



BIO - 3910

Master's Thesis in Ecology

Predation on artificial ground nests in a subarctic ecosystem



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May 2008

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Kristin Brekke Klausen

Abstract

Studies of gallinaceous bird species stress the importance of high nest losses as a factor influencing life histories and populations. Accordingly knowledge of the mechanisms affecting nest losses is essential for understanding the population dynamics. The aim of this one year study was to estimate predation rates on artificial ground nests in ptarmigan habitats, along a landscape gradient which spans from subarctic birch forest to the low-alpine zone. We particularly wanted to investigate the importance of red fox (*Vulpes vulpes*) as a nest predator, and the study area was divided in three sub-areas according to the red fox density recorded during a winter snow track survey. Artificial nests (track boards) were placed in three different habitats (birch, edge and low-alpine). Vertical vegetation structure along the gradient from the birch forest to the low-alpine zone was surveyed and analyzed to assess how the forest structure could affect the predation rates. Predation rates resulting from different species were analysed using logistic regression models.

Total predation rates over all habitats, locations and periods ranged from 47.4 % to 77.5 % and were remarkably constant over all variables. Predation by avian predators was consistently high over both trial periods (59.1 %) and mammalian predation was consistently low (5.6 %). The constant predation rate was mainly due to omnipresent corvids, especially the hooded crow (*Corvus cornix*), which dominated among the predators in all habitats and locations in the study. The high predation by avian relative to mammal predators may be due to differences in landscape use and searching effort. Differences between locations were insignificant for all species except for raven (*Corvus corax*) that showed significantly higher predation between two of the locations. Red fox played a minor role as nest predator and no relation between nest predation rates and red fox density was documented. From the perspective of nest predation risk on ground nesting birds like willow ptarmigan (*Lagopus lagopus*), they would not be expected to be selective with respect to nesting habitats.

Key words:

Artificial nest, corvids, habitat, predation, ptarmigan, red fox, subarctic birch forest

Content

1	Introduction	9
2	Material and method.....	13
2.1	Study area	13
2.1.1	Vertebrate community	15
2.2	Snow track survey	15
2.3	Experimental track boards.....	16
2.4	Vegetation structure	17
2.5	Statistical method	19
3	Results	21
3.1	Structural characteristic of the ecosystem.....	21
3.1.1	Vertebrate community.....	21
3.1.2	Vegetation structure	22
3.2	Predation rates	24
3.2.1	Spatial relation between predator species	26
4	Discussion.....	27
5	References	31

1 Introduction

Studies of gallinaceous bird species stress the importance of high nest losses as a factor influencing life histories and population dynamics (Angelstam et al. 1984, Parker 1984, Moss and Watson 2001, Baines et al. 2004). Accordingly knowledge of the mechanisms affecting nest losses is essential for understanding the population dynamics. Several studies have revealed that the most important cause for nest losses in ground breeding bird species is predation (e.g. Angelstam et al. 1984, Storch and Willebrand 1991, Hewitt et al. 2001), whereas climatic conditions play a more modest role (Sandercock et al. 2005).

Nest predation rates typically vary in both time and space. While studies of temporal variation have mainly focused on functional responses of predators, often in conjunction with switching from main prey to alternative prey (Myrberget 1974, Angelstam et al. 1984, Wegge and Storaas 1990), studies of spatial variation have mainly focused on habitat specific predation rates (Andrén et al. 1985, Storaas and Wegge 1987, Andrén and Angelstam 1988, Andrén 1992). Variation in predation rates among different habitats might result from differences in sheltering of nesting sites, density and type of predators and their prey (Andrén et al. 1985, Andrén 1989;1992, Schieck and Hannon 1993). The type and amount of edge habitat is one important landscape characteristic related to predation rates, and predation risk is documented to increase along edges (Gates and Gysel 1978, Andrén and Angelstam 1988, Batàry and Bàldi 2004, Ries et al. 2004). However, many nest predation studies have failed to detect edge effects, and state that degree of fragmentation and type of landscape, accordingly the habitat at a large scale, influence the predation rates (Angelstam 1986, Andrén 1989;1992, Lahti 2001, Storch et al. 2005). Studies have found that vegetation cover influences nest predation by affecting nest concealment, impeding predator movement and possibilities for prey to escape from predators (Schieck and Hannon 1993, Wiebe and Martin 1998, Manzer and Hannon 2005), whereas others studies find no evidence of advantages related to vegetation cover (Erikstad et al. 1982, Myrberget 1985, Brittas and Willebrand 1991, Munkebye et al. 2003).

This discrepancy may be caused by the fact that the relative importance of habitat type, vegetation cover and edge on predation rates may depend on the type of predators present, and how they use the landscape for prey searching (Andrén et al. 1985, Angelstam 1986,

Andrén 1989; 1992). Mammalian predators such as red fox (*Vulpes vulpes*) and mustelids (*Martes spp. and Mustela spp.*) relay mainly on olfactory cues to detect their prey (Whelan et al. 1994, Rangen et al. 2000), whereas avian predators such as corvids use visual cues (Picozzi 1975). Generalist predators are typically habitat generalists, and can be found in nearly all types of habitat. In contrast specialist predators are more restricted to the same habitat as their main prey (Ryall and Fahrig 2006). Several studies have also suggested that the density of generalist predators increases as the forest landscape becomes fragmented and interspersed with agriculture (Andrén et al. 1985, Angelstam 1986, Andrén 1989; 1992, Kurki et al. 1998, Kurki et al. 2000).

In northern Norway ptarmigans breeds in a range of different habitats, from sea level up to the low- and mid-alpine zones. The willow ptarmigan (*Lagopus lagopus*) is found in the lowest habitats, and the rock ptarmigan (*Lagopus muta*) in the highest, with to some extent overlapping ranges in the low- and mid-alpine zones (Andersen 1986, Pedersen and Karlsen 2007). They are both important components of subarctic birch forest and alpine ecosystems, were they particularly fill the role as prey for many of the avian and mammalian predators (Erikstad et al. 1982, Myrberget 1985, Munkebye et al. 2003). Ptarmigans are also the most popular small game species in Norway, and much effort have been invested in finding ways to manage populations in an ecological sustainable way (Brøseth and Pedersen 2000, Pedersen et al. 2002, Pedersen and Karlsen 2007). The most common nest predators in ptarmigan habitats are the generalist corvid species (*Corvus corax*, *C. cornix*, *Pica pica*), red fox and mustelids (*Martes martes*, *Mustela vison*) and specialist mustelids (*M. erminea*, *M. nivalis*) (Myrberget 1984, Angelstam 1986, Frafjord 2004). Most of the nest predation studies on gallinaceous birds are performed on forest grouse species (*Tetrao spp.*) in boreal and temperate forest ecosystems (e.g. Storaas and Wegge 1987, Marcström et al. 1988, Storaas et al. 1999, Baines et al. 2004). Only few studies we are aware of have focused on nest predation on ptarmigan in Arctic and subarctic ecosystems (Erikstad et al. 1982, Wiebe and Martin 1998, Munkebye et al. 2003, Sandercock et al. 2005, Wilson et al. 2007), and none have studied habitat specific predation rates resulting from different predator species. Studies on life histories and population dynamics on ptarmigan in Norway are mostly performed in the southern part of Norway (e.g. Erikstad et al. 1985, Myrberget 1985, Erikstad 1986, Phillips et al. 1992, Munkebye et al. 2003), although the largest populations of ptarmigan are found in the northern part of Norway according to hunting statistics (Statistics Norway 2008), hence more knowledge of limiting factors in these areas are of high importance.

