

An artificial nest experiment to unravel the interactions between forestry practices and grouse egg predation



Hazel grouse in the forest – Ferdinand Von Wright (1889)

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Abstract

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Abstract:

Populations of forest grouse – capercaillie (*Tetrao urogallus*), black grouse (*Lyurus tetrix*) and hazel grouse (*Tetrastes bonasia*) - have been declining through all of Europe. Habitat loss, fragmentation and degradation are recognized to be the most important ultimate causes behind this trend. In Fennoscandia, there is a general consensus that forestry practices have a primary role, even though the mechanisms are still not fully understood. Nest predation is generally thought to be an important proximate cause of the declines, but how nest predation relates to habitat changes remains poorly understood. I combined long-term data provided by the Natural Resources Institute Finland (LUKE) from inventory studies, both for grouses and predators, with an artificial nest experiment. I investigated a) how predation rate varies with forest age and landscape structure; b) what is the possible role of non-native mesopredator species as predators; c) how nest predation rate relates to larger scale reproductive success. In spring 2021, I placed 141 nests with two hen eggs each, in the regions of Kainuu and North Karelia for 14 days with camera traps. The nests were equally divided between mature forests (>80 years), young forests (<40 years) and edges of mature forests (in a mature forest 5m from a clearcut or a field). I found that the overall predation rate was low (~13 %)

and similar in the three sites, but predation time was faster in mature forests, suggesting that when these are scarce, they can act as an ecological trap by increasing nest detectability. However, nest predation decreased with the increasing of mature forests in the landscape around the nest, supporting the hypothesis that on a larger scale forestry may increase generalist predator densities. Areas with higher predator densities suffered higher nest losses. The main predators were pine martens, badgers and magpies, followed by bears and ravens. No nests were predated by raccoon dogs or American minks. There was no correlation between areas with higher nest predation and areas where grouse had lower reproductive success which may result from other factors, e.g., chick predation. My results add to the diverse outcomes of several studies of grouse nest predation in Europe, which together indicate large variation in nest predation, no consistency in predatory species, and weak effects of landscape composition on nest predation.

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1. Introduction

The loss of biodiversity observed worldwide as a consequence of human actions has been suggested to be the beginning of a new mass extinction. Many species are disappearing and even more are decreasing in abundance. Genetic variability is being lost, with the consequence that natural communities are now a shadow of what they used to be in the past.

Grouse are a particularly sensitive taxon and their decline observed worldwide has also led to the creation of the IUCN grouse specialist group, a network of voluntary experts seeking ways to conserve this species group. In particular, populations of European forest grouse (BOX 1) - western capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*) and hazel grouse (*Tetrastes bonasia*) – have been declining throughout all their range over the last century and they have disappeared from many localities (Jahren *et al.* 2016). However, none of them is yet considered threatened due to their large distribution (IUCN 2016). The causes of the decline are various, mirroring most of the common mechanisms found behind the biodiversity loss observed worldwide. They include overexploitation, climate change, and habitat loss and degradation. Because of the particularly strong economical and spiritual connection that exist between humans and grouse many studies have been conducted to investigate the exact mechanisms of decline and possible solutions, but only partially successfully. Money and resources have also been invested in reintroduction programs, like that of the capercaillie in Scotland (Stevenson, 2007). However, most of them have not been successful because the root problem behind their extinction has often not been rightfully addressed.

BOX 1. - European forest grouse and their importance

Grouse are medium to large sized birds in the order *Galliformes*, family *Phasianidae*, subfamily *Tetraoninae*. In Finland there are five different species, and this study focused on the three strictly forest dwelling ones – western capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*) and hazel grouse (*Tetrastes bonasia*). These three species present substantial similarities, but also some differences. They are all widespread in Fennoscandia and at higher latitude across Europe and Asia. Populations of all species are present also in the Alps. The hazel grouse is the only one to be absent from British Islands. All of them are non-migratory, ground nesting birds. Capercaillie and black grouse have accentuated sex dimorphism, with males being larger and more colourful than females, probably due to sexual selection with males showing off their displays to try to attract females

during reproductive courtships. The hazel grouse is the only one which does not use leks as a reproductive strategy. Nests are usually placed in small depressions of the ground which are filled with plant material. The female lays one clutch per season, but if this is soon lost, she is usually able to replace it with a second one (replacement clutch). Adult grouse feed on different types of vegetation, depending on the habitat and the season. In boreal forests, they are one of the few animals which eat conifer needles. However, hatchlings rely on insects during the first weeks of their lives.



Capercaillie



Black grouse



Hazel grouse

Capercaillies and hazel grouse prefer older coniferous forests, while black grouse prefer open and younger forests, also including marshes and grasslands (Sachot *et al* 2003). However, in boreal forests the selection is less strong than in the rest of Europe and the distributions of the three species overlap more, up to the point that they can be considered sympatric (Jahren *et al.* 2016). Forest grouse are known to undergo natural short term population fluctuations around an equilibrium density, both in time and space. Population dynamics are similar among the three forest grouse species in Fennoscandia, showing a cyclicity of around 6 years (Lindstrom *et al.* 1995), suggesting the presence of a common regulatory processes behind, even though it is not clear which one it could be. However, over recent years, population fluctuations of grouse have become faster (every 3-4 years) and less evident, probably due to the lower population densities (Ludwig 2007).

Grouse are important species of the boreal forest, both for ecological and cultural reasons. Capercaillie in particular is considered to be an umbrella species, i.e. a species with high demanding habitat and area requirements, whose preservation guarantees conservation of smaller and more abundant species (Pakkala *et al.* 2003). Grouse have always occupied an important place in the Finnish traditions, originating a number of myths and beliefs. Nowadays, they are still a highly important game bird with a substantial economic value. For all these reasons, their conservation should be a priority of the Finnish management system.

1.1 The decline of European forest grouse

The declines of European forest grouse across their range seem to be more associated with a lowered reproductive success rather than with a lower adult survival (Jahren *et al.* 2016). Slight differences are found between populations from British Islands, lowland Europe, the Alps and Fennoscandia. In the latter, the trend has been particularly alarming, with the average net reproductive output having decreased by a factor of four for the capercaillie and of two and a half for the black grouse (Jahren *et al.* 2016). Consequently, large scale population declines are observed. Many different interacting factors have been recognized to cause the decline of grouse in Europe. These include hunting, climate change and habitat loss.

Human hunting is one of the oldest anthropogenic pressures on forest grouse (Ludwig 2007). Grouses are highly important game birds, which were once an essential food source for many populations. Nowadays they still retain an important economic value, particularly in Finland where every year censuses are made and used to decide guidelines on how many individuals can be shot. However, a study made in the Kainuu region (Eastern Finland) showed that more hunting occurs than that recommended by authorities guidelines, since the number of bird shots was not entirely dependent on population sizes (Lampila *et al.* 2011).

On the other hand, one of the newest threats to forest grouse is climate change. In particular, the asymmetry of climate change in high latitude regions at the edge of their distribution is detrimental for them (Ludwig *et al.* 2006). This asymmetry is indicated by the phenomenon of advancing of warm springs, but not of early summers. Therefore, early springs cause a phenological shift in egg laying and hatchings to match the climatic conditions. Hatchlings then face colder conditions than what they are adapted to and, consequently, their mortality increases.

However, the most important causes in the decline of the forest grouse throughout their distribution are arguably habitat loss, fragmentation, and degradation (Storch 2000; Jahren *et al.* 2016).

1.2 Habitat loss, fragmentation and degradation

Habitat loss, fragmentation and degradation affect grouse through numerous mechanisms (Fig. 1) which might change from place to place. In Fennoscandia, forestry practices are the main leading cause of habitat alteration and there is a general consensus about their importance in the decline of forest grouse, capercaillie in particular (Miettinen *et al.* 2008; Jahren *et al.* 2016). Large scale

forestry practices begun after the second World War, when selective cuttings were replaced by clear-cuts and these expanded to previously untouched areas (Sirkiä *et al.* 2010). As a consequence, the estimated percentage of old-growth forests left in Finland today is less than 3% (FAO 2010).

