

NORWEGIAN UNIVERSITY OF LIFE SCIENCES



Preface

First we would like to thank our supervisors Associate Professor Emeritus Olav Hjeljord and Professor Emeritus Per Wegge for giving us the opportunity of doing the thesis. Olav Hjeljord especially for the trip to Russia, Per Wegge especially for conducting the field work at Varaldskogen, and both for assistance, guidance, feedback, and patience.

Andrey and Albina Sivkov, we appreciate the great hospitality and friendship. Also, we thank Andrey for conducting the field work near Pinega Village and Albina for her great cooking.

We also wish to thank Emil Halvorsrud for conducting the field work at Varaldskogen with Per. Also, we wish to thank Vidar Selaas for helping us through some statistical obstacles and giving good advices en route.

Also, we wish to thank the Norwegian Directorate for Nature Management for financial support.

Last, but not least, we wish to thank all the people at Sørhellinga, former and present classmates, teachers, professors, and all the people at the Norwegian University of Life Science.

Not to mention, we wish to thank each other for good company in the Russian wilderness, late white nights playing chess and sharing stories, and the great experience this has been.

Ås, 14.05.2011

Vebjørn Oppegaard Pollen

Halvor Ingul

Abstract

We used artificial nests to measure predator abundance and predator composition between Varaldskogen in southeastern Norway and two areas in Pinega in northwestern Russia. Varaldskogen is heavily influenced by commercial forestry and has a high density of red fox *Vulpes vulpes*, whereas the remote Pinega Forest Reserve is in a pristine state and red fox is absent. Pinega Village is close to human settlements and is therefore more disturbed by human activities. The artificial nests, consisting of two brown domestic hen eggs, were placed both on the ground and on 1.5 m poles in order to assess the relative importance of avian and mammalian predators. They were put out and monitored during the time when grouse nests are incubated. We measured how well the nests were covered from detection by sight predators. Total predation (ground and pole combined), and ground predation alone, was highest at Varaldskogen. There, ground nests also suffered higher predation than pole nests. In Pinega, there were no differences in predation between the two areas, and no differences between pole and ground predation. The results indicated that mammalian predators were more important than avian predators at Varaldskogen, whereas they were equally important in both areas in Pinega. From linear models (GLM and LMEM), canopy cover was shown to be the best explanatory variable, whereas habitat had no explanatory value at Varaldskogen. This indicated that canopy cover reveals something about the forest structure that is not explained by habitat. In Pinega Reserve, habitat and ground cover were the best explanatory variables. This could be explained by the different predators' preference or avoidance of certain habitats, whereas the importance of ground cover indicated that sight-oriented predators such as Siberian jay *Perisoreus infaustus* and red squirrel *Sciurus vulgaris* are important. In Pinega Village, habitat and canopy cover were the best explanatory variables, which probably reflect the low predation rate in the extremely dense young forest and the high predation rate in the open mature forest. The results about nest cover were highly variable, and the only negative correlation between nest predation and canopy cover was in young forest in Pinega Reserve and in mature forest at Varaldskogen. This could be due to larger corvids finding it difficult to navigate within the dense young forest in Pinega Reserve. In the Reserve, nests with good cover survived better than poorly covered nests. There was no correlation between small rodent abundance and nest predation, possibly because of other alternative prey, or high densities of predators. Higher predation at Varaldskogen than in Pinega Reserve was probably due to a higher density of generalist predators owing to its more southerly geographical location and especially the presence of red fox, which could be related to forestry practices and easily accessible food sources in proximity to human settlements.

Sammendrag

Vi benyttet kunstige reir for å sammenligne predator tetthet og predatorsammensetning mellom Varaldskogen i sørøst-Norge og to områder i Pinega i nordvest-Russland. Varaldskogen er sterkt påvirket av skogbruk og har høye tettheter av rødrev *Vulpes vulpes*, mens Pinega Naturresevat er tilnærmet urørt og rødrev er fraværende. Pinega Landsby ligger nær menneskelig bebyggelse og er derfor mer påvirket av menneskelig aktivitet. De kunstige reirene bestod av to brune hønseegg og ble plassert både på bakken og på 1.5 meter høye påler for å kunne se den relative predasjonen av flygende predatorer og pattedyrpredatorer. De ble plassert på den tiden skogsfuglen ruger i de to hovedområdene. Vi målte hvor godt dekket reirene var for synspredatorer. Total predasjon (påle og bakke kombinert) og bakkepredasjon alene var høyest på Varaldskogen. Der var også bakkepredasjon også høyere enn pålepredasjon. I de to områdene i Pinega var det ingen forskjell hverken i total predasjon eller mellom pålereir og bakkereir. Disse resultatene indikerer at bakkepredatorer var viktigere enn flygende predatorer på Varaldskogen, mens de var like viktige i de to områdene i Pinega. Ved lineære modeller (GLM og LMEM) fant vi at kronedekning var den beste forklaringsvariablen, mens habitat ikke hadde noen forklaringsverdi på Varaldskogen. Dette tyder på at kronedekning kan forklare noe av skogstrukturen som habitat ikke fanger opp. I Pinega Naturresevat var habitat og bakkedekning de beste forklaringsvariablene trolig fordi ulike predatorer foretrekker eller unngår visse habitater og at synspredatorer slik som lavskrike *Perisoreus infaustus* og ekorn *Sciurus vulgaris* er viktige. I Pinega Landsby var kronedekning og habitat de beste forklaringsvariablene, noe som trolig gjenspeiler den lave predasjonsraten i den ekstremt tette ungsbogen og den høye predasjonsraten i den åpne gammelsbogen. Det var ingen klar sammenheng mellom reirdekning og predasjon og den eneste negative korrelasjonen mellom reirpredasjon og kronedekning var i ungsbog i Pinega Naturresevat og i gammelsbog på Varaldskogen. Dette har trolig sammenheng med at større kråkefugl har vanskeligheter med å bevege seg i ungsbog i Pinega Naturresevat. Det var ingen korrelasjon mellom antall smågnagere og reirpredasjon, muligens på grunn av andre alternative byttedyr, eller på grunn av høy tetthet av predatorer. Høyere predasjon på Varaldskogen enn i Pinega var trolig på grunn av høyere tetthet av generalistpredatorer grunnet en mer sørlig geografisk beliggenhet og spesielt tilstedeværelsen av rødrev, noe som kan knyttes opp mot intensivt skogbruk og lett tilgjengelige matkilder i nærheten av menneskelig bebyggelse.

Contents

Preface.....	II
Abstract	IV
Sammendrag.....	VI
1. Introduction	1
2. Material and methods	4
2.1 Study area at Varaldskogen.....	4
2.2 Study area in Pinega State Forest Reserve, Russia.....	5
2.3 Methods.....	8
2.3.1 Nest placement in Pinega Reserve and Pinega Village	8
2.3.2 Nest placement at Varaldskogen	9
2.3.3 Nest site measurements	10
2.3.4 Nest numbers and visitations.....	11
2.4 Analyses	13
3. Results	14
3.1 Total predation and nest type	14
3.1.1 Total predation rate.....	14
3.1.2 Predation rate and nest types	15
3.2 Model testing and the importance of habitat and nest concealment.....	16
3.2.1 Model testing.....	16
3.3 The effect of habitat and nest cover within the study areas.....	22
3.3.1 Predation, habitat, and mean canopy cover	22
3.3.2 Predation and cover	24
4. Discussion	26
4.1 Total predation and nest type	26
4.1.1 The effect of geography and landscape composition on total predation pressure	26
4.1.2 Small rodent cycles in relation to predation pressure	29
4.2 Model testing and the importance of habitat and cover.....	30
4.2.1. Model testing.....	30
4.2.2 The importance of habitat and cover	30
5. Conclusion.....	33
References	34

1. Introduction

Eurasian forest grouse, in this context the species capercaillie *Tetrao urogallus*, black grouse *Tetrao tetrix* and hazel grouse *Bonasa bonasia* are ground-nesting birds that are distributed throughout large parts of the boreal forests of Central and Northern Europe, Britain and Siberia. Incubation period is between 21 and 27 days, and hatching takes place in early June in the south and later in June in the north. The number of eggs in the clutch decreases with body size, i.e. the larger capercaillie lay about 7 eggs, while the relatively smaller hazel grouse lay 8-9 eggs (Lindstrøm 1994, Watson & Moss 2008).

Several forest grouse populations in Central Europe and Britain have shown declining trends over the last decades and some are even on the verge of extinction (Storch 2007).

Traditionally, these declining trends have been related to habitat degradation and fragmentation caused by forestry (Klaus 1991). Modern forestry was introduced in Fennoscandia around 1950 and clear-cutting and replanting became the dominant forest management regime (Wegge & Rolstad 2011).

Recent studies from Fennoscandia, however, show that forestry per se may not be detrimental to forest grouse (Sirkiä et al. 2010). Despite radical changes in forest age, structure and composition, a recent study in Norway showed that capercaillie numbers and breeding success have been more or less stable during the last 30 years (Wegge & Rolstad 2011).

However, clearcuttings fragment areas and remove large proportions of old forest (Kurki et al 2000). As clear cuts are regarded as suitable habitats for certain small rodents (Hansson 1994) they may support a high density of predators, i.e. a numerical response (Wegge & Rolstad 2011) and furthermore, fragmentation may have made it easier for generalist predators to find their prey, i.e. a functional response (Storaas et al. 1999, Borchtchevski et al. 2003).

Both mammalian and avian generalist predators have a negative effect on forest grouse and several studies have stressed the importance of nest predation as an important factors limiting reproductive success and affecting population dynamics (Storch 1991, Svobodova et al. 2004, Klausen et al. 2010). Previous studies have reported nest losses in capercaillie and black grouse to vary between 30 and 90 % (Wegge & Storaas 1990), 65 % in hazel grouse (Saniga 2002) and between 10 and 80 % in willow grouse (Hannon et al. 1988). There is little knowledge, however, about which predators that cause nest losses, but predation rates probably vary with both predator composition and predator density (Angelstam 1986, Kurki et

al. 1998) and may also vary with the degree of human-related habitat change and alteration of ecosystems (Storch & Leidenberger 2003, Støen et al. 2010).