The aim of this study was to study habitat specific predation on artificial ground nests in ptarmigan habitats, along a landscape gradient spanning from subarctic birch forest to the low-alpine zone. The gradient is characterised by large variation in vegetation composition and structure, and probably also in different predator and prey composition. Thus, a consistent variation in predation pressure and those predators responsible for predation could be expected. The epizootic sarcoptic mange (*Sarcoptes scabiei*) in the late 1970s and 1980s demonstrated that red fox was an important predator on grouse species (Lindström et al. 1994). Following this we particularly wanted to investigate the role of red fox as a nest predator, to assess how the strong increase in red fox populations after the recovery from the mange epidemic can affect the ptarmigan. To achieve this, the study area was divided in three sub-areas according to the red fox density recorded during a winter snow track survey.

2 Material and method

2.1 Study area

The study was performed in the municipalities of Tromsø, Balsfjord and Karlsøy (69° N, 18-19° E) in Troms County in Northern Norway (Figure 1). The study area was further divided in three sub-areas covering the mainland of Tromsø municipality (hereafter called Mainland) and two large islands, Kvaløya and Ringvassøya. The study area lies in the subarctic birch forest and the low-alpine zone.

The forests are dominated by mountain birch (*Betula pubescens*). In areas with rich soil, rowan (*Sorbus aucuparia*) and willow species (*Salix spp.*) are also found, whereas in areas with poorer soil common juniper (*Juniperus communis*) is often present. The forest reaches to the tree line, approximately 400 m.a.s.l. on the Mainland and approximately 200-300 m.a.s.l. on the islands, but the altitude of the tree line is highly variable over short distances due to a rugged topography. The edge habitat between the birch forests and the low-alpine zone consists mostly of low growing birch and willow. The bottom- and field layer in the birch forest and edge habitat are dominated by mosses, shrubs, different tall and low growing herbs and grasses. The low-alpine zone reaches from the tree line to the upper altitudinal limit of the dwarf shrubs and heath. This habitat is characterized by alteration between barren ridges, lee-sides and snow bed vegetation, and dominated by nutrient poor species like mosses, lichens and heath (Moen 1998, see also Figure 3).

The area between sea level and the base of the mountains on the Mainland is wider than on the islands, and consequently a more extensive vegetation zone is present before reaching the steep and rugged mountains. In general, there are small sparse settlements along most of the coastline in the study area. The climate is typically subarctic oceanic with cool summers (mean July 11.8°C) and mild winters (mean January temperature -3.4°C). Annual precipitation varies between 850-1450 mm, and the area is usually snow-covered from October until May (Norwegian Meteorological institute 2008, data from 1961-1990).

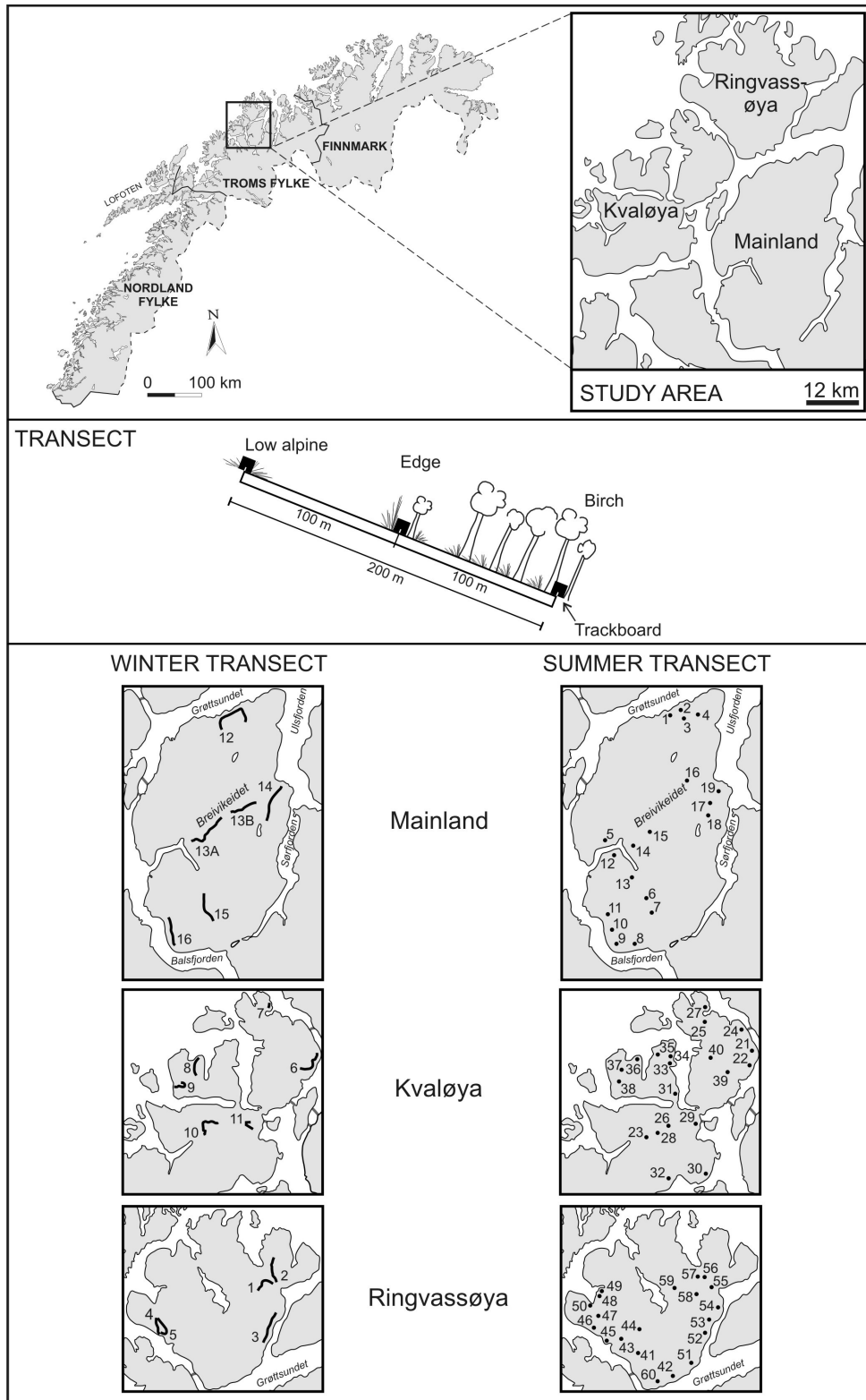


Figure 1. Upper panel: Map of northern Norway with inset showing the study area with the three sub-areas covering the Mainland, Kvaløya and Ringvassøya. Middle panel: Drawing showing the transect design with placement of baited track boards along the landscape gradient (birch, edge, low-alpine). Lower panel: Map of the three sub-areas with approximate placement of snow track transect lines in winter and baited track boards in summer. Numbers refer to respective transect or track board.

2.1.1 Vertebrate community

Ground breeding birds in the study area are among others black grouse (*Tetrao tetrix*), willow ptarmigan, rock ptarmigan, waders and passerines (Erikstad et al. 1982, Parker 1984, Hogstad 1991 a; b;1992). Mammalian nest predators are mainly the generalist red fox and pine marten and the specialists, stoat and least weasel. Other potential predators are otter (*Lutra lutra*) and mink (Erikstad et al. 1982, Parker 1984, Johansson and Frislid 1990, Frafjord 2004). Pine marten and least weasel are only located on the Mainland. The Mainland contains a higher density of red fox than Kvaløya, and red fox is not documented on Ringvassøya. Avian nest predators are raven, hooded crow and black-billed magpie (Erikstad et al. 1982, Parker 1984, Hogstad 1992). Beside ground breeding birds important prey species are mountain hare (*Lepus timidus*) (only located at the Mainland and southern Kvaløya) and small mammals. On the Mainland the small mammal community consists of Norwegian lemming (*Lemmus lemmus*), red vole (*Myodes rutilus*), field vole (*Microtus agrestis*), grey-sided vole (*Myodes rufocanus*), common shrew (*Sorex araneus*) and pygmy shrew (*S. minutus*). On Kvaløya and Ringvassøya the small mammal community consists of the two first mentioned above in addition to root vole (*Microtus oeconomus*) (Yoccoz and Ims pers comm., personal observations). Moose (*Alces alces*) and domesticated reindeer (*Rangifer tarandus*) are also found in the study area.