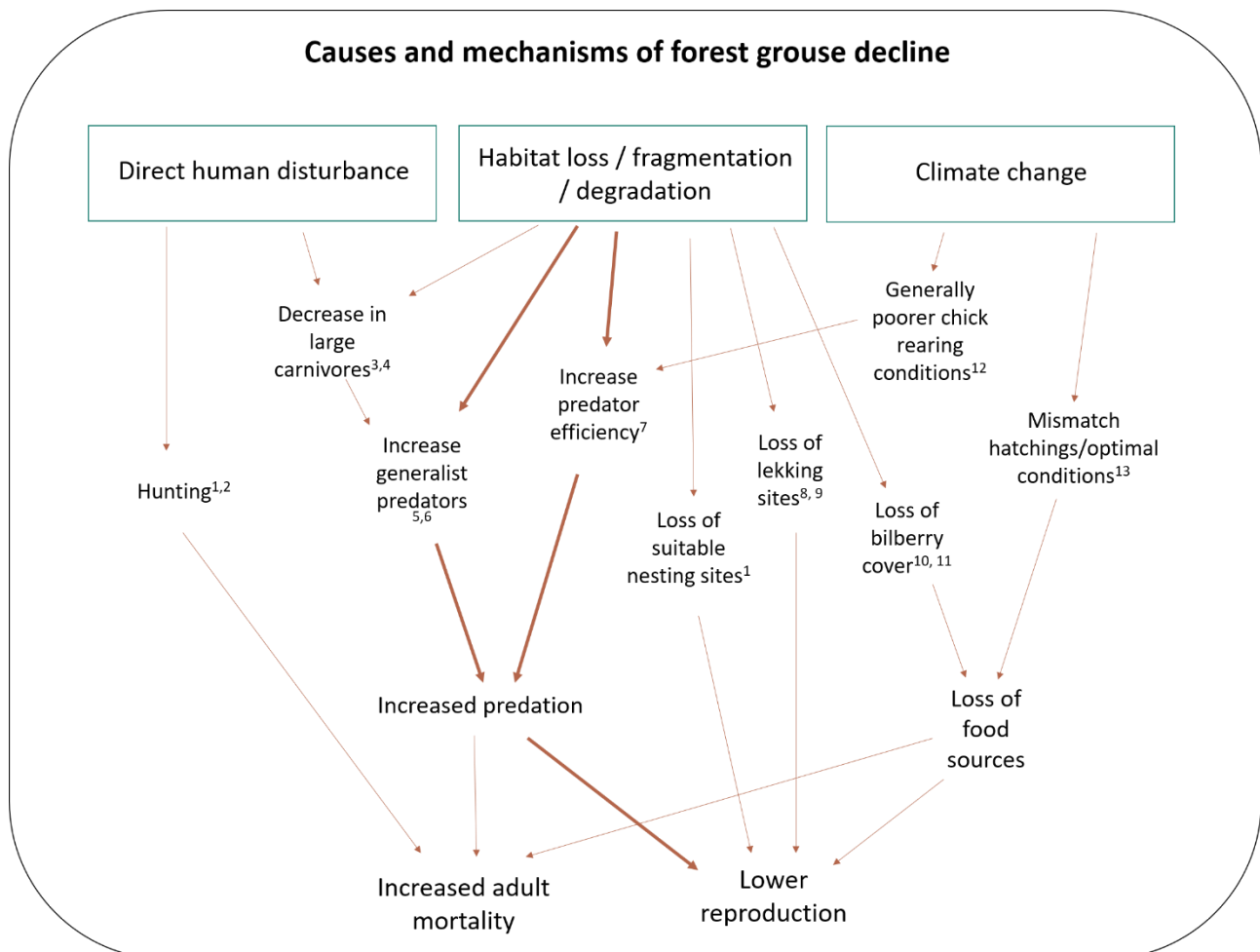


Figure 1. Possible interactions between ultimate and proximate causes behind the decline of European forest grouse. The bold arrows represent the relations investigated in the present study. References: ¹ Storch, 2000; ² Jähren *et al.* 2016; ³ Ludwig 2007; ⁴ Ritchie and Johnson 2009; ⁵ Hansson 1994; ⁶ Kurki *et al.* 1998; ⁷ Storaas *et al.* 1999; ⁸ Sjöberg, 1996; ⁹ Helle *et al.* 1994; ¹⁰ Storch 1993; ¹¹ Ludwig *et al.* 2010; ¹² Swenson *et al.* 1994; ¹³ Ludwig *et al.* 2006.

The relationship between forest grouse and forestry has been regarded as very complex (Sjöberg 1996). In Finland, although it has been demonstrated that both fragmentation and decreased percentage of older forests are correlated with decreasing of breeding success of capercaillie, (Kurki *et al.* 2000), the mechanisms through which forestry affects grouse are still not fully understood, making the extrapolation of general rules difficult. For example, forestry changes tree and ground

composition, especially through draining (Sjöberg 1996). The latter one can be particularly detrimental because it may reduce the bilberry cover (Kardell 1979) which is one of the main drivers of habitat selection for capercaillie (Storch 1993). Besides, it is critical for chick survival of each species during the first weeks, since it provides Lepidopteran larvae for their diet (Ludwig *et al.* 2006). In addition, male capercaillie select for lekking sites in older and larger forest patches (Helle *et al.* 1994) and they start to use plantations only when these reach 60 years (Wegge and Gjerde 1992).

Nonetheless, the most detrimental impact of forestry may come from its disruption of natural ecological processes such as predator-prey interactions, in particular on eggs and chicks (Sjöberg 1996; Storaas *et al.* 1999). In fact, nest predation is likely to be one of the most important proximate causes of reproductive failure and therefore decline, throughout most of the forest grouse distribution (Caizergues and Ellison 2000; Ludwig *et al.* 2010).

1.3 Predation and landscape influence

The habitat may indirectly influence nest and chick predation rates by affecting predator densities or their search efficiency. Ludwig *et al.* (2010) showed that black grouse in Fennoscandia should select for undrained areas with high tree density and low visibility in order to increase the likelihood of nesting success. Fragmentation, has been shown to increase corvid species, which are well known nest predators (Andrén *et al.* 1985; Andren 1992), as well as generalist mammalian mesopredators such as foxes (Oehler and Litvaitis 1996; Kurki *et al.* 1998). In Central and Southern Finland, the proportion of agricultural land in the landscape has been found to influence the nesting success, but not chick survival, of black grouse (Kurki and Lindén 1995). Other consequences of forestry also affect predator populations in comparable ways. In fact, with intensive forestry practices such as clear-cutting, young successional forest stages increase in the landscape (Esseen *et al.* 1992; Hansson 1992). These habitats sustain higher densities of small rodents than older stands, especially *Microtus spp* (Savola *et al.* 2013). Because of the increase in their prey, also generalist predators (foxes in particular) can become more abundant in these extensively managed forest landscapes (Hansson 1994; Kurki *et al.* 1998).

The decrease in large carnivores densities observed worldwide (Wolf and Ripple 2017) has also most likely enhanced an increase in generalist smaller mammals, a process known as “mesopredator release” (Ritchie and Johnson, 2009; Ritchie *et al.* 2012). In Fennoscandia, lynxes (*Lynx lynx*) and wolves (*Canis lupus*) are important in limiting the negative effect that mesopredators have on

grouse (Ritchie and Johnson 2009). Supporting this thought, lynx recovery in recent years has been linked to an increase in grouse populations in certain areas of Finland (Ludwig 2007).

Moreover, habitat structure may increase predation independently from predator densities, by optimizing their search efficiency. Forest grouse are known to select nesting sites with some specific environmental characteristics, with some variation from species to species (Wegge and Kastdalen 2008). With the reduction of these habitats, the few remaining suitable places may act as ecological traps in which predators are more successful (Storaas *et al.* 1999).

1.4 Predator species

Since the root cause of the decline is more related to a lower reproductive success than to lower adult survival, predation is likely to influence especially chicks and eggs. Nest predation in particular is possibly the main proximate cause behind the decline of grouse, but how it relates with ultimate causes (e.g., habitat degradation) it is not entirely clear (Caizergues and Ellison 2000; Ludwig *et al.* 2010; Jähren *et al.* 2016). Among the generally recognized nest predators there are birds, such as corvids and raptors, as well as various mammalian mesopredators. Red foxes in particular have been pointed out in several studies as the main predator throughout the distribution of forest grouse (Baines *et al.* 2004; Kammerle *et al.* 2017). Regarding the Fennoscandia region, an early predatory removal experiment showed that the extirpation of the red fox (*Vulpes vulpes*) and the pine marten (*Martes martes*) from an island was positively related with the increased breeding success of forest grouse (Marcstrom *et al.* 1988). A second study based on population trends also found similar results, showing that relative densities of pine martens and red foxes were negatively correlated with grouse densities, whereas stoats (*Mustela erminea*) did not seem to have a strong influence (Kurki *et al.* 1997). The Goshawk (*Accipiter gentilis*) has also been found to be an important specialist predator of grouse in Finland, but studies focused rather on adult and chick predation, than that of eggs (Törnberg *et al.* 2012).

However, how each predator species affect grouse and how this interaction is influenced by forestry in Finland is still unknown. Besides, two non-native generalist mesocarnivores - the raccoon dog (*Nyctereutes procyonoides*) and the American mink (*Neovison vison*) – are spreading in the country (Helle and Kauhala 1991, Kauhala 1996), possibly increasing predation pressure on grouse populations even more. In fact, both of them are known to predate on bird's nest (Krüger *et al.* 2018), but their specific impact on grouse is still unclear.

1.5 Aim and study questions

The aim of this study is to investigate the role that nest predation may have in the decline of forest grouse and how it is influenced by forestry practices. I combined long-term data provided by the Natural Resources Institute Finland (LUKE) from inventory studies, both for grouses and predators, with an artificial nest experiment designed to cover variation in forest ages and distance from edge. Specifically, I aimed at answering the following questions:

1. Does predation rate vary with forest age and landscape structure?

Some studies suggest that nest predation increases in smaller forest patches (Chalfoun *et al.* 2002) and near forest edges (Hartley and Hunter, 1998), while the effect of forest age is less clear: at a larger scale young forests may increase predator densities, but at a smaller scale older natural forests may act as ecological traps by increasing nest detectability (Storaas *et al.* 1999). However, the interaction between forest age and structure remains unknown. I hypothesize that nest predation should be highest near edges and in old forest fragments. But I also expect that nest predation decreases with increasing proportion of older forests at the landscape scale.

2. Are non-native mesocarnivores more commonly preying nests than native mesocarnivores or avian nest predators?

Preliminary analysis with the Wildlife triangle data provided by the Natural Resources Institute Finland (LUKE) show that different potential predator species are abundant in the study area (Appendix, Fig. 1). Specific data on the densities of invasive species are less reliable since raccoon dogs hibernate in winter and American minks are strictly dependent on water habitats, however their presence in Eastern Finland has been documented for decades (Kauhala 1996). I hypothesize a) that areas with higher predator densities have higher nest predation and that b) the most common predators are invasive species, followed by avian predators.

3. Does egg predation rate in my experiment reflect larger scale reproductive success?

I checked if areas with lower reproductive success according to long-term wildlife triangle data are also areas where egg predation is higher. This would help understanding whether the lower reproductive success can be attributed to higher nest predation or to some other factors (e.g., chick predation). I hypothesize that areas with higher nest predation rates should also be areas where the reproductive success is lower.

Answering these questions is key in order to discriminate the mechanisms by which forestry affects reproductive success of grouse via predation. Besides, the possible matching of my data to other data independently obtained from long-term monitoring would further support my findings and help to have a better overview of what is possibly causing the decline of grouse. This information could be valuable for future conservation management plans aimed at preserving these species.

2. Methods

2.1. Study area

The study took place in Eastern Finland, in the regions of Kainuu (22,687 km²) and North Karelia (21,584.41 km²) (Fig.2). Boreal forest covers most of the area, with the two dominant tree species being the Norway spruce (*Picea abies*) and the Scots pine (*Pinus sylvestris*). Due to extensive forestry practices, young successional mixed forests are widespread. Forests reach the age of 200 years only in few and scattered exceptions (MS-NFI, 2019). The area is mostly flat with abundant lakes and peatlands, although many of the latter ones have been drained over the last decades (Turunen 2008).

Large carnivore (wolf, brown bear, wolverine, lynx) densities are the highest in all Finland, and moose and wild forest reindeer are abundant as well (Kojola *et al.* 2004). American minks reach the highest densities of the country (Kauhala 1996) and also raccoon dogs are relatively common in the southern part of the study area, but less in the Northern one (Helle and Kauhala 1991). All forest grouse are present and they followed similar trends in population cycles and dynamics over the last 10 years (Appendix, Fig. 2).