In addition to predator density and predator composition, nest losses probably also vary with the availability of alternative prey. The alternative prey hypothesis (Hagen 1952, Angelstam et al. 1984) states that predators switch from their main prey (small rodents) to their alternative prey (forest grouse), when small rodent populations crash. Thus, nest losses are expected to vary between years in relation to the small rodent cycle, i.e. low nest losses in years with abundant small rodents and higher nest losses with low small rodent numbers, as was confirmed in a Norwegian study (Wegge & Storaas 1990).

Predator abundance and predator composition also differ between habitats and between regions, and predation risk will therefore vary with local- and regional spatial scales (Andrén 1992, Brzezinski et al. 2010, Kurki et al. 1998). Andrén et al. (1985) and Kurki et al. (1997) found that the reproductive success of forest grouse decreased when moving southwards in Fennoscandia which was negatively correlated with predator densities. Several studies have found increased predation in habitat edges which has been described as the “edge-effect” (Andrén & Angelstam 1988, Paton 1994, Batary & Baldi 2004), and increased predation has also been found in forest areas in proximity to agricultural land (Andrén 1992).

Mammalian predators detect their prey mainly by smell (Hughes et al. 2010, Whelan et al. 1994) and species like pine marten *Martes martes*, stoat *Mustela erminea*, red fox *Vulpes vulpes* and badger *Meles meles* are reported to act as nest predators on forest grouse (Angelstam 1986, Park et al. 2002). In North-America, the American red squirrel *Tamiasciurus hudsonicus* have also reported to act as major nest robbers on spruce grouse *Falci pennis canadensis* (Boag et al. 1984).

Corvids rely on visual cues when searching for food (Picozzi 1975, Storaas 1988). In the boreal forests of northern Europe, magpie *Pica pica*, hooded crow *Corvus corone*, jackdaw *Corvus monedula*, Eurasian jay *Garrulus glandarius*, Siberian jay *Perisoreus infaustus*, and raven *Corvus corax* are the most common corvids and all are known to depredate nests (Andrén et al. 1985, Angelstam 1986). The first three are most numerous in proximity to farmland and human settlements, whereas the latter three are more common in more remote forest and mountain areas (Andrén 1992, Angelstam 1986).

For more than half a decade, artificial nests have been used to understand nest predation and nest predator behavior (Rearden 1951, Balser et al. 1968), mainly because artificial nests are less time consuming and easier to control, both in numbers and placement, compared to natural nests. However, the validity of using artificial nests to measure predation on grouse nests has later been questioned (Storaas 1988, Willebrand & Marcström 1988).

To avoid the danger of misinterpretation, we did not use artificial nests to mimic real nest predation, but as a measure of predator abundance. This approach is similar to that of Storch (1990) and Støen et al. (2010).

In this study, we used artificial nests to compare nest loss in a large Russian nature reserve, the Pinega Reserve, where forestry impact have been negligible and red fox is absent, and at Varaldskogen, which is heavily influenced by modern forestry and where red fox is common. We also placed nests in the forests close to a small village outside Pinega Reserve. In our experiment we placed nests alternately on ground and on poles, thus allowing us to separate the predation from ground predators and avian predators. In Part I we (1) compare total predation rates between the study areas and compare predation on nests placed on poles and on the ground, and (2) relate this to the relative importance of avian and mammalian predators in the two areas. As for (1) we hypothesize that predation rates are highest at Varaldskogen and lowest in Pinega Reserve, with Pinega Village in between, because of more generalist predators at Varaldskogen due to habitat modifications from commercial forestry and closer proximity to human settlements. In Part II we investigate the effect of habitat and nest cover on nest predation rates.

2. Material and methods

2.1 Study area at Varaldskogen

The study area at Varaldskogen (Fig.1) covers ca. 40 km² and is situated at 60°10'N, 12°30'E in Hedmark County, Norway. Altitude varies between 200 and 400 m a.s.l. Snow covers the ground from late November to April and mean yearly air temperature is 3.9°C. Mean air temperature in January and July are -6.0°C and 12.3°C, respectively (Meteorologisk Institutt 2011). Annual mean precipitation is 700 mm.

Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* are the dominant tree species, accounting for 40% and 58% of the standing volume, respectively, interspersed by birch *Betula* spp. and aspen *Populus tremula*. Because of the forest practice up to the late 1980s, clearcuts typically were followed by pure even-aged conifer stands, whereas newer stands are often mixed coniferous (Wegge & Rolstad 2011).

In the spruce dominated forest, bilberry *Vaccinium myrtillus* typically dominates the field layer. After logging, the bilberry is largely replaced by *Deschampsia* and *Calamagrostis* spp. In the pine dominated forest, heather *Calluna vulgaris* and Cowberry *Vaccinium vitis-idaea* typically dominate the field layer. These species are not as affected by logging as bilberry (Wegge & Rolstad 2011).

The area has been intensively managed for several hundred years. For the past 40-50 years, the logging method has been clearcuts harvested in blocks. The average block size is 4ha, although the largest blocks are 50ha (Rolstad et al. 2009).

Spring density of capercaillie is approximately 2.5 and of black grouse 3.3 per km² (P Wegge 2011, pers. comm., 3 May). Nest predation has been studied both on natural and artificial nests in the 1980s (Storaas & Wegge 1987; Storaas 1988; Wegge & Storaas 1990). Known mammalian nest predators are red fox, badger, pine marten, Eurasian red squirrel *Sciurus vulgaris*, stoat, weasel, and mink *Mustela vison*. Known avian nest predators are raven, hooded crow, and Eurasian jay.

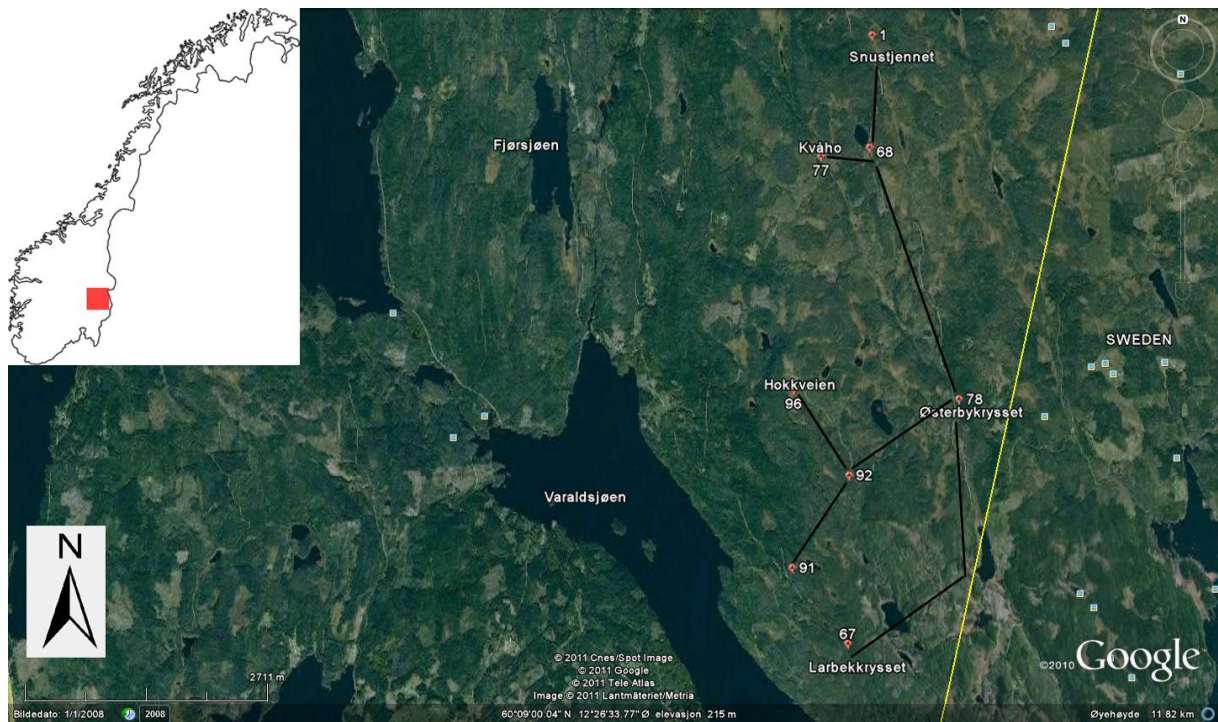


Fig.1: The study area at Varaldskogen, Norway. Black lines are transects where nests were placed. Light patches are clearcuts or bogs, green areas are forests, whereas blue areas are lakes. Numbers indicate nest numbers.

2.2 Study area in Pinega State Forest Reserve, Russia

This 515 km² study area (Fig.2) is located in the upper drainage of the Pinega River approximately 300 km south of Archangelsk in Northeast Russia (64° 35 'N 43°02' E). The area is in the northern taiga subzone at altitudes from 50 to 150 m a.s.l. Lying 200 km south of the polar circle, the long-term average air temperature is 0.16°C. Mean air temperature in January and July are -14.7°C and 14.3°C, respectively. Total yearly precipitation is about 600mm. Snow covers the ground from November to mid-May. The main study was conducted in the reserve with a supplementary experiment carried out in a logged area outside, near Pinega Village.

The Pinega State Forest Reserve (Pinega Reserve)

Siberian spruce *Picea obovata* and *P.obovata*×*P.abies* is the dominant tree species, covering about 75 % of the landscape either in pure stands or intermixed with Scots pine and Siberian larch *Larix sibirica*. Pine, birch, and aspen also grow in pure stands. The latter two form such stands after natural forest fires, often with scattered, surviving, tall larch trees.

Dominant vegetation types are *Vaccinium* spruce forest, moist spruce forest, herb spruce forest, and pine bog, accounting for 54, 10, 10, and 21 % of the forest covered landscape,

receptively (Wegge et al. 2005). Open peat bogs and lakes makes up the remaining 11%. Much of the spruce dominated forest is flooded during the spring break. Old forest is typically two-layered, with trees older than 120 years dominating the overstory and trees of 40-60 years in the understory (Wegge et al. 2005).

In the *Vaccinium* and moist spruce forest, the ground layer is dominated by ericaceous shrubs such as bilberry, Northern bilberry *Vaccinium uliginosum*, and cowberry together with *Melampyrum* spp. and others. The herb spruce forest ground layer is dominated by herbs such as wood cranesbill *Geranium sylvaticum*, arctic starflower *Trientalis europaea*, and marsh hawkbird *Crepis paludosa* together with other herbaceous and flowering plants (Wegge et al. 2005). Because of the limestone bedrock, many orchids thrive within the reserve.

