

Faculty of Biosciences, Fisheries and Economics (BFE)

Department of Arctic and Marine biology (AMB)

Can ground nesting birds escape predation by breeding in less productive habitats?

A large-scale artificial nest study from Finnmark, Northern Norway

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Mari Jacobsen

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Abstract

Predation is known to be one of the most important causes of nest failure in ground nesting birds, and many populations are experiencing a decline in breeding success worldwide. Predator abundance are expected to be highest closer to productive areas (i.e. Ecosystem exploitation hypothesis), and vary according to the availability of other prey (i.e. Alternative prey hypothesis). I hypothesized that ground-nesting birds can escape predation by breeding in less productive habitats, and that predation rates will vary according to small rodent abundances. To test these hypotheses artificial nests were deployed in nine study areas in Finnmark, northern Norway, over a four-year period along replicated distance-gradients from the forest border and into tundra plateaus (n=180*4 years). Predation rates varied annually according to small rodent abundances in support of the alternative prey hypothesis. Highest predation rates were found on nests placed furthest away from the forest border, and are therefore not in support of my productivity hypothesis. Ground nesting birds that breed on the tundra experience higher predation pressure than birds breeding in more productive habitats (e.g. forests), which might be a result of higher visibility of nests, and responses to the abundance of main prey or subsidies in nest predators.

Key words: Artificial nest; EEH; Alternative prey hypothesis; Ground nesting birds; Nest predation; Subsidies

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1. Introduction

During the last decades increased focus has been directed to the recent changes seen for many populations of ground nesting birds, with a decline in breeding success worldwide (Storch and Willebrand 1991, Summers et al. 2004, Pedersen and Karlsen 2007, Storch 2007). Predation is thought to be the most important cause of nest failure in ground nesting birds (Jehl 1970, Myrberget 1984, Steen and Haugvold 2009), and predation rates are known to vary between years and locations (Storch and Willebrand 1991, Munkebye et al. 2003, McKinnon and Bety 2009). McKinnon et al (2010) found a twofold increase in nest predation risk on artificial nests across a latitudinal gradient in Canada from high Arctic to sub-arctic tundra near boreal forests. They suggested that the cost of migration of high-arctic waders was offset by lower predation risks in high latitude ecosystems.

Arctic terrestrial ecosystems are generally thought to be less productive than boreal ecosystems. The ecosystem exploitation hypothesis predicts that predator abundance should increase with increasing primary productivity (Oksanen and Oksanen 1981). Killengreen et al. (2012) found some predators to be associated with birch forest, suggesting a neighborhood effect of forest on species richness of scavengers in the tundra of Finnmark, northern Norway. One of the species that contributed to this pattern - the hooded crow (*Corvus cornix*) – is known to be a very efficient nest predator (Erikstad et al. 1982, Pedersen et al. 2009, Klausen et al. 2010). The stoat (*Mustela erminea*) and least weasel (*Mustela nivalis*) are rodent specialists that occasionally predate bird nests, and their distribution has also been suggested to depend on the productivity of surrounding areas (Oksanen et al. 1992). This is supported by a later study on spatial patterns and dynamic responses of arctic food webs in Finnmark, which additionally suggested that the red fox (*Vulpes vulpes*) had high activity in the most productive parts of their study areas (Aunapuu et al. 2008). Thus even across short distances

an increase in predation pressure on tundra bird nests with decreasing distance to forest should be expected by several predators.

Many predators on ground nesting birds respond to the abundance of their main prey, a typical example being small rodents like voles and lemmings that exhibit large-amplitude multi-annual population density cycles, especially in boreal and arctic regions (Ims et al. 2011). Both avian and mammalian predators respond numerically and functionally to the main prey's population peaks and then switch to alternative prey species when their main prey becomes scarce (Hagen 1952, Lack 1954, Angelstam et al. 1984, Smith et al. 2007). Alternative prey often includes eggs and juveniles of ground nesting birds (Steen et al. 1988, Valkama et al. 2005). Multi-annual production cycles of many ground-nesting birds are generally attributed to the phenomenon of indirect interactions in food webs driven by predator-prey dynamics (Lack 1954, Holt and Lawton 1994).

The aim of this study was to test these expectations regarding spatio-temporal patterns of nest predation based on the ecosystem exploitation hypothesis and the alternative prey hypothesis, through the placement of artificial nests along replicated distance-gradients from the forest border and into tundra plateaus. I hypothesized that ground-nesting birds can escape predation by breeding in less productive habitats, and expected therefore a decrease in predation rates with increased distance from forest. The study was conducted in the coastal peninsulas of sub-arctic and low-arctic Finnmark in northernmost Fennoscandia. It extended over four summers, which included most phases of the small rodent population cycles in Finnmark. I expected the overall predation rates to vary annually according to small rodent abundances, with highest predation rates in the crash phase of the small rodent cycle.

2. Material and methods

2.1 Study area

The study was carried out during the early summer in 2010-2013 in Finnmark County, northern Norway. A total of nine study blocks were selected and situated from the Porsanger peninsula in the west to the Varanger peninsula in the east, covering all four low arctic peninsulas in Finnmark (fig. 1). Finnmark consists of a mosaic of sub-arctic birch forest, sub-arctic mountain tundra and low arctic tundra, but about half (50%) of the area is situated above the tree limit (Moen et al. 1999).