2.2 Snow track survey

Snow tracking has been used in many studies to investigate relative abundance and estimate population sizes of mammals and ground dwelling birds (e.g. Thompson et al. 1989, Kauhala and Helle 2000, Frafjord 2004, Linnell et al. 2007). Understanding spatial patterns of predation requires information about the predator and prey community, thus a snow track survey was performed in the study area from February 14th to March 4th 2007. We selected systematically 17 transects for snow tracking on the Mainland (n = 6), Kvaløya (n = 6) and Ringvassøya (n = 5). The lengths of each transect varied from 1 to 7.9 km, and the total length for Mainland, Kvaløya and Ringvassøya was 26.3, 21.3 and 24.0 km respectively. Each transect was placed approximately 100 m below the tree line in to obtain information about the composition of the vertebrate community in the areas where artificial ground nests were to be placed in summer. Transect lines were surveyed at a minimum of 24 hours since last snowfall (Lindèn et al. 1996).

Tracks were registered by 9 observers on skis, and the positions of all tracks crossing the transect lines were recorded by a GPS unit (GARMIN GPS, eTrex). Tracks of predators registered within 1.5 meter from the ski track were considered as a crossing. Tracks of mammals and birds were determined to species according to Aronson and Eriksson (1992) and Bang (2000). Small mammals were classified as voles (field vole, red vole, root vole and grey-sided vole), Norwegian lemming and shrew (common shrew and pygmy shrew), due to difficulties distinguishing the tracks from these species on snow. A track index for each species was calculated as number of tracks crossing the transect line per kilometre line and corrected for days since last snowfall (Lindèn et al. 1996).

2.3 Experimental track boards

To identify the predators present and the relative predation rates, we used artificial ground nests (n = 180). Nest studies with suitable design, although the nest is neither defended by adult birds or concealed as natural nests, can give information about predator assemblage and relative predation rates (Angelstam 1986, Storch 1991), despite their many shortcomings (King 1999, Thompson et al. 1999, Burke et al. 2004, Moore and Robinson 2004). We selected 60 transects for placement of artificial nests in the study area, and distributed 20 transects on the Mainland, Kvaløya and Ringvassøya respectively. The transect represents a natural gradient in vegetation composition and structure from the birch forest to the low-alpine zone. Selection of transects were based on the following criteria's: a) short distance and possibility to walk to the tree line, b) minimum of 2-3 km between each transect, and c) minimum of 2-3 km from settlements or popular leisure areas to minimize human disturbance. Hence, random sampling was not possible owing to steep and rugged terrain, making both walking to the transects and placement of artificial nests difficult. A transect consist of three artificial nests placed along a 200 m long line perpendicular to the tree line (Figure 1). One nest was placed in each end of the line, 100 m into the birch forest and the low-alpine zone respectively, and the last nest at the centre of the line coinciding with the tree line (edge habitat). The tree line was defined as the boarder line where there are scattered trees with height less than 2 m (Børset 1962).

Each artificial nest consisted of one track board (0.6 × 0.6 m, 3 mm thick chip board) and the boards were baited with one common quail (*Coturnix coturnix*) egg in the middle. The track board was smeared with a thin layer (approximate 2- 3 mm) of non-toxic lubrication grease (Mobile grease FM 102) and covered with a thin layer of soil (0.5 l), to ensure that predators

would leave tracks when removing the egg (Angelstam 1986). The forest- and edge track boards were placed under a tree or shrub in order to increase cover, but there were no cover in the low-alpine habitat. The track boards were only slightly concealed with surrounding vegetation in the field layer and highly visible for predators using visual cues. Mammalian predators using olfactory cues can locate nests after visits of an investigator (Whelan et al. 1994). We attempted to minimize human scent by wearing rubber boots within a distance of 100 m, leaving field equipment 10 m from the track board, and used plastic gloves and bags when handling the soil, eggs and boards. Since hooded crows can develop search images for nests (Picozzi 1975, Sonerud and Fjeld 1984; 1987) there was no marking of the nests, and the nests were located with a GPS unit (GARMIN GPS, eTrex).

The nests were exposed to predators for two consecutive trial periods of 10 days and each nest was checked after 10 days of exposure. Furthermore, each nest was set out in the beginning of June (1. period starting on 2nd of June and 2. period on 12th of June 2007), coinciding with the incubation period of many ground nesting birds. When preparing the nests for a new trial period additional grease and soil was supplied when needed, and the same procedure used in the first trial was repeated. The egg was considered predated if the egg was missing or damaged. Nests never found or disturbed by domestic sheep or cattle were registered as missing data. Tracks of mammalian predators were determined to species according to Aronson and Eriksson (1992). Stoat and least weasel can in some cases be hard to distinguish and incorrect registrations can occur. Avian predators were identified according to Bang et al. (2000) and hooded crow and raven foot samples were measured according to Pedersen et al. (submitted).

2.4 Vegetation structure

Nest cover, i.e. surrounding vegetation can affect nest predation rates (Schieck and Hannon 1993, Wiebe and Martin 1998, Manzer and Hannon 2005). Therefore we analysed the vertical vegetation structure along the transect to assess how the forest structure vary along the landscape gradient. The vegetation variables (Table 1) were measured along the transect line in a unit of 2 m, with the midpoint of the track board as the centre of the first and last measuring unit. This was repeated every 10 m along the transect, in total 21 sampling stations (Figure 2). Vegetation variables (Table 1) were classified in the following layers: bottom (ground level), field (< 1 m), shrub (0-2 m) and tree layer (0-2 m, 2-4 m and 4-10 m). The most dominating species or species group in each vegetation layer, intersecting the unit of 2 m, was recorded.

Table 1. Classification of vegetation variables in four vertical layers.

Category	Variable	Species/Group
Bottom layer		
Ground level	moss	moss/lichen
	hl	herb litter
	ll	leaf litter
	open	open field
	wa	water
	snw	snow
Field layer		
< 1 m	tall.herb	tall herb
	low.herb	low herb
	grass	grass
	bilberry	bilberry shrub
	heath	heath
	srh	sedge/rush/horsetail
	cotton	cotton grass
Shrub layer		
0- 2 m	dwarf.b	dwarf birch
	jun.	juniper
	prost.will	prostrate willow
	will	other willow
Tree layer		
0- 2, 2- 4, 4-10 m	b	birch
	d	other deciduous trees
	dead	dead trees