2.2. Complementary data

A series of complementary data has been collected to plan the exact location of the artificial nests beforehand. The data was open and visualized in QGIS (version 3.18, QGIS.org 2022).

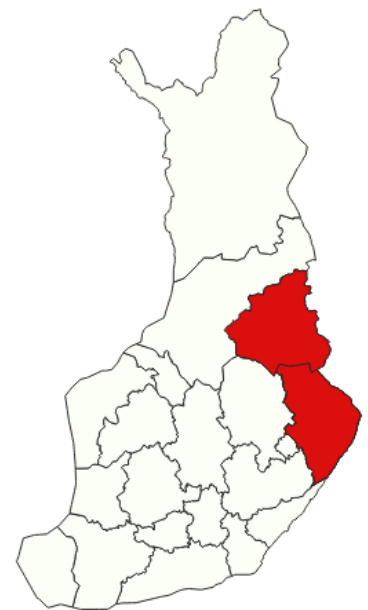


Figure 2. Study area (red). The experiment took place in the regions of Kainuu and North Karelia (Eastern Finland)

➤ 2.2.1 Wildlife triangle data

Wildlife triangle data have been provided by LUKE and it covered 10 years of censuses (2010-2020). Finland has a strong tradition of wildlife monitoring due to the connection of Finns with hunting and the consequent need of sustainable harvesting techniques. Systematic data have been collected since the beginning of the 20th century and in 1989 the wildlife triangle scheme, which is still used nowadays, was introduced. This is a monitoring technique based on winter tracks.

Censuses are made by thousands of volunteers every year by conducting transects which consist of equilateral triangles with 4 km sides ($A=6,928 \text{ km}^2$). Transects are repeated during two consecutive days and new tracks are recorded. Over 30 different species are registered, including native mesopredators and large carnivores. Usually, data about raccoon dogs and American minks is not entirely reliable, the first one because it hibernates in winter, the second one because it is strictly dependent on water habitats (Pellikka *et al.* 2005). Moreover, in late summer, further censuses specific for grouse and bear are made. Transects are conducted by three people, covering a band of 60 m wide, and all direct observation are recorded.

I used this data for multiple purposes. Firstly, I estimated predator abundance. This allowed me to place nests with a stratified design covering areas with different predator pressures. Since not all triangles are done every year due to logistic reasons, to ensure that the estimations were fair, I excluded data coming from less than 4 repetitions. From the remaining ones, I calculated the mean number of tracks over the years and used this number for the actual planning of the experiment. Moreover, I used the data to relate it to the observed predation rate to check if this can be used as a fair predictor of areas where predation pressure on grouse is higher. Additionally, I also used it to estimate grouse reproductive success which I then compared to the observed predation rates.

➤ 2.2.2. Standing forest age

A map of the standing forest age in Finland of 2019 of public domain (MS-NFI 2019) was used to equally divide the number of nests between different forest classes. In particular, I created the following three classes using the raster processing function on QGIS:

1. Young forests: stand age < 20 years
2. Intermediate forests: stand age between 20 and 40 years
3. Mature forests: stand age > 80 years

To answer my study question about the relationship between nest predation and forestry, it would have been ideal to also have old-growth forests (>150 years at least) which are the natural environment in the study area, but these were too scarce. Mature forests older than 80 years were already challenging to find and reach. Since the map was from 2019, it often happened that when I reached the site of a mature forest, I found a clear-cut instead.

➤ 2.2.3. Protected areas permit

To conduct field works in protected areas in Finland, a permit from Metsähallitus must be obtained. I overlapped a map of the protected areas of Finland (syke.fi, 2022) with the stand forest age map and the triangle data. By doing this, I found that four suitable nest locations were inside protected areas (Huurunvaaran, Kansikkovaara, Tulisuo-Varpusuon, Mesiönvaaran). Therefore, I requested and obtained a research permit from Metsähallitus to conduct the study in these areas.

2.3. Experimental design

I placed the nests with a systematic design in order to analyse areas with different relative predator pressures and different forestry impacts. Every sampling site coincided with a 1,5 km buffer around a specific wildlife triangle of 5 km radius (area = 78,54 km²). The area was divided into three further subsites. In each subsite, three locations were chosen: one in a young forest, one in a mature forest and one in a mature forest next to an edge (5 m from a field, a clearcut, or a powerline). The sites in the young and mature forests were at least 50 m from an edge (Fig. 3a).

Natural grouse nests can be easily simulated since they are simple structures consisting of ground depressions filled with leaves and sometimes twigs and feathers. Each nest was baited with two brown hen eggs, which were shown to simulate with enough precision real grouse nests (Yahner and Mahan, 1996). Eggs were handled with rubber gloves and locations were approached with rubber boots to minimize human scent in the area. A motion-activated camera trap was strategically placed at each nest in order to have information on which animals visited the place and when (Fig. 3b). In total, 52 cameras were available for the study (four different models: Browning dark OPS HD Max Plus, Browning dark OPS HD Pro X 20 MP, Bushnell Trophy Cam HD Essential). Camera traps were set to take three consecutive pictures when triggered and with an interval of 5 minutes before the next possible activation.

Artificial nests were placed between May and June 2021, a period coinciding with the real nesting season of grouse in the area. Since the number of cameras and the sampling time were limited, I had to determine whether to get more data by either sampling more locations with a shorter exposure time or sampling less locations, but for a longer time. To do so, I first placed six nests in a triangle in the southern part of the study area for two weeks. After collection, I checked if a rough accumulation curve of predation was present in a week time. Since this was not the case, I decided to maintain a two-week exposure time for the rest of the study. The final sample size consisted of $n=141$ nests.

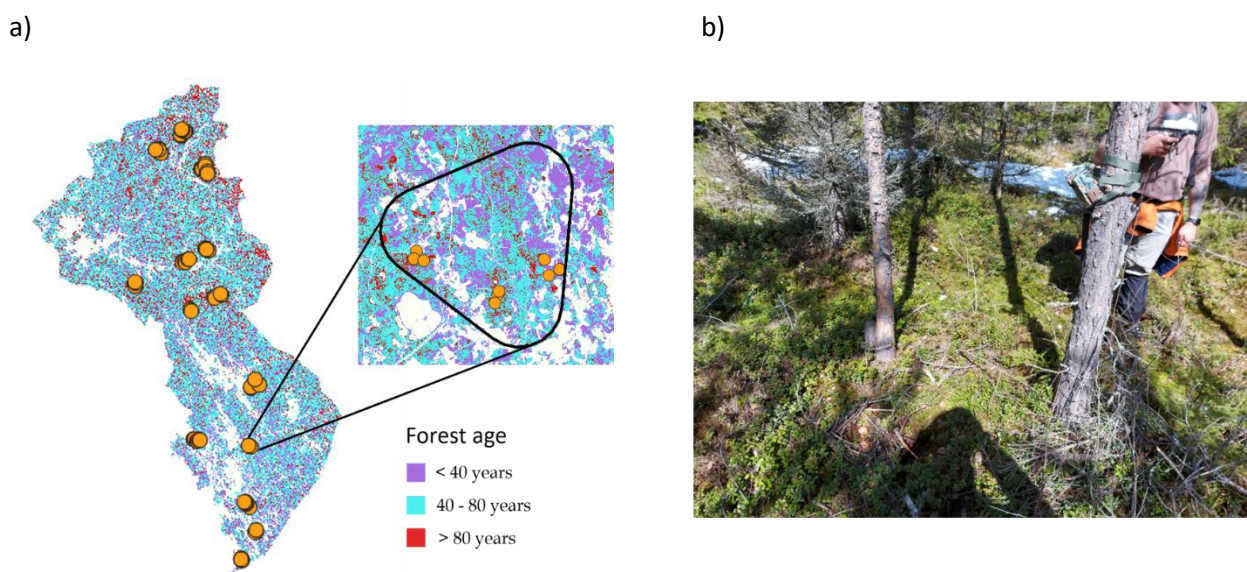


Figure 3: a) Nest locations and study design. The triangle represent the buffer of the wildlife triangle data, the orange dots are the locations of the nests. b) Experimental set up of the artificial nest with the camera trap.

➤ 2.3.1. Variations of the experiment

Over the course of the study, I performed some minor variations in the experiment settings to test whether the type of chicken eggs or the presence or the absence of the camera would make any difference. I built $n = 95$ nests with brown chicken eggs from the supermarket (in Finland they are sold unwashed) and $n = 36$ nests with brown chicken eggs from local farmers. Since the latter ones were sometimes slow to get, I also tried a third option, i.e., leaving some supermarket eggs with local chickens so that they would take their smell. Those were put in the same category as the locally farmed eggs because the latter ones were too few to make up a proper category (9 nests) and I assumed that the odour of the two was similar enough.

Additionally, some nests were placed without a camera trap (n=27) to test whether its presence would deter or scare the predators

2.4. Limits and advantages of an artificial nest experiment

Gathering extensive and systematic data on natural nests is a challenging task, since they are often hard to identify and scattered at very low densities. Therefore, artificial nests can give an important contribution to knowledge that would otherwise be impossible to get. However, it must be acknowledged that artificial nests have some limits in simulating natural conditions with high precision. In particular, the incubating hen can sometimes aggressively defend the eggs discouraging possible predators (Bell 2011) and natural nest concealment is better than what can be simulated artificially (Storaas 1988). On the other hand, it is also possible that the presence of the hen may facilitate the identification of a nest by a predator. Moreover, the scent in the two sites will be very different. In the natural one there will be the scent left by the hen, while in the artificial one it is likely that some human scent will be present, even if all precautions to reduce it are taken (e.g., handling eggs with rubber gloves, approaching sites with rubber boots). The different scent in the two cases have been reported to lead to contrasting results. Willebrand (1988) stated that the scent left by the hen attracted mesopredators more, whereas other authors stated that it was the human scent that attracted mesopredators more (e.g., Major and Kendal 1996). These apparently contrasting results are probably context and species dependent. Some species may present a certain level of neophobia whereas others may be more used to humans and attracted by their scent which may be associated to food.

Nonetheless, artificial nests provide reliable data regarding the relative importance of predation by different species and information about spatial and temporal trends. Most of the accepted theories about nest predation have been built on studies made with artificial nests.

2.5. Data analysis

All analysis were performed in R (version 1.2.5042, R Core Team 2021) and QGIS (version 3.18, QGIS.org 2022).