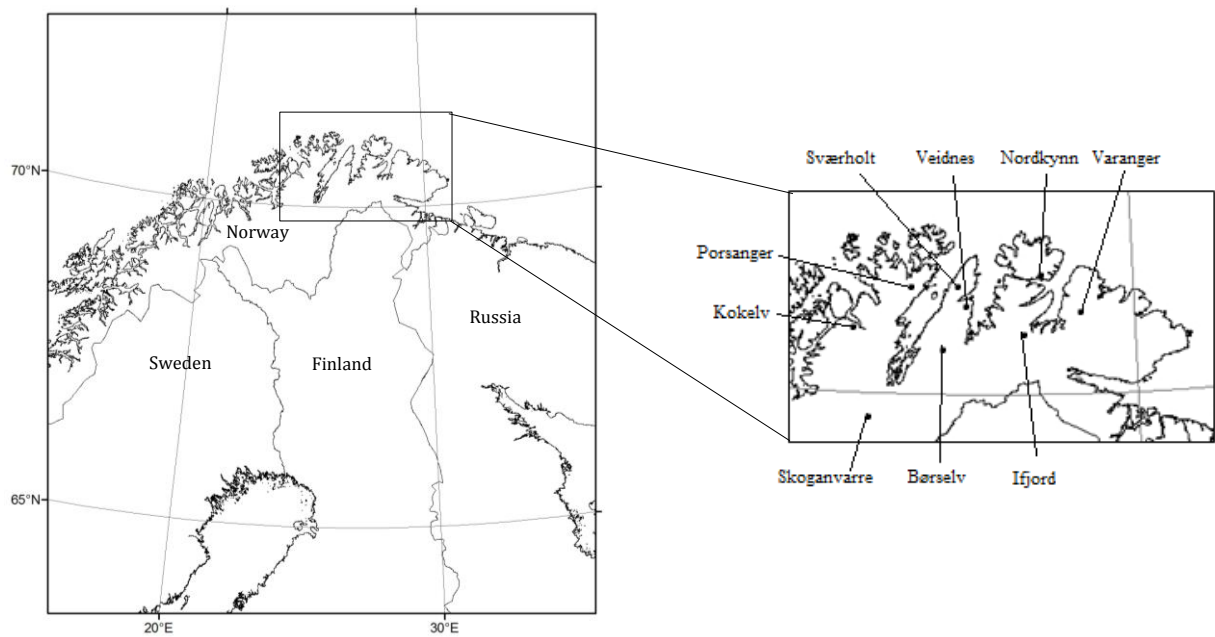


Figure 1. Map of Northern Fennoscandia. The box indicates the location of the study area in Finnmark County, Northern Norway, including the approximate locations of the nine different study blocks (Kokelv, Porsanger, Skoganvarre, Sværholt, Veidnes, Børselvfjellet, Nordkynn, Ifjordfjellet and Varanger). More detailed map of each study block is represented in figure 3.

The main ground nesting birds in the study area are willow (*Lagopus lagopus*) - and rock (*L. mutus*) ptarmigan, in addition to several species of waders, ducks, and passerines

(Killengreen et al. 2007, Ims and Henden 2012). Expected predators of ground nests in the area are avian omnivores like the common raven (*Corvus corvus*), hooded crow, and magpie (*Pica pica*). The red fox is the only expected mammalian generalist predator. In addition, some rodent specialist predators are potential nest predators, such as the long-tailed skua (*Stercorarius longicaudus*), the arctic fox (*Alopex lagopus*), the least weasel, and the stoat (Angelstam 1986, Frafjord 2004, Killengreen et al. 2007).

The rodent community in the study area consists mainly of grey-sided vole (*Myodes rufocanus*), tundra vole (*Microtus oeconomus*) and the Norwegian lemming (*Lemmus lemmus*) (Killengreen et al. 2007). Small rodent populations in Finnmark exhibit spatially synchronous 4-5 year density cycles (Oksanen and Oksanen 1981, Killengreen et al. 2007). The four year duration of the study made it possible to assess predation rates on the artificial nests in the pre-peak (2010), peak (2011), crash (2012) and low (2013) year of the cycle (fig.2).