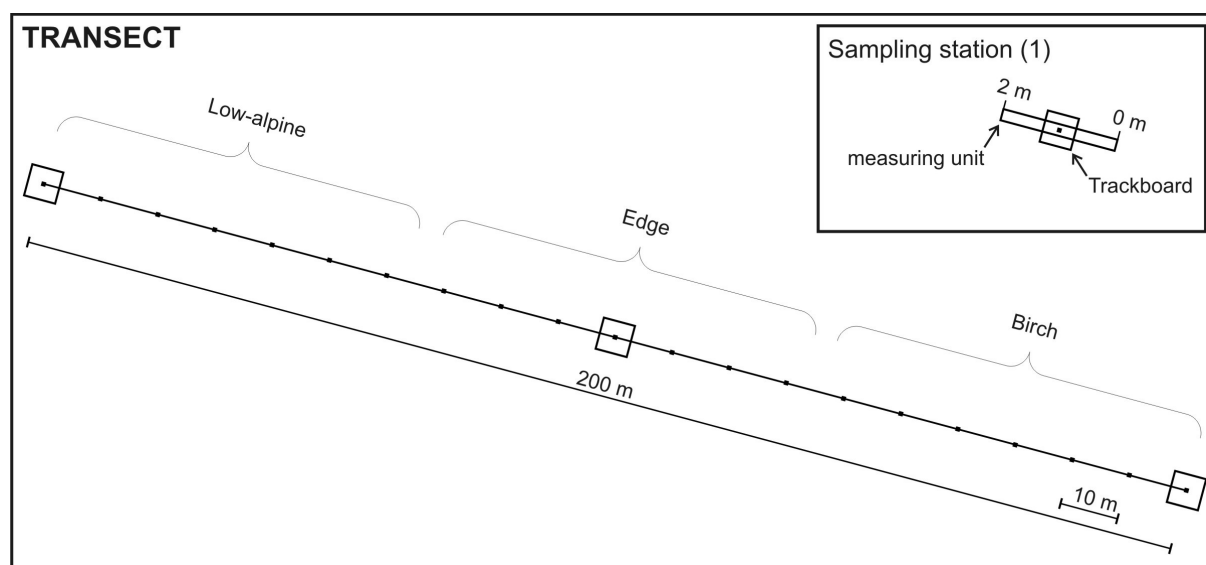


Figure 2. An example of a transect line with the distribution of 21 sampling stations. Inset showing sampling station 1 (birch habitat) with the measuring unit of 2 m on the track board.

2.5 Statistical method

Predation rates resulting from the different predator species were analysed using generalised linear mixed effect models assuming a binomial distribution for the response variable (Lewis 2004). Models were fitted in R (R Development Core Team 2008) using the lme4 package (Pinheiro and Bates 2000) and transects were treated as random factor in the analysis. The following design variables were included as fixed predictor variables: *Period* (two consecutive trial periods of 10 days), *location* (Mainland, Kvaløya, Ringvassøya) and *habitat* (birch, edge, low-alpine). Only two-way interactions considered to have biological importance were included in the analysis (*period*location* and *location*habitat*). All possible model combinations were tested using the library (dRedging) in R. Model selection was performed using the Akaike's Information Criterion corrected for small sample size (AIC_c) and AIC_c-weights (Anderson and Burnham 2002, Burnham and Anderson 2004). Variable importance (VI) was assessed using the sum of the AIC_c weights for the models including this variable (Anderson et al. 2001). Among the predators identified with certainty, we had only sufficient data for statistical analysis of predation rates of the avian predators; hooded crow, black-billed magpie and raven. For comparing locations or habitats, estimates of effect sizes are given as odds ratios (OR) with 95 % confidence intervals (CI). Spearman's rank correlation coefficients based on transect specific predation were computed to test for potential correlation between presence of different predator species at the transect level (n = 60). For this analysis data were aggregated over habitats and periods within transects, excluding eggs eaten or removed by domestic animals and other unidentified sources.

To analyse the vegetation at habitat level (birch, edge, low-alpine) the variables were averaged over sampling stations 1-7 to characterize the birch habitat, sampling stations 8-14 to characterize edge habitat and sampling station 15-21 to characterize low-alpine habitat (Figure 2). The vegetation data was processed by fuzzy coding procedures (Chevenet et al. 1994) to identify the underlying structure of the vegetation composition based on the vegetation variables (see Table 1). The resulting frequencies were further analysed by a Principle Component Analysis (PCA) (Jongman et al. 1995), with respect to instrumental variables (PCAIV) (Rao 1964), implemented in the ade4 package for R (Chessel et al. 2004). The instrumental variables were *habitat* (birch, edge, low-alpine) and *location* (Mainland, Kvaløya, Ringvassøya).

3 Results

3.1 Structural characteristics of the ecosystem

3.1.1 Vertebrate community

Snow tracks from 9 mammal species/species groups (red fox, pine marten, stoat, least weasel, mountain hare, voles, Norwegian lemming, shrew and moose) and 2 bird species/species group (black grouse and ptarmigan) were recorded during the study period. In addition we also recorded domestic reindeer. The Mainland contained most species/species group (8), followed by Ringvassøya (6) and Kvaløya (5). The highest total track index (all species) were recorded at the Mainland (55.7 track index), followed by Kvaløya (54.0 TI) and Ringvassøya (49.5 TI) (Table 2). The dominant predator species for the entire study area was stoat, followed by red fox. Kvaløya contained the highest amount of stoat, followed by Ringvassøya and the Mainland. As expected the density of red fox tracks was higher on the mainland than on the islands. The dominant prey species for the entire study area was ptarmigan, followed by shrew and voles. The Mainland had the highest amount of ptarmigan, while Kvaløya and Ringvassøya had the highest amount of shrew and vole (Table 2).

Table 2. Snow track index (no. tracks/(days after last snowfall*km)) for the predator and prey communities in the three sub-areas of the study area.

* Average refers to average snow track index for each species/species group pooled over all locations.

Species	Mainland	Kvaløya	Ringvassøya	Average*
Red fox	2.49	0.63	0.21	0.20
Pine marten	0.88	0.00	0.00	0.05
Stoat	2.54	5.68	5.52	0.81
Least weasel	0.78	0.06	0.55	0.08
Mink	0.10	0.00	0.00	0.01
Total predators	6.70	6.37	6.27	1.14
Mountain hare	12.24	0.02	0.00	0.72
Black grouse	0.00	0.00	0.55	0.03
Ptarmigan	28.13	14.25	20.94	3.72
Vole	6.12	12.94	10.83	1.76
Shrew	2.23	20.42	10.95	1.98
Lemming	0.16	0.00	0.00	0.01
Total prey	48.88	47.63	43.27	8.22

3.1.2 Vegetation structure

The principle component analysis with respect to instrumental variables (PCAIV) showed that different habitats within a location (Mainland, Kvaløya and Ringvassøya) represented the expected gradient in vegetation structure spanning from birch forest to the low-alpine zone. The habitats were ordered along the first principle component (x-axis in Figure 3 B) that describes a gradient spanning from tall birch trees (birch habitat), through lower trees and shrubs (edge habitat) to mainly open habitats with dwarf-shrubs and mosses (low-alpine habitat) (Figure 3 B, see Table 1 for classification of vegetation variables).

Consistent differences in vegetation structure were also seen between locations with the largest difference between Ringvassøya and the Mainland (Figure 3 A). The location differences were mainly described by the second principle component (y- axis in Figure 3 A) and were most pronounced for the birch habitat, where there was a tendency for higher birch trees and low herbs on Kvaløya, lower species like bilberry, grasses and prostrate willow on the Mainland, and tall herbs and low birch trees on Ringvassøya. The low-alpine zone on the Mainland was characterized by higher growing species like willows and dwarf birch compared to Kvaløya and Ringvassøya which were characterized by mosses and heath (Figure 3 A and B).