➤ 2.4.1. Predation rate, habitat and landscape

For the daily survival rate, I used the formula from Shaffer (2004) seen in equation 1:

$$\text{Daily survival rate} = \frac{1 - \text{failed nests}}{\text{exposure days}}$$

Equation 1.

To answer the question whether mature forest may act as an ecological trap for nesting grouse, I checked for differences in the predation rates and in the time until predation in different habitat types. To check for the temporal differences, I used a gamma generalized linear model with a log link function. As response variable I had the number of days until the predation event and as an explanatory variable the habitat type.

To check for the influence of the landscape on different scales, buffers were created around each nest in QGIS of 50 m, 250 m, 500 m, 1 km, 5 km and 25 km. Inside each buffer, I obtained the number of pixels without forest and with young, intermediate and mature forest, using the zonal histogram tool. I then exported these files as csv (comma separated values) files in R. Here, I performed a binomial generalized linear model with a *cloglog* function link, that fits when the probability of an event is very small, for each of the buffer sizes. The fate of the nest (predated/not predated) was used as response variable and the relative proportion of each forest class in the buffer (young, intermediate, mature) as explanatory variable.

I also tested whether the egg type (locally farmed, supermarket) could have influenced the results due to different scents by performing a chi-square goodness-of-fit test between the proportion of predated eggs of each type. Similarly, I also used a chi square test to test whether artificial nests without a camera trap were predated more.

➤ 2.4.2. Wildlife triangle data analysis

The wildlife triangle data was used to place the results into a broader perspective. To obtain values referring to the abundance of predators around the artificial nests, I used the snow index (number of tracks / 10 km transect / "snow day") for fox, marten, polecat and wolverine and the densities from the summer counts for the bear. I have only used the data from 2020. I excluded the stoat because it had strong outliers in the data and it was shown to have no negative influence on the reproductive success of grouse in Finland (Kurki *et al.* 1997). The weasel was excluded as well, since it is even smaller than the stoat and I assumed that its impact on grouse would be even lower. I also excluded raccoon dog and badger because they hibernate in winter, and American mink because it is too

strictly dependant on water habitats to give reliable statistics. Finally, I excluded the specialist large carnivores, *i.e.* the lynx and the wolf, because they are not strong egg predators. I then created buffers of 25 km around each triangle where I put the nests and selected all other triangles lying inside these. Subsequently, I did an inverse distance weighted average of the densities and the snow index values for each buffer. For this, I used the *phylin* package in R (Tarroso *et al.* 2019) using the *Modified Sheperd* Method to calculate the weights.

To answer whether triangles with higher predator densities according to the wildlife data are subject to more egg predation, I summed the obtained values from each predator species and used this as an explanatory variable in a binomial generalized linear model with the number of predated and untouched nests as response variable. To check for the possible influence of the interactions between predator abundance and habitat type, I ran a generalized linear mixed-effect model using the package *lme4* (Bates *et al.* 2015) with the habitat type of the nest as second explanatory variable and the triangle ID as random effect. For this model, I also ran a power analysis using the *simr* package (Green and Macleod 2016) to estimate how many triangles I would need to sample, with an average of 9 nests in each of them, to have statistical significance.

Subsequently, I checked if the lower reproductive success observed in the wildlife data could be explained by a higher nest predation rate. Like with the predators, I did an inverse weighted average in the 25 km buffer around the triangles containing nests of the number of adult grouse and of fledglings from census made in 2020. I then summed together the values from the three different species. Then, I ran a negative binomial generalized linear model from the package MASS (Venables and Ripley 2002) using the number of fledglings as a response variable, the percentage of predated nest in each triangle as explanatory variable, and the number of adults as an offset value.

3. Results

3.1. Predation rate, habitat and landscape

Out of the 141 nests, 18 got predated (predation rate = 12.76%). Predation did not differ between the differently aged forests nor at the edge: the number of predations were equally distributed between mature forests, young forests and edges (Fig. 4a), with a daily survival rate of 99.08 %. However, nests were predated significantly faster in old forests (Fig 4b, $t = -0.169$, $df = 14$, p -

value=0.02). It must be noted the small sample size (n=15); for three of the predated nests, it was not possible to establish the day of predation.

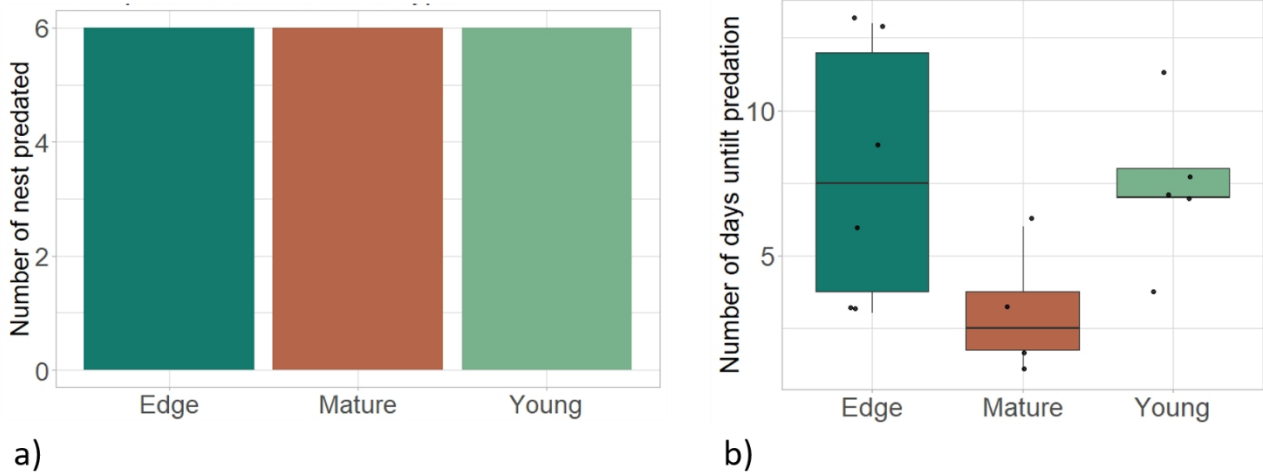


Figure 4. a) Number of nests predated per habitat type. b) Number of days until predation per habitat type. Boxplots show 25% and 75% quantiles, the black line is the median and the black dots the data points

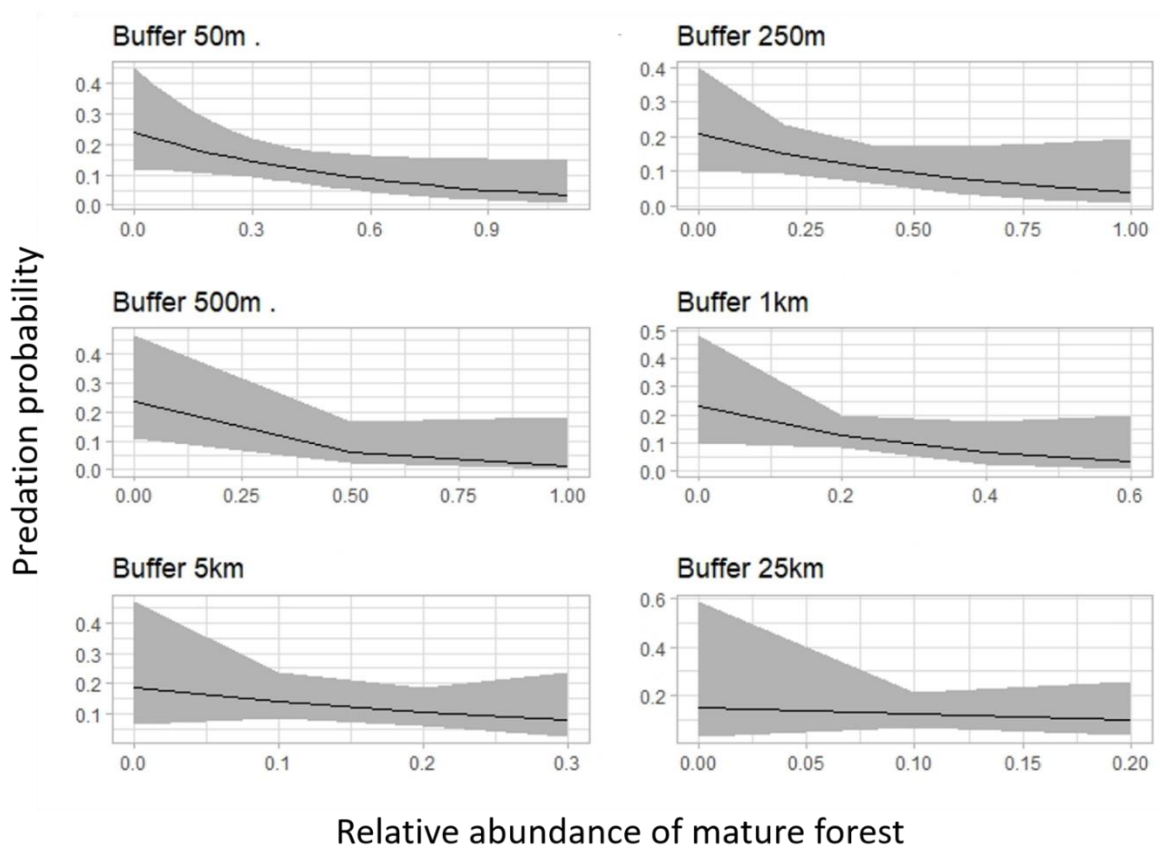


Figure 5. Predicted predation rate according to the abundance of mature forest in the landscape at different scales. The grey areas represent the 95% confidence interval. Model results have a p-value < 0.1 only for the buffer of 50m and 500m.

I found the abundance of mature and intermediate forests to be negatively correlated to predation rate, although non-significant to an $\alpha = 0.05$, in the buffer of 50 m ($z = -1.92$, $df = 140$, $p\text{-value} = 0.055$; $z = -1.84$, $df = 140$, $p\text{-value} = 0.066$) and the abundance of mature forest only in the buffer of 500m ($z = -1.729$, $df = 140$, $p\text{-value} = 0.084$). However, for each buffer size there was a trend of decreasing predation with increasing relative abundance of mature forests (Fig. 5).