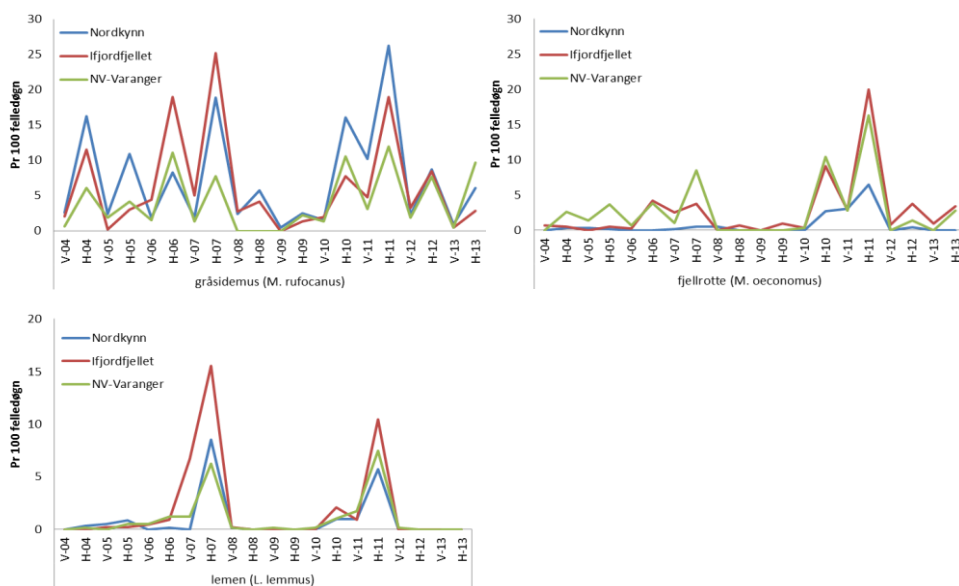


Figure 2. Small rodent trapping data (number of gray-sided vole, tundra vole and lemming caught per 100 trap nights, V = spring capture, H = autumn capture) from three of the study areas (Nordkynn, Ifjordfjellet, Varanger) (cf. Ims et al. 2011).

2.2 Study design

Within each peninsula, 1-3 study blocks were selected, ranging from the coast to the interior of the peninsulas. Within each of the nine study blocks two transects were established with a minimum distance of two kilometers between each in order to minimize the chance of predation by the same predator. The two transects were therefore considered as independent units. Each transect contained ten artificial nests (plots), resulting in 180 nests (9 blocks*2 transects*10 plots/nests) each year (fig.3). The nests were placed on a gradient from the birch forest border and roughly two kilometers into the adjacent tundra, with approximately two hundred meter spacing between each nest (fig.4).

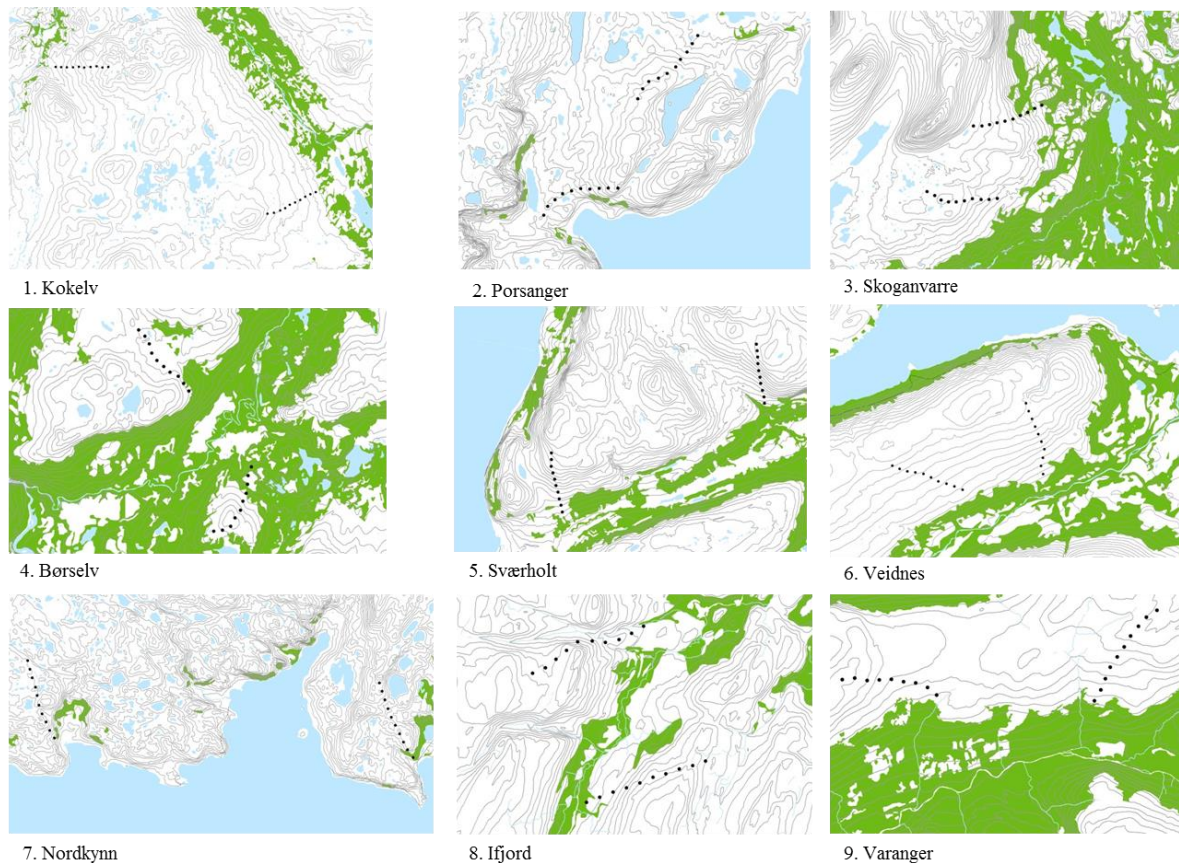


Figure 3. Maps of each of the nine study blocks in Finnmark, Northern Norway. Each study block held two transects with ten plots each, represented here by the dots (n=180).