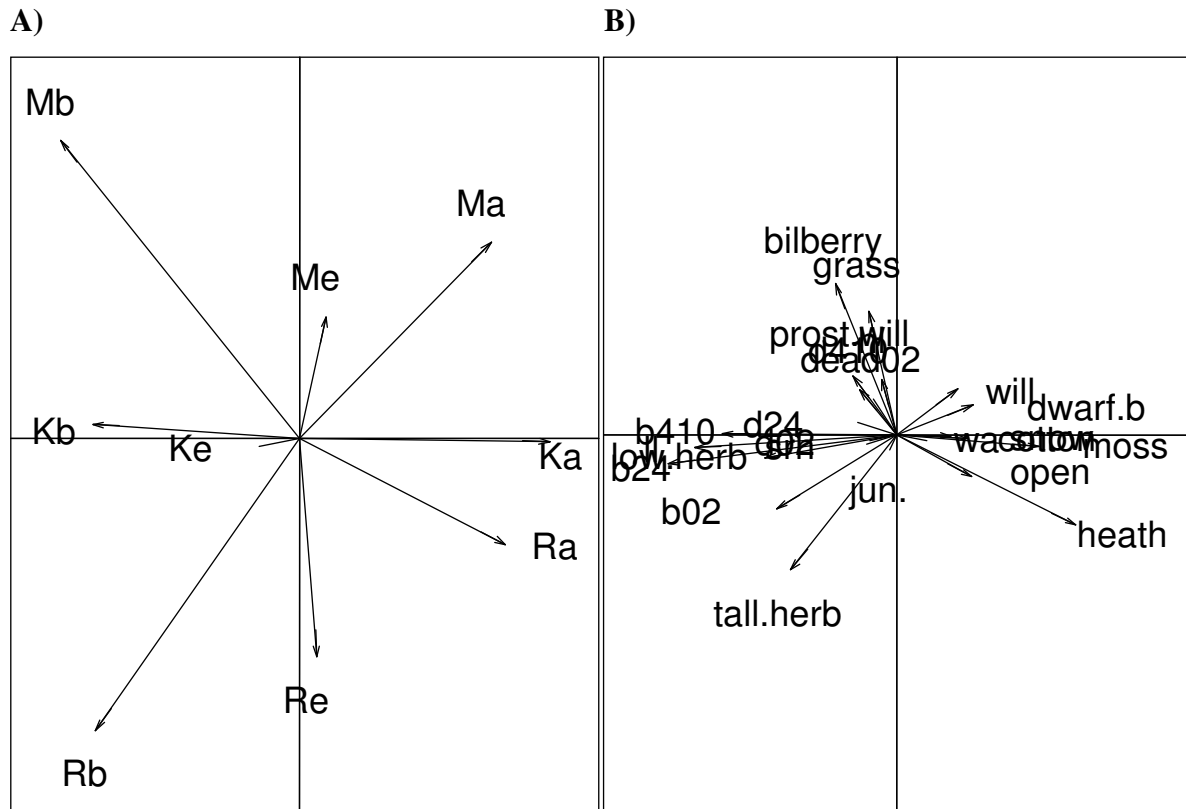


Figure 3. The two first axes of the PCA on IV explained most of the variation explained by the IV (77%). These two axes explained 46% of the variation explained by the two first axes of PCA, and the two first axes of the PCA IV were highly correlated with the two first axes of the PCA. **A)** Ordination of locations and habitats described by their correlation with the first two principle components of vegetation structure as measured by the vegetation variables listed in Table 1. Instrumental variables are M = Mainland, K = Kvaløya, R = Ringvassøya, b = birch, e = edge and a = alpine. **B)** The corresponding correlations between the vegetation variables (see table 1) and the first two principle components.

3.2 Predation rates

Total predation rates ranged from 47.4 % to 77.5 % over all habitats, periods and locations (Table 3). The best model for total predation was a constant model, although models with *location* and *period* performed almost equally well (Table 4). However, none of these variables explained a significant amount of variation in total predation rates.

Avian predators were the dominant predators and showed high and almost equal total predation rates ranging from 44.7 % to 70.0 % throughout the study. Hooded crow was the dominant predator (38.6 % predation) followed by raven (11.8 %) and black-billed magpie (3.9 %) (Table 3). For both hooded crow and black-billed magpie there was little variation between habitats, periods and locations and the best model according to AICc was a constant model (Table 4). The next best model for hooded crow predation included only the variable *habitat*. This was due to the tendency for crow predation to be lowest in the low-alpine habitat (Table 3). For raven the best model included both the variable *location* and *habitat* (Table 4). Location (Variable importance = 0.82) was the most important variable compared to habitat (VI = 0.72). Predation was higher on the Mainland (Odds ratio Mainland/Kvaløya = 4.47, Confidence interval [1.45, 13.8]) compared to Kvaløya, whereas the difference between Ringvassøya and Kvaløya was not statistically significant (OR Ringvassøya/Kvaløya = 1.89, CI [0.48, 7.52]). The low-alpine zone had the highest predation rates and there was a small decrease in predation rates downwards along the gradient (OR board birch/ board alpine = 0.40, CI [0.16, 1.01] and OR board edge/board alpine = 0.49, CI [0.20, 1.18]), although not statistically significant.

Predation by mammals was mainly represented by red fox and stoat and the total predation rates were low, ranging from 0.0 % to 10.0 %, over all habitats, periods and locations (Table 3). The predation rates for these species were too low to be analysed statistically. Unidentified predators were registered as either unidentified bird predation (1.4 %), or unidentified species predation (1.1 %). In addition some eggs were eaten or removed by domestic cattle or sheep (1.4 %) (Table 3).

Table 3. Summary of predation (no. of eggs predated) stratified by **A)** period and habitat and by **B)** location and habitat. Total predation refers to predation by all species excluding domestic animals and other unidentified sources. “Treatments” refers to total number of eggs available for predation, excluding eggs eaten or removed by domestic animals and other unidentified sources.

Predator community	A)						B)								
	Period 1			Period 2			Mainland			Kvaløya			Ringvassøya		
	Birch	Edge	Alpine	Birch	Edge	Alpine	Birch	Edge	Alpine	Birch	Edge	Alpine	Birch	Edge	Alpine
Red fox	2	1	1	1	2	2	2	3	2	1	0	1	0	0	0
Stoat	1	1	0	3	1	2	1	0	1	0	0	0	3	2	1
Least weasel	0	0	0	1	1	1	0	1	0	1	0	0	0	0	1
Black-billed magpie	5	0	1	2	4	2	2	0	1	3	1	1	2	3	1
Raven	4	5	9	6	7	11	4	8	7	4	1	6	2	3	7
Hooded crow	23	25	21	26	23	19	15	15	11	11	13	11	23	20	18
Thrush	3	0	2	1	2	0	2	0	2	1	2	0	1	0	0
Unidentified bird	1	1	2	0	0	1	1	1	1	0	0	1	0	0	1
Unidentified species	0	2	0	2	0	0	0	0	0	2	1	0	0	1	0
Domestic animal/other sources	2	1	1	0	1	0	0	0	0	2	2	1	0	0	0
Total predation	39	35	36	42	40	38	27	28	25	23	18	20	31	29	29
Treatments	58	59	59	60	59	60	40	40	40	38	38	39	40	40	40
Red fox (%)	3.4	1.7	1.7	1.7	3.4	3.3	5.0	7.5	5.0	2.6	0.0	2.6	0.0	0.0	0.0
Stoat (%)	1.7	1.7	0.0	5.0	1.7	3.3	2.5	0.0	2.5	0.0	0.0	0.0	7.5	5.0	2.5
Least weasel (%)	0.0	0.0	0.0	1.7	1.7	1.7	0.0	2.5	0.0	2.6	0.0	0.0	0.0	0.0	2.5
Black-billed magpie (%)	8.6	0.0	1.7	3.3	6.8	3.3	5.0	0.0	2.5	7.9	2.6	2.6	5.0	7.5	2.5
Raven (%)	6.9	8.5	15.3	10.0	11.9	18.3	10.0	20.0	17.5	10.5	2.6	15.4	5.0	7.5	17.5
Hooded crow (%)	39.7	42.4	35.6	43.3	39.0	31.7	37.5	37.5	27.5	28.9	34.2	28.2	57.5	50.0	45.0
Thrush (%)	5.2	0.0	3.4	1.7	3.4	0.0	5.0	0.0	5.0	2.6	5.3	0.0	2.5	0.0	0.0
Unidentified bird predation (%)	1.7	1.7	3.4	0.0	0.0	1.7	2.5	2.5	2.5	0.0	0.0	2.6	0.0	0.0	2.5
Unidentified species predation (%)	0.0	3.4	0.0	3.3	0.0	0.0	0.0	0.0	0.0	5.3	2.6	0.0	0.0	2.5	0.0
Total mammal predation (%)	5.2	3.4	1.7	8.3	6.8	8.3	7.5	10.0	7.5	5.3	0.0	2.6	7.5	5.0	5.0
Total bird predation (%)	62.1	52.5	59.3	58.3	61.0	55.0	60.0	60.0	55.0	50.0	44.7	48.7	70.0	65.0	67.5
Total predation (%)	67.2	59.3	61.0	70.0	67.8	63.3	67.5	70.0	62.5	60.5	47.4	51.3	77.5	72.5	72.5

Table 4. The three best models including the variables *period*, *location*, *habitat* and the interaction *location*habitat* according to ΔAICc and AICc weights (w). The best model is indicated in bold letters. n = number of predation events, np = number of parameters estimated, P = *period*, L = *location*, H = *habitat*, * = interactions.