➤ **3.1.1. Type of eggs and presence/absence of the camera**

The type of eggs used in the experiment appear to have some effect on predation rate, although non-significant (Tab Ia; $\chi^2 = 3.642$, $df = 1$, $p\text{-value} = 0.056$), with the farmed eggs being predated more than the supermarket ones. The presence of the camera did not have an influence on predation rate (Tab Ib; $\chi^2 = 0.270$, $df = 1$, $p\text{-value} = 0.603$).

Table I. a) Proportion of nest predated according to the egg type. b) Proportion of nest predated according to the presence/absence of the camera trap.

a)

Egg type	Number of nests	Predated
Supermarket	95	7
Locally farmed	45	11

b)

Camera	Number of nests	Predated
Present	113	16
Absent	27	2

3.2. Predator species

The predator abundance calculated from the triangle data around the nest localities tested significant in the binomial generalized linear model with the number of predated and untouched nests as the response variable (Fig. 6; $z\text{-value} = 3.336$, $df = 13$, $p\text{-value} < 0.001$). The estimate was positive, meaning that a higher abundance of predators increased the likelihood of a nest to be predated. When forest age was incorporated into the analysis, there was no significant pattern in the model results (mature forest: $z\text{-value} = -4.896$, $p\text{-value} = 0.924$; young forest = -0.184 , $p\text{-value} = 0.854$). The power analysis showed that in order to obtain significant values in regards to this, 28 triangles should have been sampled, *i.e.* twice the amount of the present sample.

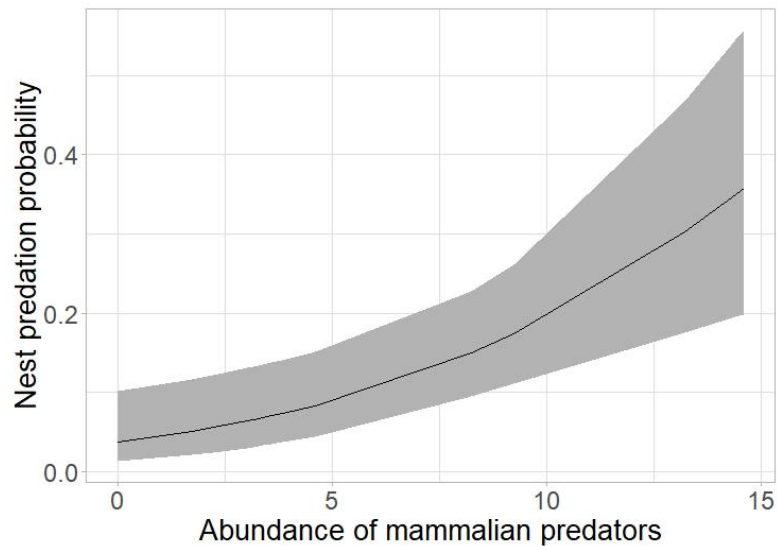


Figure 6. Abundance of potential predators and predicted nest predation rate according to the GLM with gamma errors. The grey area represents the standard error.

The three main predators were badgers, pine martens and magpies (3 nests each), followed by bears (2 nests) and then hooded crow, raven and wolverine (1 nest each) (Fig. 7). For three predation events, it was not possible to establish the predator, two because they were from nests without cameras and in the other case because from the pictures it was only possible to establish that the predator was a medium sized mammal, but not the exact species.

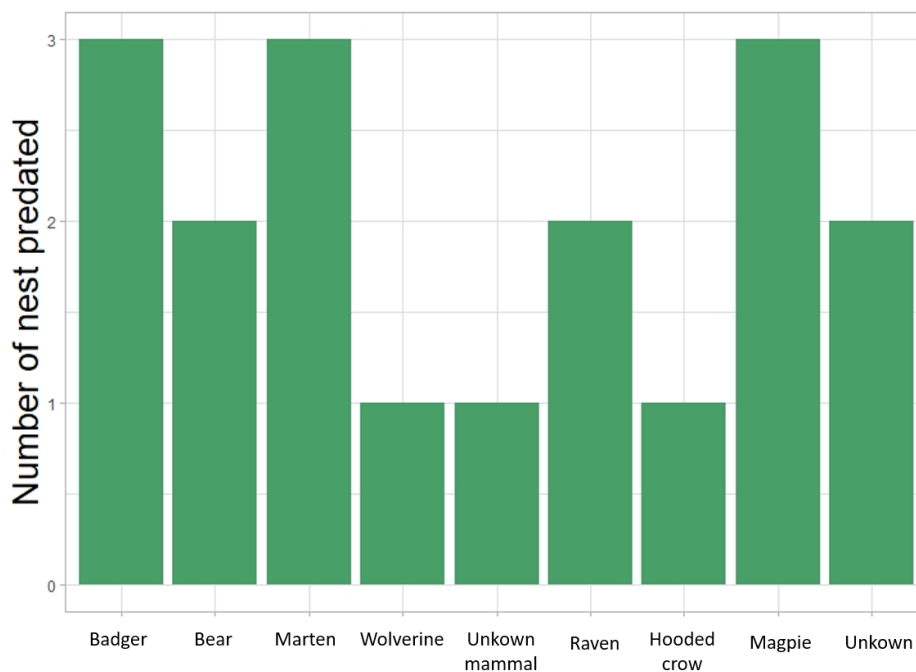


Figure 7. Number of nests predated each predator species

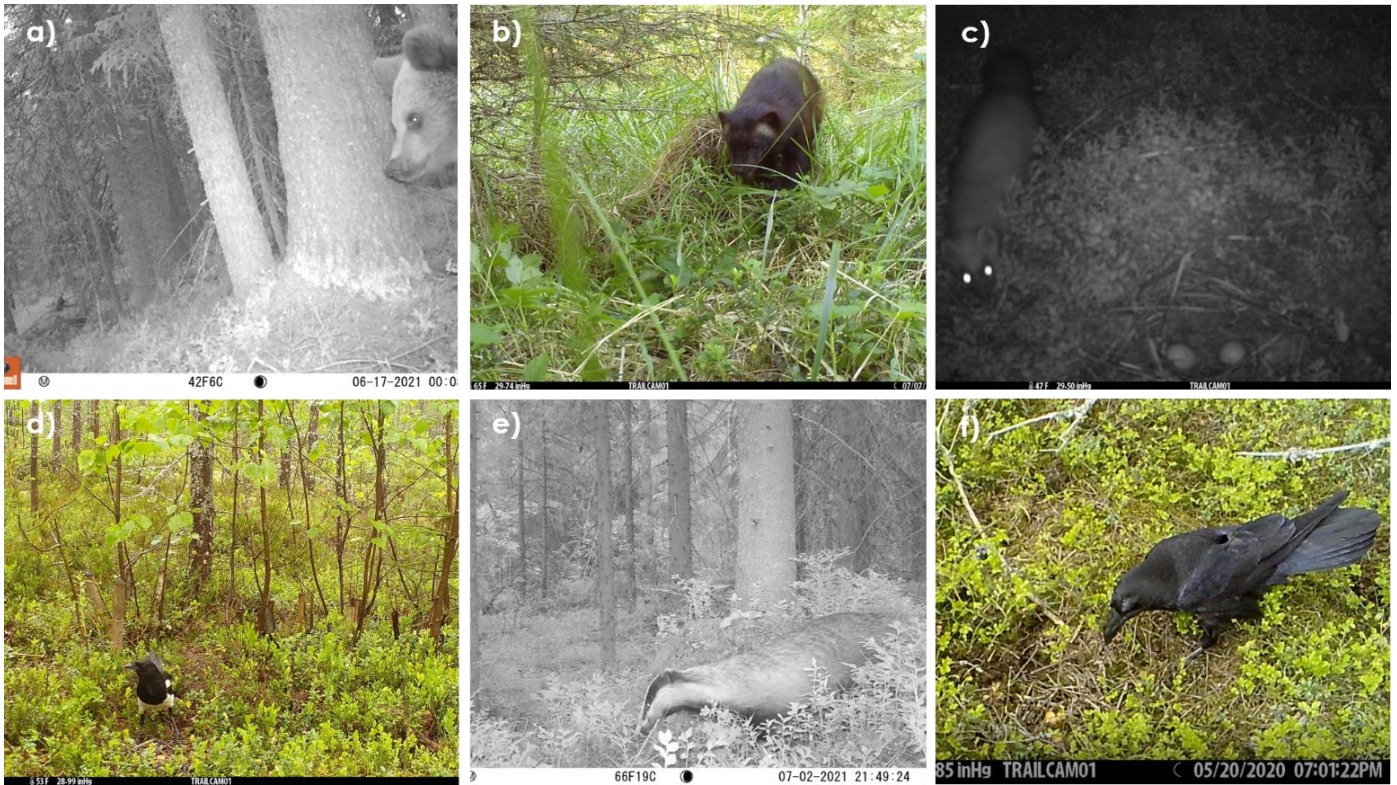


Figure 8. Some of the predator pictures taken by the camera traps. a) brown bear; b) wolverine; c) pine marten; d) Eurasian magpie; e) European badger; f) common raven.

3.3. Reproductive success and nest predation

Nest predation rate did not explain the differences in the reproductive success of grouse between different triangles in the negative binomial generalized linear model (Fig. 9; z-value = -0.439, df = 13, p-value = 0.661). The negative estimate (-0.8539) suggests that the higher the predation rate is, the lower is the number of fledglings. The standard error, however, is large (1.9) and consequently the small sample size is not enough to give statistically significant results.

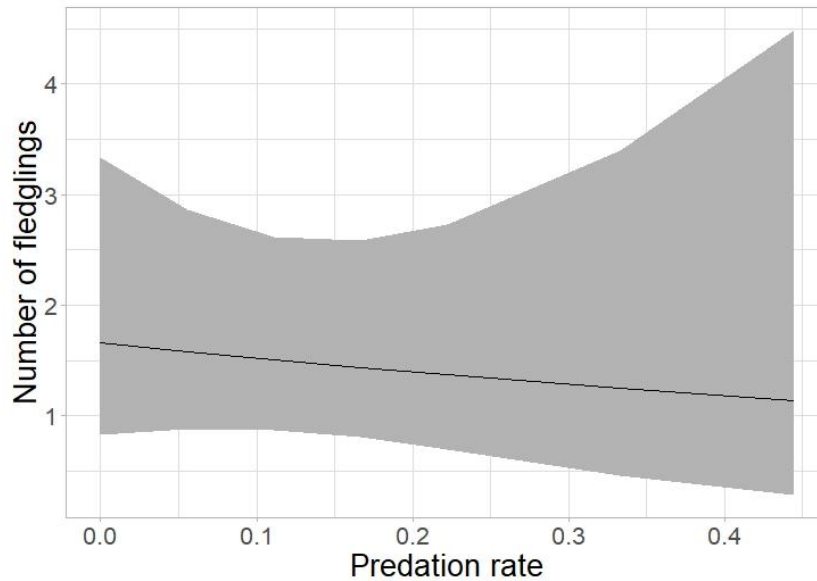


Figure 9. Prediction of the model showing the correlation between nest predation rate and number of fledglings in a 25 km buffer around the triangle where the set of nests was placed. The correlation is not significant. The grey area represents the standard error.