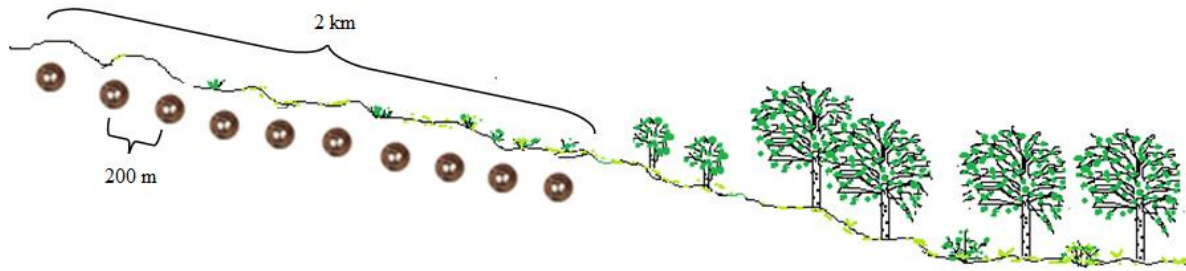


Figure 4. Sketch of the study design where the nests were deployed from the birch forest border and into the adjacent tundra. Each transect was about 2 km long, with an approximate 200 m spacing between each nest.

Thus the transects represent a gradient in terms of increasing distance from forest edge and a possible decreasing predator spill-over effect. Note, however that most of the distance gradients also represented an altitude gradient giving a positive correlation ($r=0.53$) between distance from forest and altitude (fig.5). The nests were deployed within the local nesting period for most ground nesting birds such as waders and ptarmigan in the region (between the 23rd and 30th of June) (Haftorn 1971).

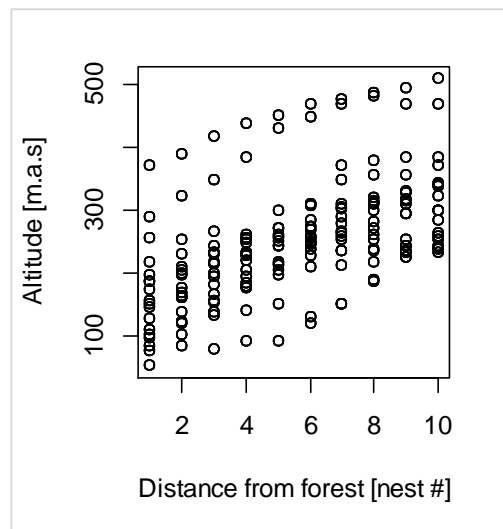


Figure 5. Correspondence between distance from forest and altitude for the 180 nests.

2.3 Artificial nests

Each artificial nest was handmade by creating a small bowl in the ground without adding any nest material, similar to the nests that ptarmigans and waders would use. Each nest contained one quail (*Coturnix sp.*) egg and one plasticine egg made to mimic a quail egg (fig. 6). Gloves were used when making the depressions in order to reduce human scent. The plasticine eggs were attached to the bottom of the nests by steel wire, and were used in order to acquire predator identity from possible bite marks (Kurucz et al. 2010). The amount of vegetation covering the nests/eggs differed greatly between the plots, but cover tended to decrease with increasing distance from forest (fig.7). To assess the effect of this variation the amount of cover was scored on a three-level nominal scale ranging from low to high degree of vegetation cover (1-3) (fig.6). The vegetation height was also measured at each nest, but correlated closely with cover ($r = 0.6$), and was therefore not used in further analysis of the data (fig.8).



Figure 6. Example pictures of the artificial nests, portraying the three different categories of vegetation cover (1-3).

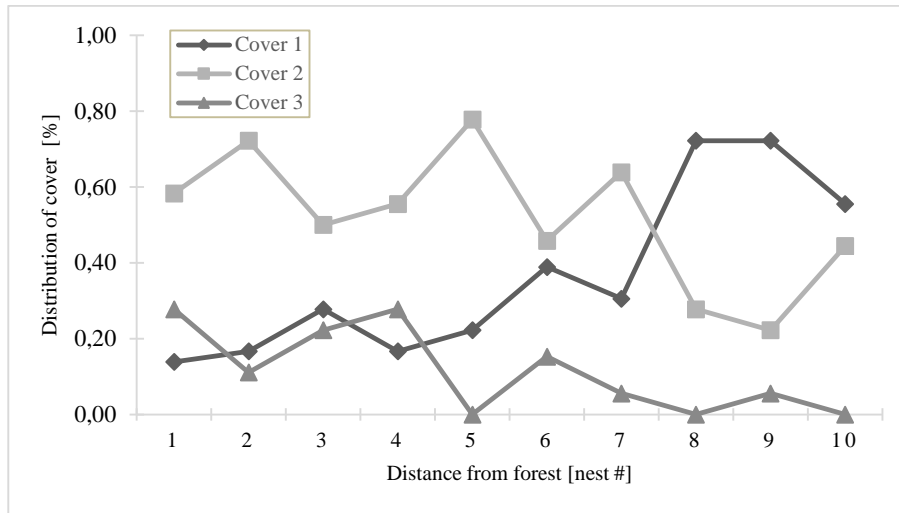


Figure 7. The proportion of nests of three different categories of vegetation cover on nests (1-3) according to distance to forest (1-10). Cover 1 represents no vegetation cover, Cover 2 medium vegetation cover, and Cover 3 large vegetation cover (fig.6).