Predator	np	P	L	H	L*H	ΔAICc	AICc (w)
Total predation (n = 230)	2	-	-	-	-	0.00	0.16
	3	x	-	-	-	0.27	0.14
	4	-	x	-	-	0.65	0.12
Hooded crow (n = 137)	2	-	-	-	-	0.00	0.30
	4	-	-	x	-	1.26	0.16
	4	-	x	-	-	1.87	0.12
Black-billed magpie (n = 14)	2	-	-	-	-	0.00	0.42
	3	x	-	-	-	1.75	0.18
	4	-	-	x	-	1.86	0.17
Raven (n = 42)	6	-	x	x	-	0.00	0.23
	4	-	x	-	-	0.87	0.15
	10	-	x	x	x	1.22	0.12

3.2.1 Spatial relation between predator species

There was no evidence for a spatial association between the individual predator species based on Spearman's rank correlation coefficients (Table 5).

Table 5. Correlation matrix of Spearman's rank correlation coefficients based on transect-specific (n = 60) predation rates resulting from different predator species. None of the coefficients were statistically significant (all $p > 0.12$).

	Red fox	Mustelid	Black-billed magpie	Raven
Mustelid*	0.01			
Black-billed magpie	-0.09	0.08		
Raven	-0.11	0.04	0.05	
Hooded crow	-0.08	0.09	-0.06	0.05

* Mustelid = stoat and least weasel predation pooled

4 Discussion

4.1 Summary of results

The total predation rates over all habitats, locations and periods were remarkably constant. The corvids, raven and especially the hooded crow, were overall the most dominant predators. There was a tendency for an opposite predation pattern along the habitat gradient for hooded crow and raven, with raven being most frequent in the low-alpine habitat and crow in the birch and edge habitat, although not statistically significant. Predation rates by all mammalian predators were low, although these predators including the red fox, were registered frequently in the winter snow track survey in the study area.

4.2 Habitat specific predation on ground nests

The total predation rates in the present study is similar to equivalent studies using artificial nests or track boards (Angelstam 1986, Storch 1991, Andrén 1992, Einarsen et al. in press, Pedersen et al. submitted), and even studies on grouse species using natural nests (Wegge and Storaas 1990, Munkebye et al. 2003). Although, the study was designed to contain a distinct habitat gradient, ranging from rather dense birch forest to open alpine habitat, differences in vegetation could not alone explain the observed predation rates. This is in line with other studies documenting that nest concealment has minor importance in nest site selection for many ground dwelling birds (Erikstad et al. 1982, Myrberget 1985, Brittas and Willebrand 1991, Munkebye et al. 2003). Hence, habitat appear to be of minor importance for predation rates on ptarmigan nests.

Habitat specific predation rates for different species might be caused by species-specific habitat requirements or presence of territorial long-lived individuals with different prey preferences. Consequently, Šàlek et al. (2004) suggested that the spatial pattern of a dominant generalist predator could be explaining the predation pattern on artificial nests. The high and constant predation rate by corvids between habitats could therefore be due the species being food- and habitat generalists. Several studies have also suggested that the density of generalist predators increases as the forest landscape becomes fragmented and interspersed with agriculture (Andrén 1992, Kurki et al. 1998, Kurki et al. 2000, Storch et al. 2005), which is the case in parts of the study area. Although not statistically significant, the hooded crow had slightly higher predation rates in the birch and edge habitat, while raven had slightly higher

predation rate in the low-alpine habitat, which may reflect the species main habitat use (Sandvik 1998, Smedshaug et al. 2002). The low predation by black-billed magpie, compared to hooded crow and raven, could be due to generally lower density of black-billed magpie in the area and the species higher preference for human settlements and agricultural landscapes than the other two species (Møller 1982, Andrén 1992, Sandvik 1998). The Mainland had the highest predation rate by raven followed by Kvaløya and Ringvassøya, even though the low-alpine zone on the Mainland had generally the highest vegetation cover and consequently poorer sight conditions from the air. The difference seen between locations could therefore be due to local differences in abundance of ravens. Thus the constant predation rates in this study could be due that the dominant nest predators are habitat and food generalist which can live at high densities.

Angelstam (1986) suggested that it should not pay predators to search specifically for nests, since the contribution of eggs to the predators` diet was less than 1 % of their food requirements. This implies that nests should only be found by chance during other feeding activities, and the most common predator species would therefore be the most important nest predator. This is in accordance with studies showing significantly higher nest predation by hooded crow, which can live at higher densities compared to raven (Angelstam et al. 1984), black-billed magpie (Møller 1982) and red fox (Frafjord 2004). However, it may pay for some predators such as the raven, which has a large home range (Angelstam et al. 1984) and therefore may encounter many nests, to develop a search image for ground nests and become a specialized nest-robber during May and early June (Andrén 1992). Thus, the importance of different species as nest predators may be affected by both density of the species and their searching effort.

It could be expected from random predation risk among different habitat types that ground nesting birds would not be selective with regard to nesting habitats. Storaas and Wegge (1987) and Schieck and Hannon (1993) found that vegetation around willow ptarmigan nests did not differ from that around a random point . On the other hand random selection of nest sites of ground nesting birds may have evolved as a strategy against predators developing a search image for specific nesting habitat (Storaas and Wegge 1987, Schieck and Hannon 1993). The predation rates were relatively stable between the two trial periods, thus there was no indication that the corvids developed a search image for the track boards in the study. This is in contrast to other studies where there has been an increase in predation rate by corvids

between trial periods (Sonerud and Fjeld 1984;1987, Einarsen et al. in press, Pedersen et al. submitted). Although, the trial periods could be too short or too few for species developing a search image.

4.3 Predator community

The high predation by corvid species is in accordance with several other studies focusing on nest predation in boreal and sub-arctic forest ecosystems (e.g. Erikstad et al. 1982, Parker 1984, Angelstam 1986, Andrén 1989, Einarsen et al. in press, Pedersen et al. submitted). The low predation rate by red fox is in contrast to other studies where red fox has been shown to be an important nest predator (Kurki et al. 1997, Baines et al. 2004). The predation rates by stoat and least weasel were also remarkable low, although this is in line with many other studies documenting these species to be of minor importance as a nest predator (Angelstam 1986, Kurki et al. 1997, Einarsen et al. in press, Pedersen et al. submitted). Stoat and least weasel are known to respond numerically to population fluctuations in boreal voles (Korpimäki et al. 1991, Hellstedt et al. 2006), and they are expected to show higher predation rates on alternative prey in the decline phase of the vole cycle (Angelstam et al. 1984, Wegge and Storaas 1990). The year of this study appeared to represent an increase year for voles in the general region (Yoccoz and Ims pers comm.) which may account for the low predation rate of the mustelids. This could affect the results in such a way that the predation rates on nests can be higher in years with lower availability of voles than observed in this study.