4. Discussion

Overall, I found low predation rate on artificial nests with only weak effect of nest location. Predation rate was in fact constant between mature forests, young forests and edges, but nests were predated faster in the mature forests. However, an increasing in the fraction of young forests in 50m-25Km around the nests increased the predation probability. Contrary to expectations, no nest was predated by non-native species, neither avian predators were more common than other mammalian mesopredators. Predator species were various, including both mesopredators (7 nests), large carnivores (3 nests) and corvids (5 nests). Egg predation seems to only partially explain the differences in reproductive success recorded in the wildlife triangle data. However, it must be taken into account that the sample sizes in my study were small and, consequently, the results may not entirely reflect the reality of the situation.

4.1. Predation rate

One of the reasons behind low sample sizes is the low predation rates encountered (12.76 %). There are a few possible reasons to explain this. As discussed in the introduction, one reason could be the high densities of large carnivores in the area which is known to be beneficial to grouse by

decreasing mesopredator densities (Ludwig 2007). However, this could explain only partially the observed rates. In fact, experiments conducted in Karstula (Central Finland) during 2021, and in Nuuksio (Southern Finland) during 2020, found 17% and 8% of predation, respectively (Uusihakala 2021). Both localities, however, have lower densities of large carnivores compared to my study area, suggesting some other reason to explain the low rates here.

Egg predation rates are also strongly influenced by vole cycles. In fact, communities in boreal forests largely depends on microtine rodents and their fluctuations (Hansson and Henttonen 1985; Hanski *et al.* 1991). Over the last years, these cycles have become less evident (Ims *et al.* 2008), but they are still maintained in Eastern Finland (Sundell *et al.* 2004). Species which predate on voles follow these cycles (Lindstrom *et al.* 1994) and therefore also the pressure on grouse eggs could vary consequently. For example, an artificial nest experiment study conducted in Norway (Pedersen *et al.* 2009) found great differences in predation rate and predator species over three years. Kurki *et al.* (1997) showed that tetraonid breeding success increased during vole cycle peak, result in accordance with the alternative prey hypothesis. This states that generalist predators increase their densities with the abundance of voles and when these decline the pressure on other preys, such as grouse, increase (Tornberg *et al.* 2012; Angelstam and Widen 1984). In fact, grouse nests are usually only a low and unpredictable food source and predators do not actively search for them. Thus, nest predation depends on predator densities and their foraging travelling distances (Wegge and Storaas 1990; Angelstam 1986). Another study that confirm the alternative prey hypothesis for grouse predators comes from Wegge and Storaas (1990) who observed higher predation on grouse nests during vole crash years and lower predation during vole peaks over 7 years of study periods. Angelstam *et al.* (1984) also showed a correlation between vole and fox densities, and increased losses in black grouse. My results support this hypothesis, since 2021 was a high vole year, even if not a peak, (Huito *et al.* 2021) and I found low predation rate which came almost exclusively from generalist species. However, it must be considered that my study area is large and stretched over a long latitudinal gradient, over which there may be some differences in the vole cycle, as well as strong predator immigration from nearby areas.

It must also be underlined that locally farmed eggs got predated more than supermarket ones, which was an unexpected result since supermarket eggs in Finland are sold unwashed and, therefore, they are expected to maintain a natural smell. However, it is unlikely that the final results would have been highly different if the study was conducted with only one constant type of egg, since the correlation was weak and the sample size small. Nonetheless, some other confounding factors may

have a role, like the period of placement of the eggs. In fact, all supermarket eggs were used at the beginning of the study and all farmed eggs at the end.

Artificial nest predation rates across studies referring to forest grouse in Europe are extremely variable, ranging from 8% (Seibold *et al.* 2013; Uusihakala 2021) to 100% (Merta *et al.* 2009), with no clear or universal factors explaining this variation. Even in the same study area large variations can be observed. It is therefore important to be critical in interpreting the results and to not take any important management decision based on one single study.

4.3. Habitat and landscape effect

Predation rates on artificial nests were equally distributed between edges, young and mature forests, even if in the latter predation happened faster. On the other hand, the presence of mature forest in the landscape around the nest positively influenced egg survival. Therefore, even if not strongly statistically significant, a pattern can be observed. On a larger landscape level, the higher amount of old forest seems to decrease nest predation, whereas, on a smaller scale, nesting in an old forest patch in a fragmented landscape increases the likelihood of predation. This is in accordance with both the postulations that forestry increases predator densities on a larger landscape scale due to the abundance of young forests (Kurki *et al.* 1998; Hansson 1994) and that the few semi-natural forests remaining can act as ecological traps for nesting forest grouse, by increasing predator searching efficiency (Storaas *et al.* 1999).

Landscape effect is a challenging variable to measure in nest predation experiments and the high variations observed among studies makes it virtually impossible to extrapolate general rules. Moreover, different predator species can vary in their response to landscape composition over different scales, further increasing the difficulties of making generalizations (Chiavacci *et al.* 2018; Ellis *et al.* 2020). For example, edge effect does not seem to be as strong in continuous forest habitats as it is in more fragmented areas (Batáry and Báldi 2004). In fact, when only studies referring to European forest grouse are considered, the edge effect is not so evident (Fig. 7a, Appendix table I). Similarly, also more fragmented areas do not show a strong increase in predation rates compared to non-fragmented areas when both potentially host forest grouse populations (Fig. 7b, Appendix table I). The effect of stand forest age is even more unclear, with some papers finding higher predation in younger stands, and another study (and the present one) lower (or slower) (Fig. 7c, Appendix table I). Interestingly, most of the studies that do not find a strong landscape effect, say that this is surprising, even if this seems to be the most common outcome. All these apparently

contrasting results are probably very much dependent on the specific landscape and the array of predators present, as well as the year the study was conducted.

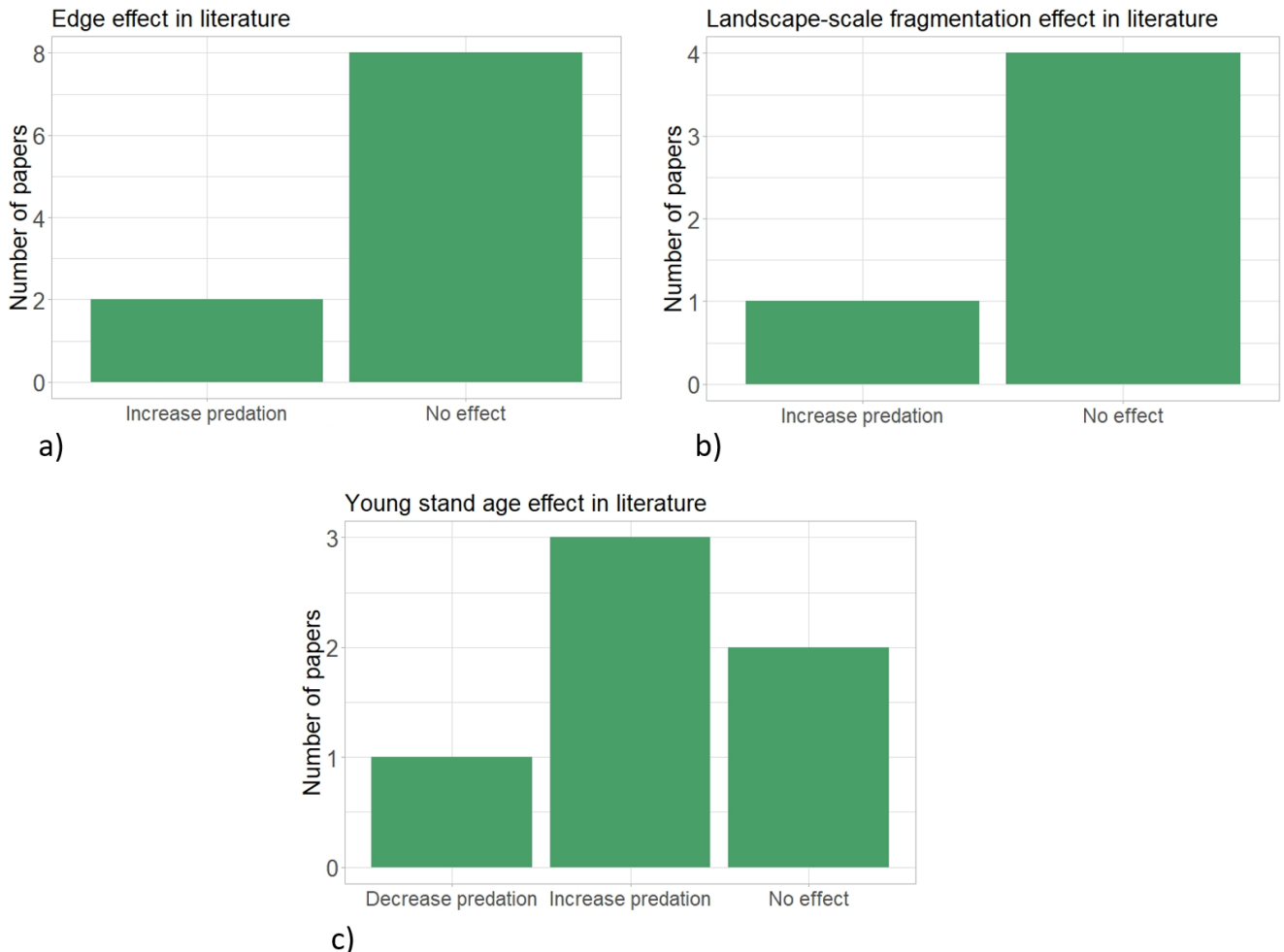


Figure 7. Number of papers that report a habitat effect on artificial nests aimed at simulating European forest grouse species: a) Edge effect, b) Landscape-scale fragmentation effect and c) Young stand age effect

4.2. Predator species

I recorded predation events from 8 different species, none of which strongly predominated. However, mammalian predation was higher than avian predation (10 nests vs 5 nests). Quite surprisingly, I did not find any predation from foxes or from non-native species. These results add to the diverse outcomes of several other nest experiments carried out in Europe. The ratio avian/mammalian predation can vary quite strongly from place to place. For example, a study conducted in Poland found over 90% of the nests to be predated by ravens alone (Merta *et al.* 2009) and even in an experiment conducted in Norway, at higher latitudes than in the present study, the

predominant predators were corvids species (Pedersen *et al.* 2009). However, this latter study was conducted in a birch forest, a quite different environment from the continuous coniferous forests that characterize this study. In fact, relative predation pressure from birds and mammals is probably very context dependent. Nour *et al.* (1993) showed that predation of birds and mammals on artificial nests presents contrasting trends, with avian pressure increasing in more fragmented areas. It has been shown that corvids become especially abundant in more open and agricultural landscapes (Andrén *et al.* 1985; Andren 1992) which were not common in my study area.