The area has been left largely untouched since the establishment of the reserve in 1974. Approximately 7% of the area was logged in the 1960's and about 21% burned prior to 1960 (Wegge et al. 2005).

Autumn density of capercaillie, black grouse, and hazel grouse has been recorded at 6.2, 5.4, and 46 birds/km², respectively (Borchtchevski et al. 2003), a slightly denser population of capercaillie and lower density of black grouse compared to Varaldskogen. The reserve also supports a population of willow grouse.

Known mammalian predators are pine martens, stoats, weasels, and Eurasian red squirrels (Borchtchevski et al. 2003). Other mammals in the Reserve are brown bears *Ursus arctos*, lynx *Lynx lynx*, mountain hares *Lepus timidus*, and wolverines *Gulo gulo*. The reserve also supports a sparse population of moose *Alces alces* as well as occasional visits of wolves *Canis lupus* and red foxes. Deep snow is probably a reason why the latter two are rare within the reserve. Avian predators are Siberian jays, ravens, goshawks, common buzzards *Buteo buteo*, and several owl species. Siberian jays and ravens are known egg predators.

Pinega State Forest Reserve was established in 1974 and is a part of the Russian zapovednik system. The decision to make it a zapovednik was based upon its karst topography caused by limestone bedrock. Only scientists and rangers are allowed to enter the reserve, and recreational hunting, fishing, berry and mushroom picking etc. is banned inside the reserve. The reserve is used by many scientists: local, national, and international in fields such as

wildlife, fisheries, and soil science. The rangers work includes maintenance work on buildings and transects, security, and assisting the scientists in their work. The scientists collect large amount of data on phenological events and animal populations, such as rodent cycles.

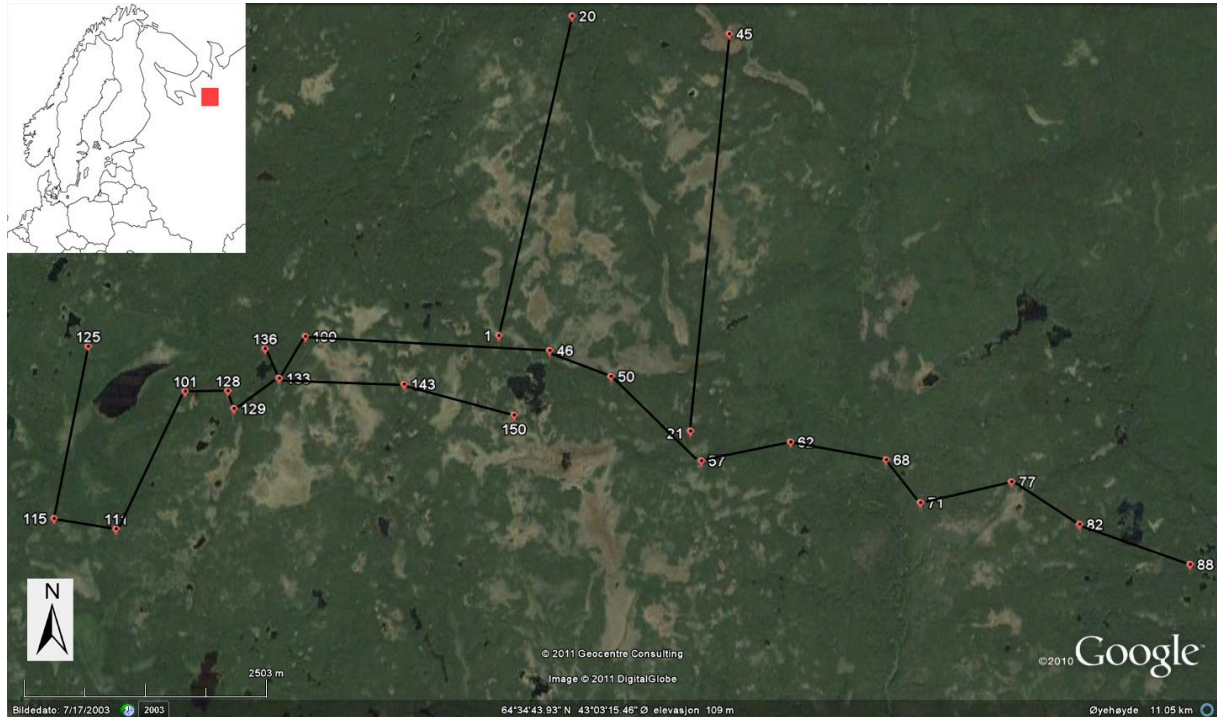


Fig.2: The study area in Pinega Reserve, Russia. Black lines are transects where nests were placed. Light areas are open bogs, green areas are forest and dark blue are lakes. Numbers indicate nest numbers.

Pinega Village

This area is located 2 km from the village of Pinega. Here artificial nests were placed in a naturally regenerated mixed forest of larch, Siberian spruce, and birch on rich soil, logged approximately 10-15 years ago, and in a dry upland pine forest, naturally regenerated after logging approximately 50 years ago. Here we expect more generalist predators like red foxes and crows, although we have no data on the predator fauna.

2.3 Methods

Artificial nests (later referred to as nests) were placed in different forest grouse habitats. We used two different nest types, one that was placed on the ground (ground nests) and one that was placed on a pole (pole nests). Pole nests were available mainly to avian predators whereas ground nests were available to both avian and mammalian predators.

In the Pinega Reserve, 75 pole nests and 75 ground nests were located at alternative sides of a maintenance road running east-west and along transects running east-west or south-north by foot. These transects are narrow clearings approximately 2 m wide.

To compare predation pressure between the reserve and the area outside of the reserve closer to the village, we placed an additional 50 ground nests and 50 pole nests in forests close to Pinega Village. These nests were placed along transects in the same manner as inside the Pinega Reserve.

At Varaldskogen, 48 ground nests and 48 pole nests were placed in the same manner as in Pinega, although following regular forest roads by car instead of walking transects. After 12 days, a second batch of 48 ground nests was placed following the same routine.

In Pinega Reserve, nests were set out between May 31 and June 8 and in Pinega Village on June 3 and 4. On Varaldskogen, all pole nests and the first batch of ground nests were set out on May 16. The second batch of ground nests were set out on May 28.

2.3.1 Nest placement in Pinega Reserve and Pinega Village

Nest sites were chosen by walking 200-paces intervals along transects and placing nests 50-paces perpendicular out from the transect alternatively on the left and the right side and alternatively as ground and pole nests, i.e. the distance between similar nest types was 400 meters. The first nest site was chosen from a random starting point at the transect. After placing the nest and doing the nest site measurements we followed the same tracks back to the transect. All this was done wearing plastic bags on boots to avoid predators following our sent trail.

Each nest contained two brown domestic hen eggs to mimic those of forest grouse. To relocate the exact nest site where the eggs had been removed because of predation, we attached a small piece of red and white flagger to the ground with a golf peg under each of the artificial nests. The peg was not visible as long as the eggs were not removed. Also, a red and white flagger was placed in the vegetation within 2 m from the nests and where we left the transect. All nests were also plotted on a Garmin GPSmap 60SCx.

At the ground nest sites we placed the eggs in a shallow depression directly on the ground, most often without much cover. At the pole nest sites we made the poles by removing the top of a tree 1.5 meter above the ground and removed all the branches from the pole. On the top of the pole we nailed a 30 x 30-cm plywood board and covered it with moss. The eggs were placed in a shallow depression in the moss. To make the eggs less visible from above, we placed a small twig from a spruce or pine over the eggs. To reveal if mammalian predators had climbed the pole and reached the eggs we put brown box sealing tape on the pole, covering the upper 30-50 cm. At most of the nest sites, we placed the pole nests 3 meters away from big trees to prevent predators such as squirrels and pine martens from jumping onto the poles. Smaller trees standing within a 3 meter radius to the pole nest were removed. On nest sites in very dense birch forest it was not possible to remove all trees within a 3 meter radius.

2.3.2 Nest placement at Varaldskogen

The nests at Varaldskogen were placed in the same manner as nests in Pinega Reserve and Pinega Village. However, instead of walking transects as in Pinega, the 200-paces between nest sites was covered riding a car along forest roads and then walking the 50-paces perpendicular to the road. Otherwise, nest type and placement methodology were the same as in Pinega.



Fig.3: Left picture shows a not-depredated pole nest, right picture a depredated pole nest. Photo by Halvor Ingul.

2.3.3 Nest site measurements

Nest site measurements were the same in all study areas. At each nest site we recorded main tree species and habitat. Habitat was categorized as open areas young forest, mature forest, and edge.

At Varaldskogen, open areas were either clearcuts up to 5 years old, treeless bogs or forested bogs with trees older than 70 years. Young forest was forest regenerated artificially after logging (planted (spruce) or seeding from residual seed trees left after logging (pine)) and was between 6 and 50 years old. Mature forest was either artificially regenerated forest older than 50 years or semi-natural pine or spruce forest older than 70 years. Edge was defined as the transition zone between forest and bog or clearcut within 10 m from the very edge.

In Pinega Reserve, open areas were either treeless or forested bogs. Young forest was 2-6 m high naturally regenerated stands, mostly after fire, birch dominated with intermixed Scots pine and spruce trees, with solitary larch trees up to 30 m. Mature forest was dominated by

spruce intermixed with larch, pine, and birch, typically two- or three-layered. Edge was defined as the transition zone from bog to the first full-grown trees in the forest.

In Pinega Village, young forest was very dense birch dominated stands, intermixed with larch and spruce, naturally regenerated after logging 10-15 years ago. Mature forest was pine dominated stands, naturally regenerated after logging approximately 50 years ago.

At ground nests, we measured nest concealment from above (NCA) and vertically from 5 m (NCV) and canopy cover. The sum of NCA and NCV is later referred to as ground cover. At pole nests, only canopy cover was measured.

When estimating NCA, we placed a 30 x 30-cm plywood board with 100 3 x 3-cm black and white squares horizontally onto the nest and counted with one eye closed the number of visible squares seen directly from above, ranging from 0, i.e. no eggs were detected, to 100, i.e. all squares were seen (= poor cover).