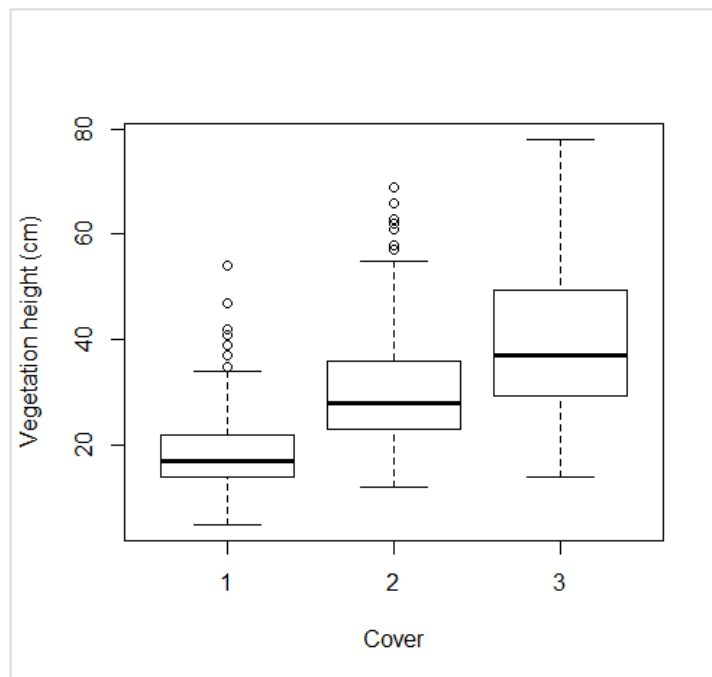


Figure 8. Vegetation height and degree of vegetation covering the nests showed a positive correlation (Cover 1-3) ($r = 0.6$).

In order to place the nests at exactly the same locations every year, UTM coordinates and a detailed description of exact placement were noted for each artificial nest. The location of the nests were also marked with blue tape, which was placed at a distance of minimum 10 meters away from the nests to reduce the chance of the tape itself attracting potential nest predators (Picozzi 1975).

The nests were left without human disturbance for about 14 days until checked and collected during the first half of July in all three years. Depredation was recorded if either one or both eggs were missing or damaged.



Figure 9. Plasticine eggs recovered in the field with beak mark from a corvid to the left and teeth marks from a fox in the middle. The picture to the right shows fresh feces from a mustelid on top of a pile of lemming pellets found next to one of the artificial nests.

Upon examination of the nest sites, mammal or avian predator was immediately classified, but pictures were also taken in order to re-identify at a later time (fig.9). The size and shape of beak and teeth marks, in addition to feces in some nests, gave reliable clues to help identify specific predators beyond the general distinction between mammal and birds (fig.9). However, it is hard to determine predator identity from beak marks, so only two different taxonomic groups of avian predators were used; corvids vs other unidentified avian predators. If there were uncertainties about the identity of the predators, or the plasticine egg was not marked or missing, it was recorded as an unknown predator.

2.4 Statistical analyses

The response variable (predation) has a binomial distribution, therefore generalized mixed effect models (GLMM) were chosen for analyzing the data (Lewis 2004, Bolker et al. 2009). Fixed effects in the model were nest-distance from forest (from now on referred to as distance) (from 1 to 10, with 1 closest to the tree line), year (2010-2013), and nest cover (1, 2, 3). The plots (each individual nest) and blocks (Kokelv, Porsanger, Skoganvarre, Børselv, Veidnes, Sværholt, Nordkynn, Ifjord, Varanger), were treated as random effects in the

models, since they represented a sample of all the possible plots and blocks available within the general study area (Bolker et al. 2009). GLMMs were fitted using the lme4 package (Bates 2012) in the software R (R Development Core Team. 2009).

The alternative expected spatio-temporal patterns were assessed with stepwise removal of fixed effect terms starting from the most complex model with *cover + year + distance + year*distance*. The *year*distance* term was included to account for annual differences in small rodent abundances and species separation in choice of habitat with lemmings often found in high densities at higher altitudes than the other small rodent species (Ims et al. 2011, Killengreen et al. 2013). The significance of each term was assessed by likelihood ratio test.

3. Results

3.1 Nest predation rates

All fixed effects terms, except for distance*year interactions were statistically significant ($p < 0.05$). Thus the model used for estimating effect sizes included the additive effects of *distance to forest*, *year* and *cover*.

The estimated predation rates showed a consistent linear increase (on the logit scale) with the distance from forest (Odds ratio per 200 m increase in distance from forest = 1.20, $p = 0.002$) (fig. 10). Removing cover from the model, which to some extent was confounded with distance, gave a larger effect of distance (Odds ratio = 1.30, $p = < 0.001$).