Surprisingly, I recorded no predation from foxes or racoon dogs. Foxes are well known egg predators (e.g., Svobodová *et al.* 2004; Šálek *et al.* 2004; Pedersen *et al.* 2009) and, in Fennoscandia, some previous studies showed a negative correlation between fox abundance and grouse reproductive success (Marcstrom *et al.* 1988; Kurki *et al.* 1997). Additionally, the wildlife triangle data for my study area showed that they were the most abundant generalist mesopredator. The lack of predation by them was therefore unexpected. One possibility is that they are particularly neophobic and suspicious of new objects and therefore do not predate on artificial nests. However, this is in contrast with many other studies that did observe fox predation (e.g., Svobodová *et al.* 2004; Šálek *et al.* 2004; Pedersen *et al.* 2009). Another possibility is that the role of the fox in limiting grouse populations in Finland has been overestimated in previous studies. In fact, most of these studies make use of the wildlife triangle data, which is biased on the mammalian species that are active in winter. For example, the presence of the badger, one of the main nest predators in the present study, is not recorded. One other possibility is that foxes move predominantly on roads (Towerton *et al.* 2016), whereas martens and badgers may move more in the forest interiors where the nests are usually found. Finally, it is also possible that foxes play a more important role as chick predators than egg predators.

I also recorded no predation by raccoon dogs, even if they are often considered an important egg predator. However, this result probably should not sound very surprising. In artificial nest experiments aimed at simulating grouse nest all around Europe, raccoon dogs have rarely been recorded to play a major role. They predated nests only in a couple of studies in Estonia, but always in low numbers (Pass *et al.* 2019; Oja *et al.* 2018). On the other hand, in studies investigating the fate of waterfowls and ground nesting farmland bird nests, raccoon dogs have been often one of the main predators (Krüger *et al.* 2018; Holopainen *et al.* 2020; Nummi *et al.* 2019), even at high latitudes (Dahl and Åhlén 2019). In fact, it is possible that raccoon dogs thrive more in fragmented landscapes, where grouse are usually already extinct for other reasons, than in continuous coniferous forests (Mulder 2012). For example, in Finland, raccoon dogs select for meadows and

gardens, while badgers select more for forests with thick canopy, even if the two species overlap to a certain extent (Kauhala and Auttila 2010). Uusihakala (2021) specifically set an experiment in Southern Finland to investigate the role of raccoon dog as potential grouse nest predator. The study recorded no predation event in a protected area made of continuous forest (Nuuksio) where grouse are present, but it did record predation by racoon dogs in much more fragmented green areas (Espoo and Vantaa), where grouse are unlikely to be present. This and my results indicate that raccoon dogs are not yet particularly threatening for the remaining forest grouse populations in Fennoscandia. Nonetheless, raccoon dog populations are on the rise (Kauhala and Kowalczyk 2011) and it is therefore possible that in the future their role as egg predator for grouse will become more predominant.

4.4. Relationship between nest predation rates and wildlife triangle data

With the use of the wildlife triangle data, I found a positive correlation between areas with higher predator densities and areas with higher nest predation. This result suggests that the triangle data can be used to predict in which areas grouse are subject to higher predation. However, one must be careful in the interpretation. In fact, only six predation events came from animals that were censused in the data (marten, wolverine and bear). In the model these abundances were simply summed to be used as response variable. Therefore, the predicted correlation in the model is not necessarily translated into actual causation. Its statistical significance could be the result of a random effect due to the small sample size or of some other hidden factor. As expected, adding the habitat to the model did not improve it. In fact, to estimate interactions, even larger sample sizes are usually needed than when estimating the effect of a single variable. The power analysis showed that sampling efforts should have been doubled in order to get a significant result from the model.

No statistically significant correlation was found between areas where grouse had lower reproductive success and areas where nest predation was higher. However, by looking at the model predictions, a weak trend was observed. This result suggests that egg predation is only partially responsible for the decreased reproductive success. Chick predation could also play an important role in the process. For example, a study in Norway found that on average, 57 % of capercaillie chicks die in the first month of life, and this is mainly due to predation (Wegge and Kastdalen 2007). Additionally, Storaas *et al.* (1999) observed chick predation to increase as a consequence of habitat fragmentation even more than egg predation. Besides, also other processes are important in

determining the reproductive success of grouse, like environmental factors such as the bilberry cover and the weather (Ludwig *et al.* 2010; Wegge and Kastdalen 2007).

4.5. Implications

My results suggest that nest predation alone is not enough to explain the low densities of forest grouse in Eastern Finland. It is possible that chick predation and adult mortality play a more important role in it. Recreative hunting in particular is extremely widespread in the study area, especially of black grouse. The game bag for this species in Kainuu and North Karelia in 2020 alone was of 28.400 individuals (statdb.luke.fi, 2022). Forestry is also known to be detrimental for grouse and my results suggest that one of the mechanisms through which it has an effect could be an increase in nest predation. Several management decisions can be taken to improve the situation. The few remaining untouched forest patches should be left as such and connected as much as possible with each other. In the remaining forests, forestry should limit clearcuts and adopt more sustainable techniques which leaves a continuous cover. Also, the clearings of understory should be avoided so that it creates shelter from predators. Finally, draining should be reduced or halted, and wetlands should be restored to provide insect-rich habitats that improve chick survival.

4.6. Conclusion

To conclude, the decline of the European forest grouse is a complex topic and it probably does not have a single clear cause. Many mechanisms, and their interaction, are likely to play a role, and nest predation is only one. In Fennoscandia, forestry is the main driver of landscape change and it is likely to be a predominant driver behind grouse declines. Non-native generalist mesopredators do not seem to have a strong negative influence as usually believed, even if the situation may change in the future. However, one must be careful in interpreting the results. In fact, with only a few nests to conduct statistical analysis, it was difficult to get strong statistical significance and the observed trends need to be confirmed by further studies. Finally, it is also worth mentioning that artificial nests experiments across Europe show many highly variable different results. Therefore, the extrapolation of general rules based on these can be difficult and they are unlikely to further increasing our knowledge about the decline of forest grouse.

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6. References

- Andren, H. 1992. "Corvid Density and Nest Predation in Relation to Forest Fragmentation : A Landscape Perspective" *Ecology* 73 (3): 794–804. <https://doi.org/10.2307/1940158>
- Andrén, H., Angelstam, P., Lindström, E., Widén, P., Andren, H., Angelstam, P., Lindstrom, E. and Widen, P. 1985. "Differences in Predation Pressure in Relation to Habitat Fragmentation : An Experiment" *Oikos* 45 (2): 273–77.
- Angelstam, P. 1986. "Predation on Ground-Nesting Birds' Nests in Relation to Predator Densities and Habitat Edge." *Oikos* 47 (3): 365–73.
- Baines, D., Moss, R. and Dugan, D. 2004. "Capercaillie Breeding Success in Relation to Forest Habitat and Predator Abundance." *Journal of Applied Ecology* 41 (1): 59–71. <https://doi.org/10.1111/J.1365-2664.2004.00875.X>.
- Batáry, P. and András B. 2004. "Evidence of an Edge Effect on Avian Nest Success." *Conservation Biology* 18 (2): 389–400. <https://doi.org/10.1111/j.1523-1739.2004.00184.x>.
- Bates, D., Martin, M., Benjamin M. B., and Steven C. W.. 2015. "Fitting Linear Mixed-Effects Models Using Lme4" - *Journal of Statistical Software* 67 (1). <https://doi.org/10.18637/jss.v067.i01>.
- Bell, C. B. 2011. Nest site characteristics and nest success of translocated and resident greater sage grouse at Clear Lake National Wildlife Refuge" - MS thesis. Humboldt State University
- Caizergues, A. and Ellison, L. N. 2000. "Age-Specific Reproductive Performance of Black Grouse Tetrao Tetrix Females." *Bird Study* 47 (3): 344–51. <https://doi.org/10.1080/00063650009461194>.
- Chalfoun, A. D., Thompson, F. R. and Ratnaswamy, M. J. 2002. "Nest Predators and Fragmentation: A Review and Meta-Analysis." *Conservation Biology* 16 (2): 306–18. <https://doi.org/10.1046/j.1523-1739.2002.00308.x>.
- Chiavacci, S. J., Benson, T. J. and Ward, M. P. 2018. "Linking Landscape Composition to Predator-