When estimating NCV, we placed the checkerboard vertically onto the nest and counted the number of visible squares from all four cardinal directions standing 5 meters away from the nest. We summarized the counts from the 4 different directions to determine how well a nest was concealed, ranging from 0, i.e. no eggs were detected, to 400, i.e. all were seen (=poor cover).

To determine canopy cover we sat down on our knees over the ground nest or as close as possible to the pole nest, leaning back and looked straight up with one eye closed and estimated how many percent of the sky that was covered by trees and branches.

2.3.4 Nest numbers and visitations

At Varaldskogen, a total of 143 nests (96 ground and 47 pole) were distributed as following: 14 in open areas (8 and 6), 44 in young forest (32 and 12), 37 in mature forest (25 and 12), and 48 in edge (31 and 17). In Pinega Reserve, a total of 150 nests were distributed with 24 in open areas (12 and 12), 28 in young forest (17 and 11), 89 in mature forest (41 and 48), and 9 in edge (5 and 4). In Pinega Village, a total of 100 nests were distributed with 25 ground nests and 25 pole nests in young forest and in mature forest.

In the Pinega Reserve, nests were checked for signs of predation 3 times at intervals of approximately 10 days. The eggs were out in the forest for 31 days, 3-5 more days than the incubation period for capercaillie. Outside Pinega Village, nests were checked after 9 and 25 days. At Varaldskogen, nests were checked 4 times at intervals of 5-10 days and were out for 24-29 days in total.

Nests were considered depredated if at least one of the two eggs was eaten on or had been removed from the nest site. When checking the nests, plastic bags were used in the same manner as when placing the nests.



Fig. 4: Left picture shows the main transect in Pinega Reserve, right picture shows transect close to nest 115. Left photo by Vebjørn Oppegaard Pollen and right photo by Halvor Ingul.

2.4 Analyses

Raw data was managed and tables made in Microsoft Office Excel® 2007 (Microsoft Corporation 2002-2007) and figures in SigmaPlot 11.0 (2008 Systat Software, Inc.).

Difference in total predation rate between areas and in predation rate between nest types within areas and between areas was done using two-way contingency tables with Pearson's χ^2 -test in R© version 2.12.1. For all statistical tests a significance level of $\alpha = 0.05$ was used, but when comparing rates between the specific study areas the α -level was Bonferroni adjusted.

For model testing, following the advice of Lewis et al. (2004), we used logistic regression. These analyses were done using R. Packages used were Rcmdr version 1.6-3 and lme4 by Douglas Bates and Martin Maechler. Generalized linear models (GLM) were used for datasets with no random variables, linear mixed-effects models (LMEM) for datasets with random variables. A potentially random variable was considered so if two-way contingency tests with Pearson's χ^2 -test revealed differences in predation rate for this variable if not otherwise stated in text.

Model selection was based on the Akaike Information Criterion corrected for small samples (AICc) and evaluated by AICc weights (w_{AICc}) as recommended by Wagenmakers & Farrell (2004). All models with $\Delta AICc$ value ≤ 2 of the best model were considered to have substantial support and further model selection was based on number of parameters.

When analyzing the effect of habitat and nest concealment separately, differences in predation rate between habitats were tested using two-way contingency tables and Fisher's Exact test in R owing to small sample sizes when splitting the data into nest type and habitat. Differences in nest cover measurements for depredated and not-depredated nests were tested with Wilcoxon or Kruskal-Wallis two-sample test and post-hoc with Dunn method for joint ranking in JMP 9 (2010 SAS Institute Inc.).

3. Results

3.1 Total predation and nest type

3.1.1 Total predation rate

Total predation rate was significantly higher at Varaldskogen compared to Pinega Reserve and Pinega Village ($\chi^2=6.24$ and 8.56 , $df=1$, $p=0.013$ and 0.003), but between the Pinega areas there was no significant difference ($\chi^2=0.46$, $df=1$, $p=0.499$) (Fig.5).

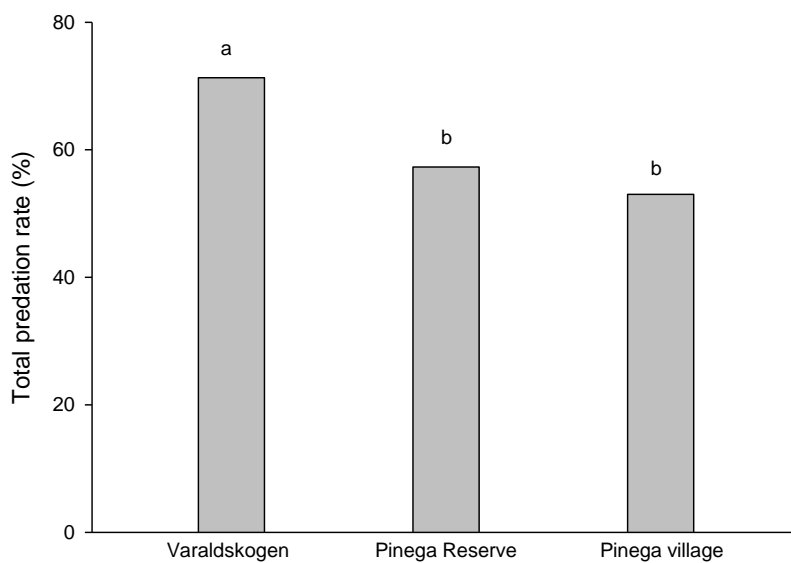


Fig.5: Total predation rates in each study area. Columns with different letters are significantly different at $\alpha=0.05$ level.

3.1.2 Predation rate and nest types

Chi square analysis' revealed that ground nests were depredated at a higher rate than pole nests at Varaldskogen ($\chi^2=32.69$, $df=1$, $p=0.001$), but no difference in predation rate between nest types in neither Pinega Reserve nor Pinega Village ($\chi^2=0.11$ and 0.04 , $df=1$, $p=0.741$ and 0.841) (Fig.6).

Predation rate on ground nests was significantly higher at Varaldskogen compared to Pinega Reserve and Pinega Village ($\chi^2=19.86$ and 18.64 , $df=1$, $p<0.001$). On pole nests there were no differences between areas ($\chi^2=24.76$, $df=2$, $p=0.146$) (Fig.6).

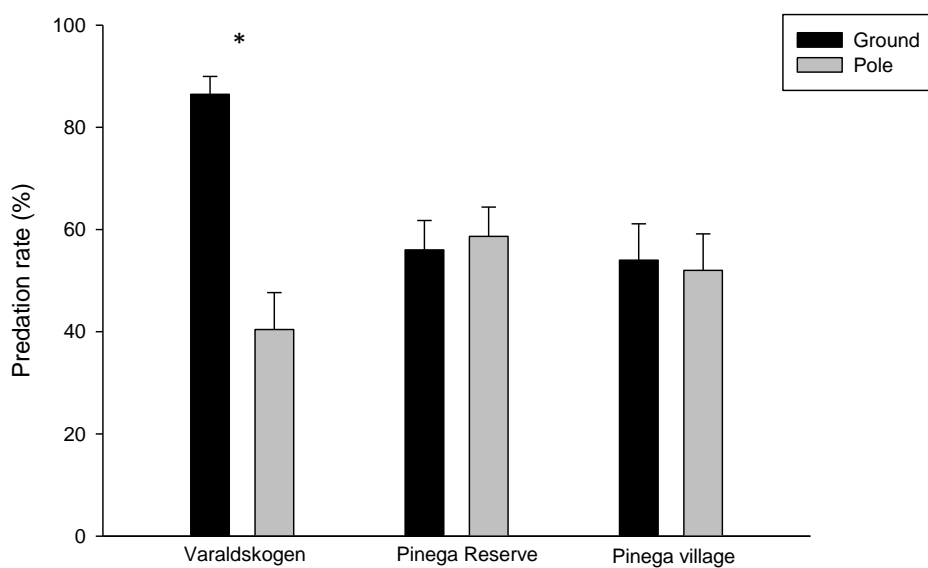


Fig. 6: Predation rate for nest types within each study area. * indicates $\alpha = 0.05$ significant difference between ground and pole nest predation rates. Means are given with SE.

3.2 Model testing and the importance of habitat and nest concealment

3.2.1 Model testing

The model testing shows which variables are best at explaining predation rates for each study area. The best model is chosen based on lowest AICc and number of variables, and the relative likelihood of being the best model is interpreted by the w AICc. The w AICc ratio between two models tells us the relative likelihood that one is the best model compared to the other.

Varaldskogen

For ground nests, predation rates used were measured after 7-10 days because of very high predation. For pole, predation rates were measured after 24 days. A total of 143 nests were placed along 4 road transects. Chi square analysis' revealed no significant difference in predation rate between transects for ground nests or pole nests ($\chi^2=2.60$ and 3.26 , $df=3$, $p=0.457$ and 0.196 , respectively). Therefore, all tests were done using GLM.

Varaldskogen, Ground nests

The dataset consisted of 96 nests. We tested 19 models, among which 4 models were ≤ 2 $\Delta AICc$. Model 1 with only canopy cover was the best model measured by both AICc and number of variables, and was 1.3 times more likely to be the best model compared with model 2 with both canopy cover and NCA as measured by the Akaike criterion (Table 1).

Table 1: Model testing for ground nest predation at Varaldskogen using generalized mixed models (GLM) and Akaike information criterion corrected for small samples (AICc). k number of observations, n number of variables, NCA Nest concealment from above, NCV Nest concealment vertically.

Model	k	n	logLik	AICc	Δ AICc	w AICc	Fixed variable	p-value
1	1	96	-	114.14	0.00	0.386	Intercept	0.0003
							Canopy cover	0.0102
2	2	96	-	114.74	0.60	0.286	Intercept	0.0002
							Canopy cover	0.0189
							NCA	0.2318
3	2	96	-	115.73	1.59	0.174	Intercept	0.002
							Canopy cover	0.0114
							Ground cover	0.4824
4	2	96	-	115.98	1.84	0.154	Intercept	0.0039
							Canopy cover	0.0105
							NCV	0.6184

Varaldskogen, Pole nests

The dataset consisted of 47 observations. Model 1 with only canopy cover was the best model and was 1.8 times more likely to be the best model compared with model 2 with both canopy cover and habitat as measured by the Akaike criterion (Table 2).