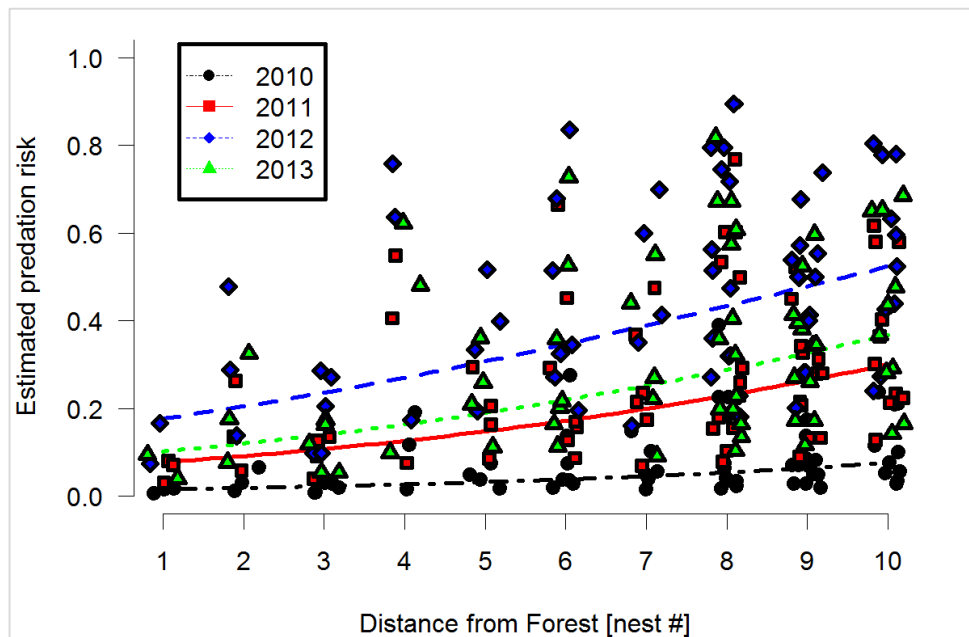


Figure 10. Predicted predation rates on nests according to distance from forest (nest # 1-10, 1 being closest to forest and where distance between successive nests are approximately 200m). Lines give the estimated fixed effect from the logistic predictor while the points include the random block and plot effects. All predictions are made conditional on Cover=1.

The overall predation rates varied significantly among years (fig.11), with the lowest predation rates occurring during the first year of the study (2010) followed by a steady increase and subsequently peaked during the lemming crash year (2012). In turn, this was followed by a reduction in predation rates during the low phase (2013; fig.11). Predation rates

increased more than a five-fold from 2010 to 2011 (Odds ratio (2010-2011) =5.2, $p < 0.001$), and in 2012 predation rates were thirteen times higher than in 2010 (Odds ratio (2010-2012) =13.3, $p < 0.001$) and almost three times higher than 2011 (Odds ratio (2011-2012) = 2.6, $p = 0.001$). In 2013 the estimated predation rates declined by 50% from 2012 (Odds ratio (2012-2013) = 0.5, $p = 0.02$), but were still 7 times higher than 2010 (Odds ratio (2010-2013) =7.0, $p < 0.001$) and slightly, but not significantly, higher than in 2011(Odds ratio (2011-2013) = 1.4, $p = 0.3$).

The highest predation rates occurred in nests with the least vegetation cover (cover 1; fig.11). These rates were three times larger than nests with higher degree of vegetation cover (fig. 11) (Odds ratio (2-1) = 2.6, $p = 0.003$. Odds ratio (3-1) = 3.0, $p = 0.07$).

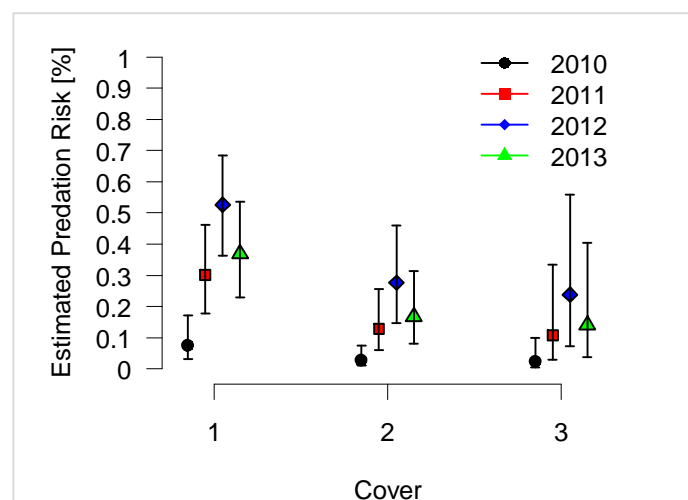


Figure. 11. Estimated nest predation risk (with 95 % CI using the function EzPredict in R) according to the degree of vegetation cover per nests for all years of the study (2010 – 2013).