Clark and Nudds (1991) stated that nest concealment was most effective when the major predators were birds, and was less important when mammals were most dominant. This could be due to different predators relying on visual and olfactory cues to locate nest, and the relative importance of either cue depends on the predator species and the ambient conditions (Andrén 1992, Rollinson and Brooks 2007). High predation rates by corvids and low predation rates by mammals may therefore be a result of predators using the landscape in different ways to locate prey and their searching effort. Mammalian predators mainly rely on olfactory cues (Whelan et al. 1994, Rangen et al. 2000), whereas avian predators rely on visual cues (Picozzi 1975). Detecting track boards, which gives a distinct shift in the bottom and field layer is much more likely by vision and may have accentuated this difference between avian and mammalian predation. Due to lack of scent from an incubating bird or nestling, mammalian predators need to be very close to the nest before detecting it, and Storaas et al. (1999) found that mammalian predators detected capercaillie nest at distance

closer than 1.6 meters from the nest. However, some avian predators appear to use movement of the female to and from the nest as a cue to locate nests (Hammond 1956, Erikstad et al. 1982). Consequently, the lack of an incubating bird could also affect the predation rates by avian predators. Several studies have also criticized the use of artificial nests because mammalian predators using olfactory cues can locate nests after visits of an investigator (Whelan et al. 1994). According we used a field method that minimized human scent. Therefore the effect of human scent would likely be of minor importance in the study. The low predation by mammals compared to avian predators could also be due to longer searching time for mammals, leading to avian predators finding these nests before the mammals. Although, the dominant predators in this study were avian predators using visual cues, the habitat and consequently the sight condition did not affect the predation rates. However, the use of track boards as artificial nests could have increased predation by avian predators compared to mammalian predators.

Conclusion

In this one year study, using artificial nests, we found nest predation rates to be remarkably constant over a distinct habitat gradient ranging from rather dense birch forest to open alpine habitat. The constant predation rates were mainly due to omnipresent corvids, especially the hooded crow, which dominated among the predators in all habitats and locations included in the study. From the perspective of nest predation risk on ground nesting birds like willow ptarmigan, they would not be expected to be selective with respect to nesting habitats.

5 References

- Andersen, J.-E. 1986. Habitat selection by Willow Grouse *Lagopus l. lagopus* in central Norway. *Fauna norvegica. Ser. C Cinclus* 9:82-94.
- Anderson, D. R., and K. R. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66:912-918.
- Anderson, D. R., W. A. Link, D. H. Johnson, and K. P. Burnham. 2001. Suggestions for presenting the results of data analyses. *Journal of Wildlife Management* 65:373-378.
- Andrén, H. 1989. Predation processes in fragmented boreal forest landscapes. *Acta Univ. Ups.* Comprehensive summaries of Uppsala dissertations from the Faculty of Science 201
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794-804.
- Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69:544-547.
- Andrén, H., P. Angelstam, E. Lindström, and P. Widén. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. *Oikos* 45:273-277.
- Angelstam, P. 1986. Predation on ground-nesting birds nests in relation to predator densities and habitat edge. *Oikos* 47:365-373.
- Angelstam, P., E. Lindström, and P. Widén. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199-208.
- Aronson, Å., and P. Eriksson. 1992. *Dyrespor: og kunsten å spore*. J.W. Cappelens Forlag a.s., Oslo, Norway (in Norwegian).
- Baines, D., R. Moss, and D. Dugan. 2004. Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology* 41:59-71.
- Bang, P., E. Østbye, and P. Dahlstrøm. 2000. *Sportegn fra pattedyr og fugler*. H. Aschehoug & Co, Oslo, Norway (in Norwegian).
- Batàry, P., and A. Bàldi. 2004. Evidence of an edge effect on avian nest success. *Conservation Biology* 18:389-400.
- Brittas, R., and T. Willebrand. 1991. Nesting habitats and egg predation in Swedish black grouse. *Ornis Scandinavica* 22:261-263.
- Brøseth, H., and H. C. Pedersen. 2000. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. *Journal of Applied Ecology* 37:182-190.

- Burke, D. M., K. Eliliott, L. Moore, W. Dunford, E. Nol, J. Phillips, S. Holmes, and K. Freemark. 2004. Patterns of nest predation on artificial and natural nests in forests. *Conservation Biology* 18:381-388.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference - understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261-304.
- Børset, O. 1962. *Skogskjøtsel*. Volume 2. Skogforlaget A/S, Oslo, Norway (in Norwegian).
- Chessel, D., A.-B. Dufour, and J. Thioulouse. 2004. The ade4 package- 1: One-table methods. *R News* 4:5-10.
- Chevenet, F., S. Dolèdec, and D. Chessel. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31:295-309.
- Clark, R. G., and T. D. Nudds. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. *Wildlife Society Bulletin* 19:534-543.
- Einarsen, G., V. H. Hausner, N. G. Yoccoz, and R. A. Ims. in press. Predation on artificial ground nests in birch forest fragmented by spruce plantations. *Ecoscience*.
- Erikstad, K. E. 1986. Relationship between weather, body condition and incubation rhythm in Willow Grouse. *Fauna norvegica. Ser. C. Cinclus* 9:7-12.
- Erikstad, K. E., R. Blom, and S. Myrberget. 1982. Territorial hooded crows as predators on willow ptarmigan nests. *Journal of Wildlife Management* 46:109-114.
- Erikstad, K. E., H. C. Pedersen, and J. B. Steen. 1985. Clutch size and egg size variation in willow grouse *Lagopus .l. Lagopus*. *Ornis Scandinavica* 16:88-94.
- Frafjord, K. 2004. Winter range of a red fox (*Vulpes vulpes*) group in a northern birch forest. *Mammalian Biology* 69:342-348.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- Hammond, M. C. 1956. Experiments on causes of duck nest predation. *Journal of Wildlife Management* 20:243-247.
- Hellstedt, P., J. Sundell, P. Helle, and H. Henttonen. 2006. Large-scale spatial and temporal patterns in population dynamics of the stoat, *Mustela erminea*, and the least weasel, *M. nivalis*, in Finland. *Oikos* 115:286-298.
- Hewitt, D. G., D. M. Keppie, and D. F. Stauffer. 2001. Predation effects on forest grouse recruitment. *Wildlife Society Bulletin* 29:16-23.
- Hogstad, O., editor. 1991a. *Norges dyr. Fuglene* 2. J.W. Cappelens Forlag a.s., Oslo, Norway (in Norwegian).

- Hogstad, O., editor. 1991b. Norges dyr. Fuglene 3. J.W. Cappelens a.s., Oslo, Norway (in Norwegian).
- Hogstad, O., editor. 1992. Norges dyr. Fuglene 4. J.W. Cappelens Forlag a.s., Oslo, Norway (in Norwegian).
- Johansson, A. S.-., and R. Frislid, editors. 1990. Norges dyr. Pattedyrene 1. J.W. Cappelens Forlag a.s, Oslo, Norway (in Norwegian).
- Jongman, R. H., C. J. F. t. Braak, and O. F. R. Van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, England.
- Kauhala, K., and P. Helle. 2000. The interactions of predator and hare populations in Finland - a study based on wildlife monitoring counts. *Annales Zoologici Fennici* 37:151-160.
- King, D. I., Degraaf, R.M, Griffin, C. & Maier, T.J. 1999. Do predation rates on artificial nets accurately reflect predation rates on natural bird nests? *J. Field Ornithol.* 70:257-262.
- Korpimäki, E., K. Norrdahl, and T. Rintajaskari. 1991. Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia* 88:552-561.
- Kurki, S., P. Helle, H. Lindèn, and A. Nikula. 1997. Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. *Oikos* 79:301-310.
- Kurki, S., A. Nikula, P. Helle, and H. Lindèn. 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology* 67:874-886.
- Kurki, S., A. Nikula, P. Helle, and H. Lindèn. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* 81:1985-1997.
- Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* 99:365-374.
- Lewis, K. P. 2004. How important is the statistical approach for analyzing categorical data? A critique using artificial nests. *Oikos* 104:305-315.
- Lindèn, H., E. Helle, P. Helle, and M. Wikman. 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finnish Game Research* 49:4-11.
- Lindström, E. R., H. Andrèn, P. Angelstam, G. Cederlund, B. Hörnfeldt, L. Jäderberg, P. A. Lemnell, B. Martinsson, K. Skold, and J. E. Swenson. 1994. Disease reveals the