Table 2: Model testing for pole nest predation at Varaldskogen using generalized mixed models (GLM) and Akaike information criterion corrected for small samples (AICc). *k* number of observations, *n* number of variables.

Model	k	n	logLik	AICc	Δ AICc	w AICc	Random variable	Fixed variable	p-value
1	47	1	-	69.02	0.00	0.578	-	Intercept	0.660
								Canopy cover	0.652
2	47	3	-	70.18	1.16	0.324	-	Intercept	0.423
								Habitat 1	1.000
								Habitat 2	0.505
								Habitat 3	0.196
3	47	4	-	72.56	3.54	0.098	-	Intercept	0.423
								Canopy cover	0.901
								Habitat 1	0.962
								Habitat 2	0.583
								Habitat 3	0.254

Pinega Reserve

In Pinega Reserve, a total of 150 nests were placed following 5 transects. Chi square analysis' revealed differences in predation rate between transects for both ground and pole nests ($\chi^2=20.91$ and 20.85 , $df=4$, $p<0.001$). Therefore, transect was treated as a random variable using linear mixed-effect models (LMEM).

Pinega Reserve, Ground nests

The dataset consisted of 75 nests. We tested 18 models, among which 6 models were ≤ 2 Δ AICc (Table 3). The best model contained only habitat. The likelihood of being the best model increased some by adding ground cover as seen in model 1, while habitat alone was 2.5 times more likely to be the best model as model 6 containing both habitat and canopy cover as measured by the Akaike criterion (Table 3).

Table 3: Model testing for ground nest predation in Pinega Reserve using linear mixed-effect models (LMEM) and Akaike information criterion corrected for small samples (AICc). *k* number of observations, *n* number of variables, *NCA* Nest concealment from above, *NCV* Nest concealment vertically.

Model	k	n	logLik	AICc	Δ AICc	w AICc	Random variable	Fixed variable	p-value
1	4	75	-41.45	95.18	0.00	0.235	Transect	Intercept	0.640
								Habitat 1	0.329
								Habitat 2	0.014
								Habitat 3	0.051
								Ground cover	0.159
2	3	75	-42.5	95.34	0.16	0.216	Transect	Intercept	0.336
								Habitat 1	0.572
								Habitat 2	0.026
								Habitat 3	0.085
3	4	75	-41.71	95.59	0.41	0.191	Transect	Intercept	0.612
								Habitat 1	0.356
								Habitat 2	0.016
								Habitat 3	0.055
								NCV	0.208
4	4	75	-41.8	95.77	0.59	0.175	Transect	Intercept	0.368
								Habitat 1	0.497
								Habitat 2	0.019
								Habitat 3	0.077
								NCA	0.227
5	5	75		96.94	1.76	0.097	Transect	Intercept	0.610
								Habitat 1	0.344
								Habitat 2	0.014
								Habitat 3	0.056
								NCV	0.312
NCA	0.346								
6	4	75	-42.5	97.17	1.99	0.087	Transect	Intercept	0.343
								Habitat 1	0.585
								Habitat 2	0.035
								Habitat 3	0.086
								Canopy cover	0.978

Pinega Reserve, Pole nests

The dataset consists of 75 observations and was analyzed using LMEM. Model 1 with habitat alone was 2.4 times more likely than model 2 with both habitat and canopy cover and 7.3 times more likely than canopy cover alone to be the best model as measured by the Akaike criterion (Table 4).

Table 4: Model testing for pole nest predation in Pinega Reserve using linear mixed-effect models (LMEM) and Akaike information criterion corrected for small samples (AICc). *k* number of observations, *n* number of variables.

Model	k	n	logLik	AICc	Δ AICc	w AICc	Random variable	Fixed variable	p-value
1	75	3	-	90.60	0.00	0.646	Transect	Intercept	0.414
								Habitat 1	0.037
								Habitat 2	0.958
								Habitat 3	0.395
2	75	4	-	92.37	1.77	0.266	Transect	Intercept	0.419
								Canopy cover	0.630
								Habitat 1	0.051
								Habitat 2	0.794
								Habitat 3	0.349
3	75	1	-	94.59	3.99	0.088	Transect	Intercept	0.406
								Canopy cover	0.458

Pinega Village

Near Pinega Village, 100 nests were placed in 2 separate areas or transects. Chi-square analysis revealed significant differences in predation rates between transects for both ground nests and pole nests ($\chi^2=35.51$ and 25.96 , $df=1$, $p<0.001$, respectively). However, as transect 6 consisted of only young forest and transect 7 of only mature forest, separating a random effect of transect from a habitat effect was not possible. Therefore, all tests were done using GLM and no random variable.

Pinega Village, Ground nests

The dataset consists of 50 observations. Using GLM, 7 models were tested among which 3 were $\leq 2 \Delta AICc$. Model 1 with habitat was the best model. Measured by the Akaike criterion, model 1 was roughly 2.4 and 2.6 times more likely to be the best model compared to model 2 and 3 which included NCA and canopy cover, respectively (Table 5).

Table 5: Model testing for ground nest predation in Pinega Village using generalized linear models (GLM) and Akaike information criterion corrected for small samples (AICc). k number of observations, n number of variables, NCA Nest concealment from above.

Model	k	n	logLik	AICc	$\Delta AICc$	w AICc	Random variable	Fixed variable	p-value
1	1	50	-	30.83	0.000	0.558	-	Intercept Habitat	<0.0001 <0.0001
3	2	50	-	32.62	1.792	0.228	-	Intercept Habitat NCA	0.0001 0.0005 0.5441
3	2	50	-	32.75	1.919	0.214	-	Intercept Habitat Canopy cover	0.0015 <0.0001 0.6166

Pinega Village, Pole nests

The dataset consisted of 50 observations and was analyzed using GLM. Habitat was found to make the best model and was only slightly improved by adding canopy cover (table 6).

Table 6: Model testing for pole nest predation in Pinega Village using generalized mixed models (GLM) and Akaike information criterion corrected for small samples (AICc). *k* number of observations, *n* number of variables.

Model	k	n	logLik	AICc	Δ AICc	w AICc	Random variable	Fixed variable	p-value
1	2	50	-	44.32	0.00	0.511	-	Intercept	0.890
								Habitat	<0.0001
								Canopy cover	0.147
2	1	50	-	44.41	0.09	0.489	-	Intercept	<0.0001
								Habitat	<0.0001
3	1	50	-	67.69	23.36	0.000	-	Intercept	0.032
								Canopy cover	0.027

3.3 The effect of habitat and nest cover within the study areas

The model testing showed us which variables best explained nest predation rates in each study area. The models, however, did not tell us how predation varies between habitats and in which direction and habitats cover influences predation rates within each study area.

3.3.1 Predation, habitat, and mean canopy cover

At Varaldskogen, Fisher's exact test revealed no difference in neither ground nor pole nest predation rates between habitats (n=96 and 47, p=0.204 and 0.384, respectively). Here, mean canopy cover was significantly lower in open areas compared to in young forest, mature forest, and edge (Z=3.89, 4.20, and 3.51, p<0.001 and 0.003, respectively) (Fig.7a).

In Pinega Reserve, there was a significant differences in predation rates between habitats for ground nests, but not pole nests (n=75, p=0.018 and 0.113, respectively). Particularly was the predation rate in open areas a lot lower than in mature forest (n=53, p=0.102). Mean canopy cover was lower in open areas compared to in young and mature forest (Z=3.81 and 4.33, p<0.001, respectively) (Fig.7b).

In Pinega Village, both nest types were depredated at a much higher level in mature forest as compared to in young forest ($n=50$, $p<0.001$). Mean canopy cover was higher in young forest than mature forest ($Z=-1.67$, $p=0.094$) (Fig.7c).

In all areas there was greater difference in predation rate between habitats for ground nests than pole nests.

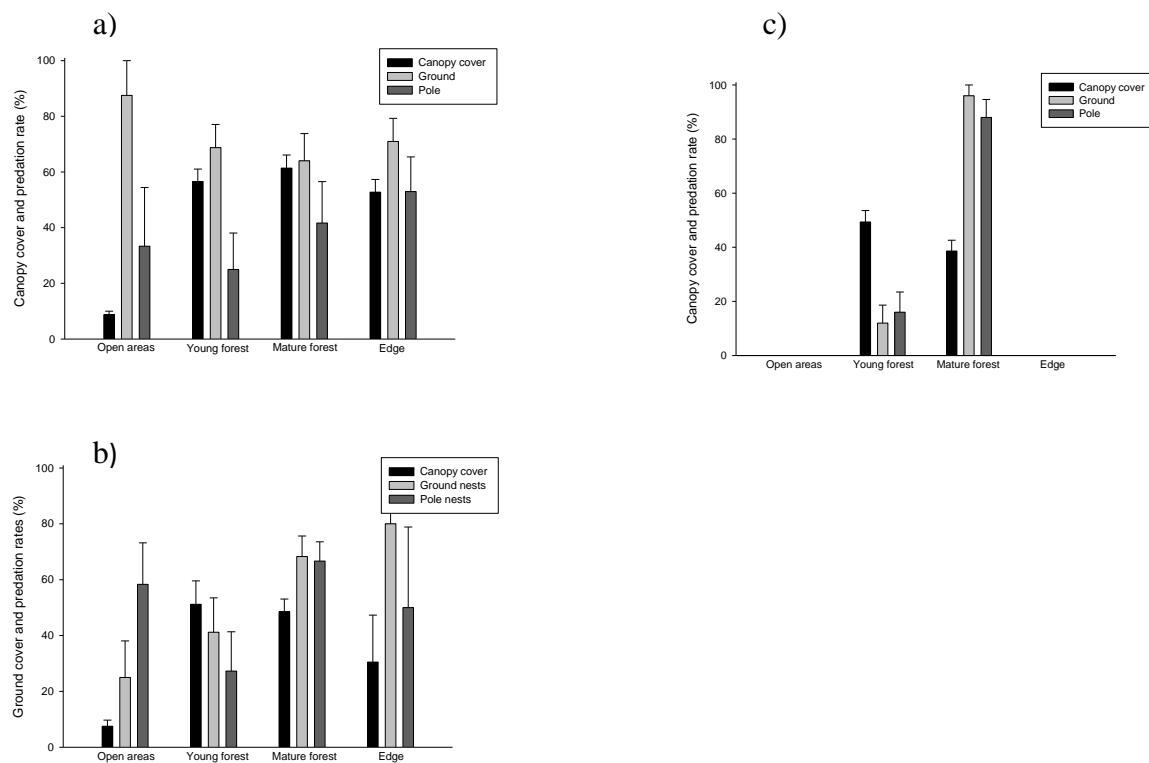


Fig.7: Mean canopy cover on ground nests and predation rates for ground and pole nests for habitats in a) Varaldskogen, b) Pinega Reserve, and c) Pinega Village. All columns show means with SE.