Although the distance*year interactions were not statistically significant, the estimated effect sizes from the model with this interaction revealed an annual variation in the influence of distance from forest. The year 2010 had the smallest effect with 1.5 % increase in predation rates per 200 m increase in distance from forest. The year of 2012 had the highest effect of distance from forest with an increase of 8.6 % per 200 m increase in distance from forest,

while 2011 and 2013 both had an increase of 2.8 % per 200 m increase in distance from forest.

3.2 Predator identity

A large proportion of the predation events could not be attributed to any known predator species or taxon (30-40 % per year; fig.12) since the plasticine eggs were either missing or untouched. Among predator taxa that could be identified based on beak and teeth marks corvids were most common in all years except 2013, followed by unidentified birds (fig.12). Mammalian predation was relatively uncommon, but was greatest in 2012 and 2013, with foxes as the main mammalian predator (fig.12). Due to the large proportion of events with unknown predator identity these data were not analyzed statistically.

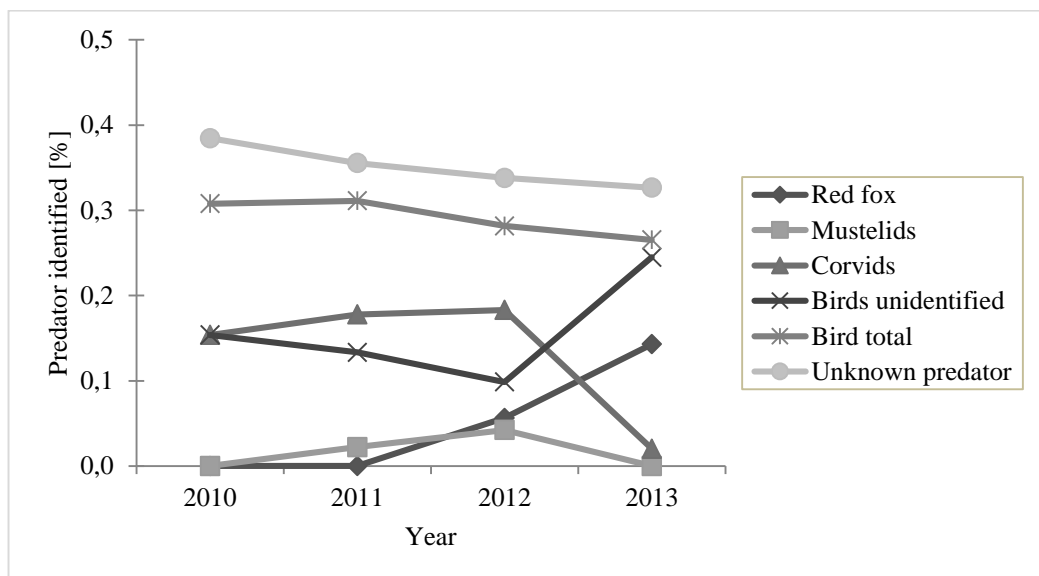


Figure. 12. Proportion of predation events attributed to the different categories of predators (including unknown) in all years of the study (2010-2013).

4. Discussion

In all years of the study predation rates were found to be highest on the artificial nests placed furthest away from the forest edge. These results were unexpected since I anticipated that the predation would be highest on the nests placed closest to the birch forest due to a spillover effect of predators (Killengreen 2011). There was an annual difference in overall predation rates, which seemed to follow the cyclicity of the local small rodent populations and therefore was in agreement with both the alternative prey hypothesis (Hagen 1952, Lack 1954) and my expectations.

A possible explanation for the unexpected increase in predation rates away from forest might be the nest predators' response to main prey abundances. Parallel to the present study, Ims et al. (2013) found the Norwegian lemming to be a much stronger predictor of increased nest predation through the alternative prey mechanism than sympatric voles. This is further supported by studies that have involved other arctic lemming species (Blomqvist et al. 2002, Smith et al. 2007). In Finnmark the Norwegian lemming differ from other small rodent species in terms of their increase in abundance with increasing altitudes and distance from the birch forest (Ims et al. 2011, Killengreen et al. 2013). If mobile predators aggregate according to abundance of the lemming this could in fact inflict higher nest predation rates at high altitudes far from the forest.

Data on small rodent abundances in the study area show that the populations of lemmings started to increase prior to the first year of the study, peaked in the second, crashed in the third, and remained low or absent in the fourth year (fig.2). The overall predation rates followed this pattern with highest predation rates in the crash year, as expected from the alternative prey hypothesis and in accordance to several other studies on nest predation (i.e. Angelstam et al. 1984, Wegge and Storaas 1990, Blomqvist et al. 2002, Smith et al. 2007, Ims

et al. 2013). Although the interaction between year and distance from forest edge was not statistically significant, the effect did vary between years with the lowest effect occurring in the pre-peak year and highest in the crash year in lemming abundances. This might reflect a numerical and functional response of predators to the increase in abundance of small rodents (Wegge and Storaas 1990), and maybe in particular lemmings.