- predator: sarcoptic mange, red fox predation, and prey populations. *Ecology* 75:1042-1049.
- Linnell, J. D. C., P. Fiske, I. Herfindal, J. Odden, H. Brøseth, and R. Andersen. 2007. An evaluation of structured snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. *Wildlife Biology* 13:456-466.
- Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: A multi-scale approach. *Journal of Wildlife Management* 69:110-123.
- Marcström, V., R. E. Kenward, and E. Engren. 1988. The impact of predation on boreal tetraonids during vole cycles -an experimental study. *Journal of Animal Ecology* 57:859-872.
- Moen, A. 1998. Nasjonalatlas for Norge. Vegetasjon. Bokbinderiet Johnsen A.S, Skien, Norway (in Norwegian).
- Moore, R. P., and W. D. Robinson. 2004. Artificial bird nests, external validity, and bias in ecological field studies. *Ecology* 85:1562-1567.
- Moss, R., and A. Watson. 2001. Population cycles in birds of the grouse family (Tetraonidae). *Advances in Ecological Research* 32:53-111.
- Munkebye, E., H. C. Pedersen, J. B. Steen, and H. Brøseth. 2003. Predation of eggs and incubating females in willow ptarmigan *Lagopus l. lagopus*. *Fauna norvegicus* 23:1-8.
- Myrberget, S. 1974. Variations in the production of the Willow Grouse *Lagopus lagopus* (L.) in Norway, 1963-1972. *Ornis Scandinavica* 5:163-172.
- Myrberget, S. 1984. Population dynamics of Willow Grouse *Lagopus lagopus* on an island in North Norway. *Fauna norvegica. Ser. C. Cinclus* 7:95-105.
- Myrberget, S. 1985. Egg predation in an island population of Willow Grouse *Lagopus lagopus*. *Fauna norvegica. Ser. C. Cinclus* 8:82-87.
- Møller, A. P. 1982. Characteristics of magpie pica-pica territories of varying duration. *Ornis Scandinavica* 13:94-100.
- Norwegian Meteorological institute. 2008. Data from 1961-1990.
http://retro.met.no/observasjoner/troms/normaler_for_kommune_1902.html.
 Norwegian
- Parker, H. 1984. Effect of corvid removal on reproduction of willow ptarmigan and black grouse. *Journal of Wildlife Management* 48:1197-1205.
- Pedersen, H. C., and D. H. Karlsen. 2007. Alt om rypa: biologi, jakt, forvaltning. Tun, Oslo, Norway (in Norwegian).

- Pedersen, H. C., H. Steen, L. Kastdalen, W. Svendsen, and H. Brøseth. 2002. Rapport fra SIP: bærekraftig høsting av bestander. Sluttrapport.
- Pedersen, Å. Ø., N. G. Yoccoz, and R. A. Ims. submitted. Spatial and temporal patterns of artificial nest predation in mountain birch forests. *Journal of European Wildlife Research*.
- Phillips, J., J. B. Steen, R. S.G., and F. Aalerud. 1992. Effects of burning and cutting on vegetation and the population of willow grouse *Lagopus lagopus* in Norway. *Fauna norvegica. Ser. C. Cinclus* 15:37-42.
- Picozzi, N. 1975. Crow predation on marked nests. *Journal of Wildlife Management* 39:151-155.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-Effects Models in S and S-PLUS* elektronisk ressurser. Springer-Verlag, New York, USA.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R foundation for Statistical Computing <http://www.r-project.org/>.
- Rangen, S. A., R. G. Clark, and K. A. Hobson. 2000. Visual and olfactory attributes of artificial nests. *Auk* 117:136-146.
- Rao, C. R. 1964. The use and interpretation of principal component analysis in applied research. *Sankhya* 26:329-358.
- Ries, L., J. Robert J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual review of ecology, evolution and systematics* 35:491-522.
- Rollinson, N., and R. J. Brooks. 2007. Marking nests increases the frequency of nest depredation in a northern population of painted turtles (*Chrysemys picta*). *Journal of Herpetology* 41:174-176.
- Ryall, K. L., and L. Fahrig. 2006. Response of predators to loss and fragmentation of prey habitat: A review of theory. *Ecology* 87:1086-1093.
- Šálek, M., J. Svobodová, V. Bejček, and T. Albrecht. 2004. Predation on artificial nests in relation to the numbers of small mammals in the Krusne hory Mts, the Czech Republic. *Folia Zoologica* 53:312-318.
- Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology* 86:2176-2186.
- Sandvik, J. 1998. Kråkefuglene- en del av naturens mangfold. Norsk Ornitologisk Forening, Klæbu, Norway (in Norwegian).

- Schieck, J. O., and S. J. Hannon. 1993. Clutch predation, cover, and the overdispersion of nests of the willow ptarmigan. *Ecology* 74:743-750.
- Smedshaug, C. A., S. E. Lund, A. Brekke, G. A. Sonerud, and T. Rafoss. 2002. The importance of the farmland-forest edge for area use of breeding Hooded Crows as revealed by radio telemetry. *Ornis Fennica* 79:1-13.
- Sonerud, G. A., and P. E. Fjeld. 1984. Searching and caching behaviour in hooded crows-an experiment with artificial nests. *Fauna norvegica. Ser. C. Cinclus* 8:18-23.
- Sonerud, G. A., and P. E. Fjeld. 1987. Long-term memory in egg predators: an experiment with a hooded crow. *Ornis Scandinavica* 18:323-325.
- Statistics Norway. 2008. Småviltjakt. Antall felte ryper. Fylke. 2001/02-2006/07. <http://www.ssb.no/emner/10/04/10/srjakt/tab-2007-08-08-01.html>. Norwegian
- Storch, I. 1991. Habitat fragmentation, nest site selection, and nest predation risk in capercaillie. *Ornis Scandinavica* 22:213-217.
- Storch, I., and T. Willebrand. 1991. Management implications of nest and brood predation in grouse. *Ornis Scandinavica* 22:271-272.
- Storch, I., E. Woitke, and S. Krieger. 2005. Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe. *Landscape Ecology* 20:927-940.
- Storaas, T., L. Kastdalen, and P. Wegge. 1999. Detection of forest grouse by mammalian predators: a possible explanation for high brood losses in fragmented landscapes. *Wildlife Biology* 5:187-192.
- Storaas, T., and P. Wegge. 1987. Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. *Journal of Wildlife Management* 51:167-172.
- Thompson, F. R., W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. *Auk* 116:259-264.
- Thompson, I. D., I. J. Davidson, S. Odonnell, and F. Brazeau. 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Canadian Journal of Zoology* 67:1816-1823.
- Wegge, P., and T. Storaas. 1990. Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway. *Oecologia* 82:527-530.
- Whelan, C. J., M. L. Dilger, D. Robso, N. Hallyn, and S. Dilger. 1994. Effects of olfactory cues on artificial- nest experiments. *The Auk* 111:945-952.
- Wiebe, K. L., and K. Martin. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behaviour* 56:1137-1144.

Wilson, S., K. Martin, and S. J. Hannon. 2007. Nest survival patterns in Willow Ptarmigan: Influence of time, nesting stage, and female characteristics. *Condor* 109:377-388.