3.3.2 Predation and cover

At Varaldskogen, canopy cover was lower for depredated nests compared to not-depredated ground nests in young and mature forest, although only significantly in the latter ($Z=2.37$, $p=0.018$) as revealed by Wilcoxon two-way test (Fig.8a). In Pinega Reserve, canopy cover was significantly lower for depredated compared to not-depredated ground nests in young forest ($Z=-2.10$, $p=0.035$) (Fig.8b).

For pole nests, canopy cover was higher for depredated nests compared to not-depredated nests in young and mature forest at Varaldskogen (Fig.8a) and lower in young forest in Pinega Village ($Z=-1.68$, $p=0.094$) (Fig.8c).

Ground cover showed very little variation between depredated and not-depredated nests at Varaldskogen (Fig.8d). In Pinega Reserve, predation rates decreased with increasing ground cover in young and mature forest, but only significantly in mature forest ($Z=2.07$, $p=0.038$) (Fig.8e).

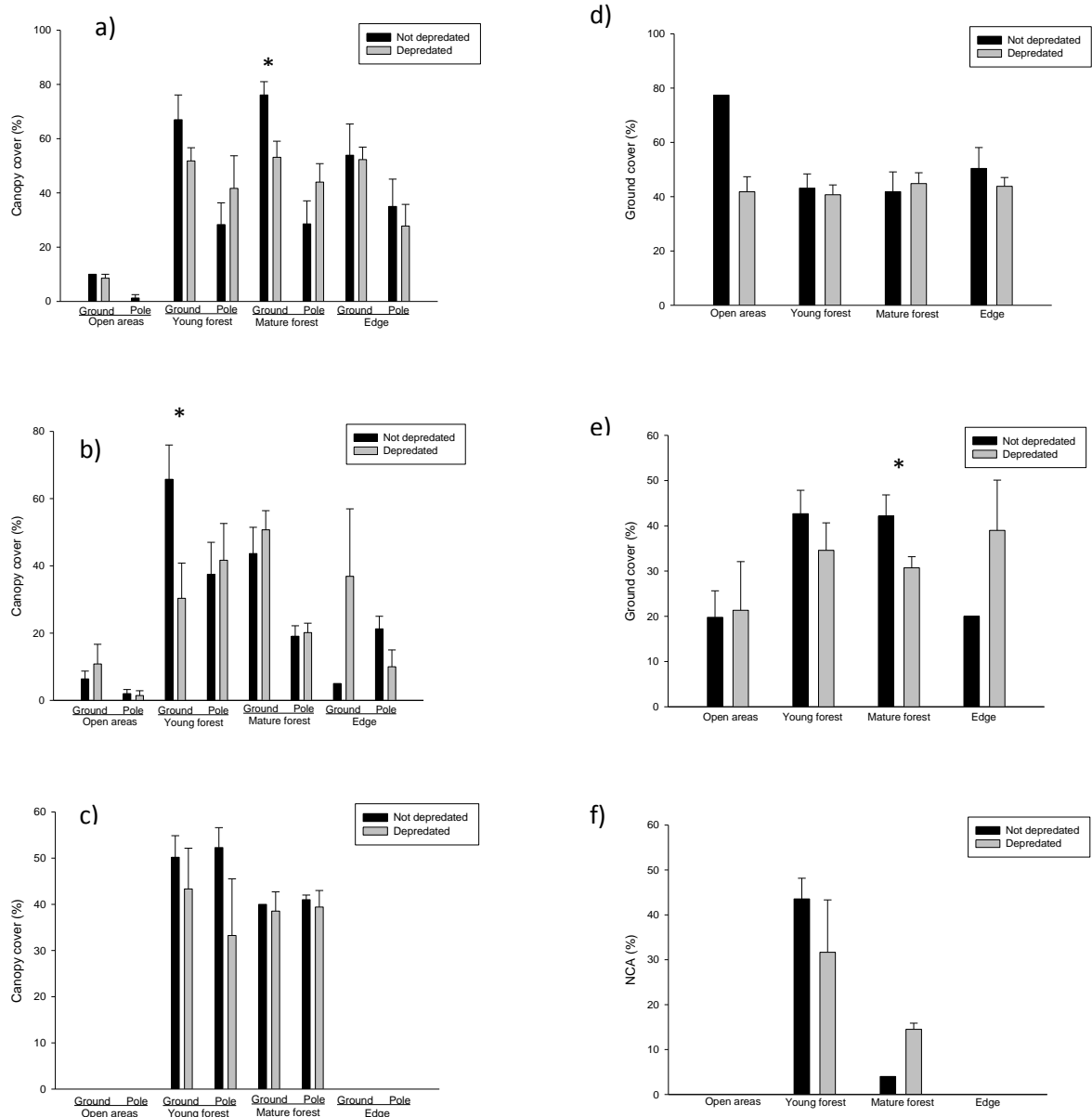


Fig. 8: a – c) canopy cover according to nest type and habitat in a) Varaldskogen, b) Pinega Reserve, and c) Pinega Village. d – e) Ground cover according to habitat in d) Varaldskogen and e) Pinega Reserve, and f) nest concealment from above (NCA) according to habitat in Pinega Village. d – f) is for ground nests only. Means are given with SE and * indicates difference between not-depredated and depredated nests at $\alpha = 0.05$ significance level.

4. Discussion

4.1 Total predation and nest type

4.1.1 The effect of geography and landscape composition on total predation pressure

Varaldskogen

Predation was significantly higher at Varaldskogen than in Pinega Reserve. This may be due to more mammalian and avian generalist predators when moving southwards in Fennoscandia (Hanski et al. 1991). This was probably a result of generally higher productivity and more landscape alterations through forestry and agriculture in the south as well as different prey communities between north and south (Andrén et al. 1985, Kurki et al. 1997). There was no significant difference in pole nest predation between the study areas, which indicate that avian predators are important regardless of geography.

Ground nests suffered higher losses than pole nests at Varaldskogen. In general, avian predators depredate nests placed in shrubs while mammalian predators depredate ground nests (Söderström et al. 1998) and we therefore believe mammalian were most important at Varaldskogen.

Recent track counts from Varaldskogen and Pinega showed that the relative density of pine marten was slightly lower at Varaldskogen than in the Pinega area, with 1.0 tracks/10km and 2.8 tracks/10km, respectively (Hjeljord et al. 2009, unpublished data) which in part may be due to winter trapping at Varaldskogen (P Wegge 2011, pers. comm., 10 May). Pine martens have been documented as nest predators by wildlife cameras, and accounted for as much as 13 % of the depredated nests in a recent study in Hedmark (T Jahren 2011, pers. comm., 10 March). With the exception of clearcuts, pine martens are not negatively influenced by modern forestry (Gundersen & Rolstad 2000). However, as their habitat use is restricted by open areas and the density of the species is relatively low, the total predation impact from pine marten should be lower than from red fox. Despite a decline in red fox numbers at Varaldskogen during the last 10 years, it is still the most important predator at Varaldskogen (Wegge & Rolstad 2011). Red foxes are considered to be habitat generalists and Gundersen & Rolstad (2000) also found a correlation between fragmentation by clearcuts and red fox numbers, perhaps as a result of higher numbers of small rodents on clearcuts (Hansson 1994).

Apart from forestry per se, Varaldskogen is influenced by hunting and other human activity. Moose numbers have exploded in Norway in the last five decades with high numbers of moose killed each year (Statistics Norway 2011), and hunting residues may therefore supply red fox populations with additional food and thus sustain higher numbers of this species.

Surprisingly, pole nests suffered lower predation than expected. Andrén (1992) found higher densities of hooded crow in landscapes where agriculture and forests intermix than in large, continuous forest areas. We had expected hooded crows to strongly influence nest predation, but the majority of hooded crows were probably confined closer to human settlements, rather than in the more remote areas at Varaldskogen. Ravens and Eurasian jays have been reported as the main nest predators in forest areas (Angelstam 1986) and these were probably the most important avian predators in our study area. Ravens are also considered to be food opportunists and may thus benefit from carcasses (Marzluff & Neatherlin 2006, Rösner & Selva 2005) which may be an important food source for these at Varaldskogen. Nests at Varaldskogen were distributed along forest roads which could function as “travel lines” for certain species. This was rejected for predators such as red foxes (Svobodova et al. 2007). However, Røttereng & Simonsen (2010) found a positive association between roads and predation from raven, and explained this by active search for road kills. It could therefore be argued that our nests in proximity to roads at Varaldskogen may have affected predation rates.

The significantly higher predation rates on ground than pole nests at Varaldskogen are probably a result of high red fox densities, with additional predation from pine marten. Avian predators, mainly ravens and Eurasian jays, have acted as important nest robbers, but because the impact from hooded crows is low, predation on pole nests was not as high as expected.

Pinega Reserve

There was no significant difference between ground and pole nests in Pinega Reserve. The human impact within Pinega Reserve is low and predators that benefit from human activity are probably absent or at very low densities. The lack of red foxes and hooded crows could therefore explain the relatively lower predation rates than at Varaldskogen.

Ravens have excellent sight and cover home ranges from 14 to 18 km² (Luginbuhl et al. 2001) and have been described as important nest predators (Angelstam 1986). Raven was observed twice during the seven weeks in the reserve and one of the times close to a nest site. Ravens

have been reported to respond opportunistically to human disturbances at waterfowl nest sites (Kelly et al. 2005) and it may therefore be argued that our movements could have attracted ravens when we placed or checked the nests.

