 (-0.101;-0.029)	-0.065 (-0.101;-0.029)	-0.065 (-0.101;-0.029)
Proportion picture with Bait (PB)	0.687 (0.644;0.731)	0.687 (0.644;0.731)	0.688 (0.644;0.731)	0.688 (0.644;0.731)	0.664 (0.622;0.706)	0.664 (0.622;0.706)	0.687 (0.643;0.731)	0.687 (0.644;0.731)	0.687 (0.644;0.731)
Vole (V)	0.123 (0.087;0.160)	0.124 (0.087;0.160)	0.122 (0.086;0.159)	0.122 (0.085;0.158)	0.115 (0.079;0.152)	0.116 (0.080;0.153)	0.123 (0.086;0.159)	0.123 (0.086;0.159)	0.123 (0.086;0.160)

Appendix C

Table C.1 Model selection for analysis of the presence of hooded crows. For each model the number of parameters (K), AICc and the difference in AICc to the best model (ΔAICc) are presented. The selected model is shown in bold and correspond to the one with the lowest ΔAICc and the highest weight.

Models	Df	AICc	ΔAICc	weight
altitude + baitnbd + lem + vole	6	149.57	0.00	0.17
altitude + lem + vole	5	150.13	0.56	0.13
altitude + baitnbd + distroad + lem + vole	7	151.11	1.54	0.08
altitude + baitnbd + lem + totalcarc + vole	7	151.29	1.71	0.07
altitude + distroad + lem + vole	6	151.42	1.85	0.07
altitude + baitnbd + distforest + lem + vole	7	151.63	2.06	0.06

Table C.2 Summary of the estimates describing variation in the predicted presence of hooded crow between 2005 and 2017 in Varanger peninsula, Northern Norway.

Fixed Effects			
Variable	Estimate	P.value	95% CI
(Intercept)	-2.960	<0.001	[-4.586 ; -1.951]
Altitude	-1.253	0.018	[-2.586 ; -0.248]
Number of days with bait	0.372	0.123	[-0.093 ; 0.863]
Lemming	-0.653	0.079	[-1.498 ; -0.003]
Vole	0.124	0.637	[-0.394 ; 0.653]

Random Effect		
	Variance	Std.Dev
cam (Intercept)	2.993	1.73