The identification of nest predators showed that avian predators were almost exclusively present the first two years of the study, which indicates that they are the drivers of this pattern. The research of Killengreen et al. (2012) indicated that the common raven, a scavenger, did not show connection to forest edge and was the most dominant predator in the area. Ravens have shown a spatial response to lemming abundances (Ims et al. 2013), and have also been suggested to show very high predation rates on nests (Andren 1992). Long-tailed skuas might also have contributed to the pattern of higher predation rates further from forest edge since they concentrate in the less productive parts of the arctic tundra (Aunapuu et al. 2008). During fieldwork of the present study, both ravens and long-tailed skuas were indeed the most frequent nest predators observed in the uppermost parts of the study areas. Hooded crows, which were expected predators on the nests, were rarely seen. This might be a result of the study areas decreased proximity to large human settlements, forest, and agricultural activity which this particular predator shows a strong connection to (Andren 1992). This is supported by other nest predation studies situated in forest and/or closer to larger human settlements which found the hooded crow to be the dominant predator (Pedersen et al. 2009, Klausen et al. 2010).

Mammals were identified as nest predators in the last two years of the study, which was the crash- and low phase in the lemming cycle (fig. 2). Some predators are suggested to show a one-year delay in the numerical and functional response to main prey abundances, and therefore inflict highest predation rates in the decline phase of the lemming cycle (Angelstam

et al. 1984, Wegge and Storaas 1990). Additionally, Oksanen et al. (1992) suggested that stoat and least weasel might move to more barren areas when there is an overexploitation of prey in the best habitats. Mammalian predation might therefore have contributed to the increased effect of distance from the forest edge on predation rates in the third year of the study. This temporal variability in nest predation by mammalian predators might be the reason why some short-term nest studies has failed to detect mammalian predation (i.e. Klausen et al. 2010).

The predation rates decreased in the last year of the study (low phase), but were still higher than I would expect in a lemming cycle low phase. This might indicate that more prey are available in these areas than first anticipated, allowing predators to stay longer than they otherwise would. The lemming abundances crashed during the winter of 2012 (fig. 2), which might have resulted in many lemming carcasses being available to carnivores after the snow melt in the following spring. This could also indicate that some predators have a 2-year time lag in the numerical response to main prey abundances. The red fox for example showed highest predation rates in the last year of the study. Additionally, most of the study blocks are summer pastures for semi-domesticated reindeer (*Rangifer tarandus*) that provides a key resource for the community of carnivores, including corvids and foxes (Killengreen et al. 2012, Hamel et al. 2013). Due to an overabundance of reindeer in some regions it is likely that reindeer carrion, and reindeer calves, provides generalist predators with a temporal food source through the winter.

Reindeers often disperse to more barren areas, i.e. the tundra, during the warm summer months in order to avoid insect harassment (Hagemoen and Reimers 2002). Studies on stomach content and scat samples from red fox have shown that their diet contains reindeer as the second main prey type next to small rodents (Frafjord 2004, Killengreen et al. 2007, Killengreen et al. 2013), and in rodent low years reindeer carrion dominate the diets (Killengreen et al. 2011). Killengreen et al. (2012) found corvids, especially ravens, and red

foxes to be the most common predators on reindeer carcasses, which were also the most common avian and mammalian predators on the artificial nests in this study. Subsidies might allow predators to stay in the area longer than they usually would after a crash in main prey abundances, and therefore would help explain the higher predation rates in the less productive parts of the transects especially during low lemming abundances. This increases the concern around the recent increase observed in abundance and distribution of generalist predators over the last decades (Storch and Willebrand 1991, Tannerfeldt et al. 2002, Storch 2007, Fletcher et al. 2010). I therefore suggest that future studies look into the effect of reindeer abundances on predation rates of ground nesting tundra birds through shared generalist predators.

In addition, degree of vegetation cover significantly effected predation rates, with highest predation rates occurring on nests with least amount of cover, which is supported by some other studies on ground nesting birds (Wiebe and Martin 1998, Munkebye et al. 2003). Vegetation cover functions as an important food source, shelter, and predator protection for many ground nesting birds (Ims and Henden 2012). Little cover might make nests easier to locate, especially for avian predators which highly depend on visual cues in order to locate prey (Klausen et al. 2010 and citations therein), and some species may even develop search images for nests (Erikstad et al. 1982, Sonerud and Fjeld 1987). There was a tendency towards less vegetation covering the nests with increasing distance from the forest edge (fig.7), which might suggest that these were easier to locate. However, the effect of distance from forest was independent of vegetation cover, and can therefore not be explained by degree of vegetation cover alone.

Conclusion

A recent study on common montane birds in northern Europe show a decline in many ground nesting bird species that occur in my study area (Lehikoinen et al. 2014), and mentioned that climate change can potentially result in loss of breeding range due to an

increase in the altitudinal tree line, threatening especially tundra species. On the scale of Finnmark County, Norway it seems like ground nesting birds do not escape predation by breeding in less productive habitats. Ground nesting species that make their bird nests in the tundra experience higher predation pressure than birds breeding in more productive habitats (e.g. forests). This might be a result of higher visibility of nests, in particular to avian predators, responses to abundance of main prey species, or responses to availability of alternative prey such as reindeer further away from forest. Together with an increase in generalist abundance and distribution this might cause some species of ground nesting tundra birds to be even more dependent on the regular release from predation pressure during the peak phase of the lemming cycle.

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