Based on number of observations, Siberian jay was the most numerous corvid in the reserve. According to Gienapp & Merilä (2011), Siberian jays are associated with old-growth forest, but this should not have hindered Siberian jays from entering adjacent younger forest stands. Siberian jays and ravens also show different search patterns, as the Siberian jays are confined to the lower layers in the forest, whereas ravens also may search for food by flying above the forest. Siberian jays generally avoid open areas because of predation risk from goshawks (Griesser & Nystrand 2009) but there is no such evidence for ravens. Thus, Siberian jays and ravens were probably both important avian predators, leading to high pole nest losses in all habitat types.

As red foxes are absent within the reserve and badgers are rare in northwestern Russia other mammalian species have acted as nest predators within the reserve. Squirrels have been reported to act as major nest predators on spruce grouse (Boag et al. 1984) and Hjeljord et al. (2009, unpublished data) reported high numbers of squirrels within the reserve. Squirrels are positively correlated to forest interiors and spruce share on a landscape scale and similar to pine martens, they avoid open areas (Andrén & Delin 1994, Brainerd & Rolstad 2002). Hence, together with pine martens, they have probably been important nest predators in the reserve. However, because red foxes are absent, total predation rates were lower than at Varaldskogen.

Two of our nests were depredated by brown bears. Even though this constitutes only a small proportion of the robbed nests, it clearly shows that brown bear may act as a depredator within the reserve.

Presumably, pine martens and squirrels were not able to exert the same predation pressure as the combination of red fox and pine marten at Varaldskogen. Conversely, avian predators appeared to be as abundant as at Varaldskogen, but here the European jay was replaced by the Siberian jay. The results that ground and pole nests suffered similar predation but ground nests survived better than at Varaldskogen supports the idea of lower total nest predation pressure within the reserve. With red fox absent, they also supports the inference that red fox is a main nest predator on grouse nests in areas where it occurs.

Pinega Village

Pinega Village is situated close to human settlements and the surrounding forests are heavily influenced by forestry. We therefore expected predation to be similar to Varaldskogen. However, total predation was significantly lower than at Varaldskogen. Predation rates in the young forest were extremely low compared to mature forest. The young forest was extremely dense and this could have prevented the predators' movements within the forest and thus cause low predation rates. Therefore, it is probably the forest structure and not the lack of predators in Pinega Village that has led to low predation in this habitat.

Like in the reserve, pole and ground nests suffered similar predation rates in Pinega Village. Based on Söderström et al. (1998) we believe that avian predators and mammalian predators were equally important, the latter consisting mainly of pine martens and squirrels, as red fox is rare in this area (Hjeljord et al. 2009, unpublished data).

The study site in Pinega Village is situated close to human settlements and hooded crows were probably more important here than at Varaldskogen. Also, the forests surrounding Pinega Village should also support raven and Siberian jay populations (Angelstam 1986, Gienapp & Merilä 2011). Thus, the equal impact from mammalian and avian predators could be explained by the presence of ravens, hooded crows and Siberian jays as well as pine martens, squirrels and red foxes.

4.1.2 Small rodent cycles in relation to predation pressure

We had expected nest losses to vary according to the alternative prey hypothesis (Hagen 1952, Angelstam et al. 1984) but despite a peak year for small rodents in 2010 at Varaldskogen (P Wegge 2011, pers. comm., 10 May) predation was still high. Predators probably do not search actively for nests as they constitute a rather low and unpredictable food source (Storaas & Wegge 1987). Our artificial nests were probably found "by chance" as olfactory cues should be low. Certain predators may have immigrated to the study area in response to the increasing number of small rodents in the prepeak and peak years, i.e. a numeric response, leading to high predator densities and consequently high nest losses. In Pinega, small rodent numbers have been low for several years (A Sivkov 2011, pers. comm.) and predators have therefore not responded numerically and consequently nest losses remained low. Also, Helldin (1999) and Rosselini et al. (2008) found that pine martens may

increase consumption of mountain hares and young squirrels when small rodent numbers are low. Thus, a high density of squirrels within the reserve may have functioned as alternative prey for pine martens.

4.2 Model testing and the importance of habitat and cover

4.2.1. Model testing

The model testing showed that canopy cover was the main explanatory variable for both ground and pole nests Varaldskogen, whereas habitat was most important in the Pinega areas.

The effect of both habitat and cover on the predation rate on artificial nests is uncertain. Svobodova et al. (2004) found no effect of habitat, whereas Storch (1990) found predation rates to increase with successional stages, but to be independent of ground cover. Einarsen et al. (2008) also found predation rates to increase with successional stage, whereas Storaas (1988) and Svobodova et al. (2004) found an effect of nest cover.

One possible explanation when there is no habitat effect is the presence of habitat generalist predators, as with corvid birds and red foxes at Varaldskogen. In Pinega, pine martens, Eurasian red squirrels, Siberian jays, and ravens were probably the major nest predators. Pine martens (Gundersen & Rolstad 2000; Brainerd & Rolstad 2002) and Siberian jays (Griesser & Nystrand 2009) are known to avoid open areas and Eurasian red squirrels are known to prefer habitats with high proportions of Norway spruce (Delin & Andrén 1999). These species can thus be considered habitat specialists, while ravens are found to scavenge irrespectively of habitat (Rösner & Selva 2005). Thus, different composition of predators – mainly generalists at Varaldskogen and specialists in Pinega – may explain why we found an overall effect of habitat in Pinega Reserve but not at Varaldskogen.

4.2.2 The importance of habitat and cover

Varaldskogen

At Varaldskogen, predation rates were highest in open areas and in general high for ground nests. Canopy cover was negatively correlated with predation on ground nests in both young and mature forest, and it also explained predation rates between habitats.

The high predation on ground nests in open areas was probably a combination of habitat and predator fauna. We believe red foxes were the main predator here, and earlier studies have found red foxes to prefer (Hansson 1994) or use clearcuts equally (Gundersen & Rolstad 2000) to forest interiors and edge habitats. The general lack of a significant habitat effect is also supported by Svobodova (2004), whose study was conducted in an area with clearcuts and red foxes.

When we compared mean canopy cover and predation in each habitat, we found that they were negatively correlated. Equally, Einarsen et al. (2008) found predation rates to decrease as the coniferous canopy closed in. At Varaldskogen, this was not only the case for the whole area, but also when we compared depredated and not-depredated nests in young and mature forest. Between habitats, our results indicated that canopy cover described predation rates in each habitat as well as habitat itself. In addition, it gave information on predation on nests inside habitats, making the overall explanatory value of canopy cover quite high. The effect of canopy cover but not of ground cover in young and mature forest suggested that forest structure was more important than nest cover. This is further supported by the relative importance of mammalian versus avian predators revealed by the ground – pole predation ratio. The missing effect of ground cover was similar to Huhta et al. (1996) and Martin (1987), but Storaas (1988) found higher predation on artificial nests with poor cover than nests with good cover. This was possibly because Storaas deliberately placed nests with very good or very poor cover, whereas most of the nests in our study had medium cover.

Pinega Reserve

In contrast to Varaldskogen, predation on ground nests was low in open areas in Pinega Reserve. We believe this was a combination of pine martens and red squirrels preferring forested habitats and more or less avoiding low productive bogs. Also, we believe the ground nests were less visible than our ground cover measurements indicated in this habitat. First, there was no difference in ground cover for depredated and not-depredated nests in contrast to what we found in young and mature forest. Secondly, pole nests were depredated to a much higher extent than ground nests in open areas. An explanation is that the eggs partly sunk into the bog surface, making them less visible than the ground cover measurements implied. In young forest in the reserve, predation on ground nests was higher and on pole nests lower than in open areas. The first supports the predator habitat preference hypothesis. Compared to

at Varaldskogen, predation on ground nests in young forest was lower in Pinega Reserve. Canopy cover was negatively correlated to predation on ground nests, but not on pole nests. The young forest in Pinega reserve was very dense with a high proportion of birch and high mean canopy cover. Huhta et al. (1996) suggests that predators may prefer habitats with a high proportion of conifers, so maybe the high proportion of birch made young forest less suitable for predators compared to the more Norway spruce and Scots pine dominated stands at Varaldskogen. Especially for corvid birds may the dense young forest with low height have been unsuitable, explaining the low predation on pole nests. On ground nests, predation decreased with higher canopy cover, but as the pole nests were deliberately placed more openly, the lack of an effect of canopy cover on pole nests inside the habitat was expected. The effect of canopy and ground cover on ground nests in young forest and of ground cover in mature forest suggests that sight-oriented predators have played an important role. Besides corvid birds, this may also have included small tree-dwelling mammals such as pine martens and squirrels.

Pinega Village

In Pinega Village, predation rates were much higher in mature forest compared to young forest, similar to in Pinega Reserve and for pole nests at Varaldskogen. Also, canopy cover was higher and NCA significantly higher in young compared to mature forest. Thus, when comparing habitats, predation rate was negatively correlated both with canopy cover and NCA, with the latter being most important.

Further, tree height in young forest was low, the proportion of deciduous trees high, and tree density extreme, so like in Pinega Reserve, we believe both avian and mammalian predators may have found the habitat unsuitable. The lack of a cover effect between depredated and not-depredated nests within the habitats underpins the importance of habitat per se. However, few nests were depredated in young forest and almost all nests were depredated in mature forest, so caution should be taken before concluding upon the importance of nest cover within the habitats.

5. Conclusion

As expected, total predation was higher at Varaldskogen than in Pinega. Comparing ground and pole nests, mammalian predators seems to be most important at Varaldskogen whereas avian predators are equally or more important than mammalian in Pinega. Red foxes are abundant at Varaldskogen, probably because of its southern location and human influence, and are likely to be the most important predator here. In Pinega, red foxes are more or less absent, leaving pine martens and red squirrels as well as Siberian jays and ravens as the main predators.

The model testing revealed that canopy cover was best at explaining nest predation rates in the whole Varaldskogen study area, whereas habitat was best in the Pinega areas. This is consistent with generalist predators being most important at Varaldskogen and specialists in Pinega. When explaining predation within habitats, both canopy and ground cover found only limited and inconsistent support.

References

- Andrén, H.** (1992). Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. *Ecology* 73: 794-804.
- Andrén, H. & Angelstam, P.** (1988). Elevated predation rates as an edge effect in habitat islands: Experimental evidence. *Ecology* 69: 544-547.
- Andrén, H. & Delin, A.** (1994). Habitat selection in the Eurasian red squirrel, *Sciurus vulgaris*, in relation to forest fragmentation. *Oikos* 70: 43-48.
- Andrén, H., Angelstam, P., Lindström, E. & Widén, P.** (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., Lindström, E. & Widén, P.** (1984). Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62: 199-208.
- Balser, D.S., Hill, H.H. & Nelson, H.K.** (1968). Effect of predator reduction on waterfowl nesting success. *The Journal of Wildlife Management* 32: 669-682.
- Batary, P. & Baldi, A.** (2004). Evidence of an edge effect on avian nest success. *Conservation Biology* 18: 389-400.
- Boag, D.A., Reeb, S.G. & Schroeder, M.A.** (1984). Egg loss among spruce grouse inhabiting lodgepole pile forests. *Canadian Journal of Zoology* 62: 1034-1037.
- Borchchevski, V.G., Hjeljord, O., Wegge, P. & Sivkov, A.V.** (2003). Does fragmentation by logging reduce grouse reproductive success in boreal forests? *Wildlife Biology* 9: 275-282.
- Brainerd, S.M. & Rolstad, J.** (2002). Habitat selection by Eurasian pine martens *Martes martes* in managed forests of southern boreal Scandinavia. *Wildlife Biology* 8: 289-297.
- Brzezinski, M., Zmihorski, M. & Barkowska, M.** (2010). Spatio-temporal variation in predation on artificial ground nests: a 12-year experiment. *Annales Zoologici Fennici* 47: 173-183.
- Delin, A.E. & Andrén, H.** (1999). Effects of habitat fragmentation on Eurasian red squirrel (*Sciurus vulgaris*) in a forest landscape. *Landscape Ecology* 14: 67-72.
- Einarsen, G., Hausner, V.H., Yoccoz, N.G. & Ims, R.A.** (2008). Predation on artificial ground nests in birch forests fragmented by spruce plantations. *Ecoscience* 15: 141-149.
- Gienapp, P. & Merilä, J.** (2011). Sex-specific fitness consequences of dispersal in Siberian jays. *Behavioral Ecology and Sociobiology* 65: 131-140.

- Google. Google Earth®.** (2011). Version 6.0.1.2032 (beta). California, USA.
- Griesser, M. & Nystrand, M.** (2009). Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. *Behavioral Ecology* 20: 709-715.
- Gundersen, V. & Rolstad.** (2000). Rev *Vulpes vulpes* og mår *Martes martes* i boreal skog: Har habitatfragmenteringen medført økt predasjonstrykk? *Fauna* 53: 186-199.
- Hagen, Y.** (1952). Rovfuglene og viltpleien. Gyldendal norske forlag, Oslo, Norway.
- Hannon, S.J., Martin, K. & Schieck, J.O.** (1988). Timing of reproduction in two populations of willow ptarmigan in Northern Canada. *The Auk* 105: 330-338.
- Hanski, I., Hansson, L. & Henttonen, H.** (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* 60: 353-367.
- Hansson, L.** (1994). Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. *Landscape Ecology* 9: 105-115.
- Helldin, J.-O.** (1999). Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography* 22: 324-336.
- Hughes, N.K., Price, C.J. & Banks, P.B.** (2010). Predators are attracted to the olfactory signals of prey. *PLoS ONE* 5: 1-4.
- Huhta, E., Mappes, T. & Jokimaki, J.** (1996). Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. *Ecography* 19: 85-91.
- Kelly, J.P., Etienne, K.L. & Roth, J.E.** (2005). Factors influencing the nest predatory behaviors of common ravens in heronries. *The Condor* 107: 402-415.
- Klaus, S.** (1991). Effects of forestry on grouse populations: Case studies from the Thuringian and Bohemian forests, Central Europe. *Ornis Scandinavica* 22: 218-223.
- Klausen, K.B., Pedersen, Å.Ø., Yoccoz, N.G. & Ims, R.A.** (2010). Prevalence of nest predators in a sub-Arctic ecosystem. *European Journal of Wildlife Research* 56: 221-232.
- Kurki, S., Helle, P., Lindén, H. & Nikula, A.** (1997). Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. *Oikos* 79: 301-310.
- Kurki, S., Nikula, A., Helle, P. & Lindén, H.** (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., Nikula, A., Helle, P. & Lindén, H.** (2000). Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* 81: 1985-1997.
- Lewis, K.P.** (2004). How important is the statistical approach for analyzing categorical data? A critique using artificial nests. *Oikos* 104: 305-315.

- Lindström, J.** (1994). Tetraonid population studies – state of the art. *Annales Zoologici Fennici* 31: 347-364.
- Luginbuhl, J.M., Marzluff, J.M., Bradley, J.E., Raphael, M.G. & Varland, D.E.** (2001). Corvid survey techniques and the relationship between corvid relative abundance and nest predation. *Journal of Field Ornithology* 72: 556-572.
- Martin, T.E.** (1987). Artificial nest experiments: Effects of nest appearance and type of predator. *The Condor* 89: 925-928.
- Marzluff, J.M. & Neatherlin, E.** (2006). Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. *Biological Conservation* 130: 301-314.
- Meteorologisk institutt.** (2010). eKlima. <http://eklima.met.no> [Lesedato: 05.03.2011].
- Microsoft Corporation.** (2007). Microsoft Office Excel[®], Version 2007. Washington, USA.
- Park, K.J., Booth, F., Newborn, D. & Hudson, P.J.** (2002). Breeding losses of red grouse in Glen Esk (NE Scotland): Comparative studies, 30 years on. *Annales Zoologici Fennici* 39: 21-28.
- Paton, P.W.C.** (1994). The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8: 17-26.
- Picozzi, N.** (1975). Crow predation on marked nests. *The Journal of Wildlife Management* 39: 151-155.
- R Foundation for Statistical Computing.** (2010). R[®], Version 2.12.1. Vienna, Austria.
- Rearden, J.D.** (1951). Identification of waterfowl nest predators. *The Journal of Wildlife Management* 15: 386-395.
- Rolstad, J., Wegge, P., Sivkov, A.V., Hjeljord, O. & Storaunet, K.O.** (2009). Size and spacing of grouse leks: Comparing capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) in two contrasting Eurasian boreal forest landscapes. *Canadian Journal of Zoology* 87: 1032-1043.
- Rosselini, S., Barja, I. & Pintero, A.** (2008). The response of European pine marten (*Martes martes* L.) feeding to the changes of small mammal abundance. *Polish Journal of Ecology* 56: 497-504.
- Rösner, S. & Selva, N.** (2005). Use of bait-marking method to estimate the territory size of scavenging birds: A case study on ravens *Corvus corax*. *Wildlife Biology* 11: 183-191.
- Røttereng, L.C.M. & Simonsen, M.** (2010). Predation on artificial nests in relation to human activity and willow ptarmigan density along landscape gradients in a boreal ecosystem. Master thesis – Department of ecology and natural resource management, Norwegian university of life sciences.

Saniga, M. (2002). Nest loss and chick mortality in capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) in West Carpathians. *Folia Zoologica* 51: 205-214.

SAS Institute Inc. (2010). JMP[®], Version 9.0. North Carolina, USA.

Systat Software Inc. (2008) SigmaPlot[®], Version 11.0. California, USA.

Sirkia, S., Lindén, A., Helle, P., Nikula, A., Knape, J. & Lindén, H. (2010). Are the declining trends in forest grouse populations due to changes in the forest age structure? A case study of Capercaillie in Finland. *Biological Conservation* 143: 1540-1548.

Statistics Norway (2011). Felte elg, Norge. 1889-2010. <http://www.ssb.no/elgjakt/fig-2011-03-24-01.html>. Norwegian.

Storaas, T. (1988). A comparison of losses in artificial and naturally occurring capercaillie nests. *The Journal of Wildlife Management* 52: 123-126.

Storaas, T., Kastdalen, L. & Wegge, P. (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. & Wegge, P. (1987). Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. *The Journal of Wildlife Management* 51: 167-172.

Storch, I. (1990). Habitat fragmentation, nest site selection, and nest predation risk in Capercaillie. *Ornis Scandinavica* 22: 213-217.

Storch, I. (2007). Grouse: Status survey and conservation action plan 2006 – 2010. Gland, Switzerland: IUCN and Fordingbridge, UK: World Pheasant Association. 114 pp.

Storch, I. & Leidenberger, C. (2003). Tourism, mountain huts and distribution of corvids in the Bavarian alps, Germany. *Wildlife Biology* 9: 301-308.

Svobodova, J., Albrecht, T. & Salek, M. (2004). The relationship between predation risk and occurrence of black grouse (*Tetrao tetrix*) in a highly fragmented landscape: An experiment based on artificial nests. *Ecoscience* 11: 421-427.

Svobodova, J., Salek, M. & Albrecht, T. (2007). Roads do not increase predation on experimental nests in a highly fragmented forest landscape. *Folia Zoologica* 56: 84-89.

Støen, O.G., Wegge, P., Heid, S., Hjeljord, O. & Nellemann, C. (2010). The effect of recreational homes on willow ptarmigan (*Lagopus lagopus*) in a mountain area of Norway. *European Journal of Wildlife Research* 56: 789-795.

Söderström, B., Pärt, T. & Rydén, J. (1998). Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and review. *Oecologia* 117: 108-118.

- Wagenmakers, E.J. & Farrell, S.** (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review* 11: 192-196.
- Watson, A. & Moss, R.** (2008). Grouse. The natural history of British and Irish species. Harper Collins, London, England. 529 pp.
- Wegge, P., Olstad, T., Gregersen, H., Hjeljord, O. & Sivkov, A.V.** (2005). Capercaillie broods in pristine boreal forest in northwestern Russia: The importance of insects and cover in habitat selection. *Canadian Journal of Zoology* 83: 1547-1555.
- Wegge, P. & Rolstad, J.** (2011). Clearcutting forestry and Eurasian boreal forest grouse: Long-term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *T.tetrix* reveals unexpected effects on their population performances. *Forest Ecology and Management* 261: 1520-1529.
- Wegge, P. & Storaas, T.** (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., Dilger, M.L., Robson, D., Hallyn, N. & Dilger, S.** (1994). Effects of olfactory cues on artificial-nest experiments. *The Auk* 111: 945-952.
- Willebrand, T. & Marcström, V.** (1988). On the danger of using dummy nests to study predation. *The Auk* 105: 378-379.