- Specific Nest Predation Requires Examining Multiple Landscape Scales.” *Journal of Applied Ecology* 55 (4): 2082–92. <https://doi.org/10.1111/1365-2664.13090>.
- Dahl, F. and Åhlén, P. A. 2019. “Nest Predation by Raccoon Dog *Nyctereutes Procyonoides* in the Archipelago of Northern Sweden.” *Biological Invasions* 21 (3): 743–55. <https://doi.org/10.1007/s10530-018-1855-4>.
- Ellis, K. S., Randy T. L., and Koons, D. N. 2020. “The Importance of Functional Responses among Competing Predators for Avian Nesting Success.” *Functional Ecology* 34 (1): 252–64. <https://doi.org/10.1111/1365-2435.13460>.
- Esseen, P., Ehnstrom, B. and Ericson, L. 1992. “Boreal Forests-The Focal Habitats of Fennoscandia.” - *Ecological principles of nature conservation* (pp. 252-325)
- Food and Agriculture Organization of the United Nations (FAO). 2010. "Global forest resources assessment 2010: Main report." Rome: Food and Agriculture Organization of the United Nations. <https://www.fao.org/3/i1757e/i1757e.pdf>
- Forest resource maps and municipal statistics. 2019. “Forest resource maps and municipal statistics. Natural Resources Institute (Luke), Finland.” <https://kartta.luke.fi/opendata/valinta-en.html> [retrieved on 29/04/2022]
- Green, P. and Macleod, C. J. 2016. “SIMR : An R Package for Power Analysis of Generalized Linear Mixed Models by Simulation” *Methods in Ecology and Evolution* 7.4: 493-498. <https://doi.org/10.1111/2041-210X.12504>.
- Hanski, I., Hansson, L. and Henttonen, H. 1991. “Specialist Predators , Generalist Predators , and the Microtine Rodent Cycle” *The Journal of Animal Ecology*: 353-367.
- Hansson, L. 1992. “Landscape Ecology of Boreal Forests.” *Trends in Ecology and Evolution* 7 (9): 299–302. [https://doi.org/10.1016/0169-5347\(92\)90227-3](https://doi.org/10.1016/0169-5347(92)90227-3).
- Hansson, L. 1994. “Vertebrate Distributions Relative to Clear-Cut Edges in a Boreal Forest Landscape.” *Landscape Ecology* 9 (2): 105–15. <https://doi.org/10.1007/BF00124377>.
- Hartley, M. J. and Hunter M. L. 1998. "A meta-analysis of forest cover, edge effects, and artificial nest predation rates." *Conservation Biology* 12.2: 465-469
- Helle, E. and Kauhala, K. 1991. “Distribution History and Present Status of the Raccoon Dog in Finland.” *Ecography* 14 (4): 278–86. <https://doi.org/10.1111/j.1600-0587.1991.tb00662.x>.
- Helle, P., Helle, T. and Lindén, H. 1994. “Capercaillie (*Tetrao Urogallus*) Lekking Sites in Fragmented Finnish Forest Landscape.” *Scandinavian Journal of Forest Research* 9 (1–4): 386–96. <https://doi.org/10.1080/02827589409382856>.
- Holopainen, S., Väänänen, VM. and Fox, A. D. 2020. “Artificial Nest Experiment Reveals Inter-Guild Facilitation in Duck Nest Predation.” *Global Ecology and Conservation* 24. <https://doi.org/10.1016/j.gecco.2020.e01305>.
- Huito, O., Niemimaa, J. and Henttonen, H. 2021. " Myyräkannat alhaiset suurimmassa osassa Suomea". *Luke* (17/06/2021). <https://www.luke.fi/fi/uutiset/myyrakannat-alhaiset-suurimmassa-osassa-suomea> [last checked: 29/04/2022]
- Ims, R. A., Henden, J. A. and Killengreen, S. T. 2008. “Collapsing Population Cycles.” *Trends in Ecology and Evolution* 23 (2): 79–86. <https://doi.org/10.1016/j.tree.2007.10.010>.
- IUCN 2016. 2016 IUCN Red List Of Threatened Species. Available at <https://www.iucnredlist.org/> [retrieved on 01/05/2022]
- Lindström, ER and Hörnfeldt, B. 1994. “Vole Cycles , Snow Depth and Fox Predation” *Oikos* 70 (1): 156–60.
- Jahren, T., Storaas, T., Willebrand, T., Fossland, M. P. and Hagen, B. R.. 2016. “Declining Reproductive Output in Capercaillie and Black Grouse-16 Countries and 80 Years.” *Animal Biology* 66 (3–4): 363–400. <https://doi.org/10.1163/15707563-00002514>.
- Kammerle, J. L., Coppes, J., Ciuti, S., Suchant, R. and Storch, I. 2017. “Range Loss of a Threatened Grouse Species Is Related to the Relative Abundance of a Mesopredator.” *Ecosphere* 8 (9). <https://doi.org/10.1002/ecs2.1934>.

- Kardell, L. 1979. "Occurrence and Production of Bilberry, Lingonberry and Raspberry in Sweden's Forests." *Forest Ecology and Management*. [https://doi.org/10.1016/0378-1127\(79\)90055-0](https://doi.org/10.1016/0378-1127(79)90055-0).
- Kauhala, K. 1996. "Distributional History of the American Mink (*Mustela Vison*) in Finland with Special Reference to the Trends in Otter (*Lutra Lutra*) Populations." *Finnish Zoological and Botanical Publishing Board* 33 (2): 283–91.
- Kauhala, K. and Auttila, M. 2010. "Habitat Preferences of the Native Badger and the Invasive Raccoon Dog in Southern Finland." *Acta Theriologica* 55 (3): 231–40. <https://doi.org/10.4098/j.at.0001-7051.040.2009>.
- Kauhala, K. and Kowalczyk, R. 2011. "Invasion of the Raccoon Dog *Nyctereutes Procyonoides* in Europe: History of Colonization, Features behind Its Success, and Threats to Native Fauna." *Current Zoology* 57 (5): 584–98. <https://doi.org/10.1093/czoolo/57.5.584>.
- Kojola, I., Huitu, O., Toppinen, K., Heikura, K., Heikkinen, S. and Ronkainen, S. 2004. "Predation on European Wild Forest Reindeer (*Rangifer Tarandus*) by Wolves (*Canis Lupus*) in Finland." *Journal of Zoology* 263 (3): 229–35. <https://doi.org/10.1017/S0952836904005084>.
- Krüger, H., Väänänen, VM, Holopainen, S. and Nummi, P. 2018. "The New Faces of Nest Predation in Agricultural Landscapes—a Wildlife Camera Survey with Artificial Nests." *European Journal of Wildlife Research* 64 (6). <https://doi.org/10.1007/s10344-018-1233-7>.
- Kurki, S., Helle, P., Lindén, H. and Nikula, A. 1997. "Breeding Success of Black Grouse and Capercaillie in Relation to Mammalian Predator Densities on Two Spatial Scales." *Oikos*: 301-310
- Kurki, S. and Lindén, H. 1995. "Forest Fragmentation Due to Agriculture Affects the Reproductive Success of the Ground-nesting Black Grouse *Tetrao Tetrix*." *Ecography* 18 (2): 109–13. <https://doi.org/10.1111/j.1600-0587.1995.tb00330.x>.
- Kurki, S., Nikula, A., Helle, P. and Lindén, H. 1998. "Abundances of Red Fox and Pine Marten in Relation to the Composition of Boreal Forest Landscapes." *Journal of Animal Ecology* 67 (6): 874–86. <https://doi.org/10.1046/j.1365-2656.1998.6760874.x>.
- Kurki, S., Nikula, A., Helle, P. and Lindén, H. 2000. "Landscape Fragmentation and Forest Composition Effects on Grouse Breeding Success in Boreal Forests." *Ecology* 81 (7): 1985–97. [https://doi.org/10.1890/0012-9658\(2000\)081\[1985:LFAFCE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1985:LFAFCE]2.0.CO;2).
- Lampila, P., Ranta, E., Mönkkönen, M., Lindén, H. and Helle, P. 2011. "Grouse Dynamics and Harvesting in Kainuu, Northeastern Finland." *Oikos* 120 (7): 1057–64. <https://doi.org/10.1111/j.1600-0706.2010.18788.x>.
- Hansson, L. and Henttonen, H. 1985. "Gradients in Density Variations of Small Rodents: The Importance of Latitude and Snow Cover," *Oecologia*, 67(3), 394-402. <https://doi.org/10.1007/BF00384946>
- Lindstrom, J., Ranta, E., Kaitala, V. and Linden, H. 1995. "The Clockwork of Finnish Tetraonid Population Dynamics" *Oikos* 74 (2): 185–94. <https://doi.org/10.2307/3545647>
- Ludwig, G. X. 2007. *Mechanisms of Population Declines in Boreal Forest Grouse*. PhD Thesis. University of Jyväskylä
- Ludwig, G. X., Alatalo, R. V., Helle, P., Lindén, H., Lindström, J. and Siitari, H. 2006. "Short- and Long-Term Population Dynamical Consequences of Asymmetric Climate Change in Black Grouse." *Proceedings of the Royal Society B: Biological Sciences* 273 (1597): 2009–16. <https://doi.org/10.1098/rspb.2006.3538>.
- Ludwig, G. X., Alatalo, R. V., Helle, P. and Siitari, H. 2010. "Individual and Environmental Determinants of Daily Black Grouse Nest Survival Rates at Variable Predator Densities." *Annales Zoologici Fennici* 47 (6): 387–97. <https://doi.org/10.5735/086.047.0602>.
- Major, R. E. and Kendal, C. E. 1996. "The Contribution of Artificial Nest Experiments to Understanding Avian Reproductive Success: A Review of Methods and Conclusions." *Ibis* 138 (2): 298–307. <https://doi.org/10.1111/j.1474-919x.1996.tb04342.x>.
- Marcstrom, V., Kenward, R. E. and Engren, E. 1988. "The Impact of Predation on Boreal

- Tetraonids During Vole Cycles: An Experimental Study.” *The Journal of Animal Ecology* 57 (3): 859. <https://doi.org/10.2307/5097>.
- Merta, D., Bobek, B., Furtek, J. and Kolecki, M. 2009. “Distribution and Number of Black Grouse, Tetrao Tetrix in Southwestern Poland and the Potential Impact of Predators upon Nesting Success of the Species.” *Folia Zoologica* 58 (2): 159–67.
- Miettinen, J., Helle, P., Nikula, A. and Niemelä, P. 2008. “Large-Scale Landscape Composition and Capercaillie (Tetrao Urogallus) Density in Finland.” *Annales Zoologici Fennici* 45 (3): 161–73. <https://doi.org/10.5735/086.045.0301>.
- Mulder, L. 2012. “A Review of the Ecology of the Raccoon Dog.” *Lutra* 55(2), 101-127.
- Nature protected areas. 2021. Finnish Environment Institute (SYKE). https://www.syke.fi/en-US/Open_information/Spatial_datasets/Downloadable_spatial_dataset [retrieved on 29/04/2022]
- Nour, N., Matthysen, E. and Dhondt, A. A. 1993. “Artificial Nest Predation and Habitat Fragmentation: Different Trends in Bird and Mammal Predators.” *Ecography* 16 (2): 111–16. <https://doi.org/10.1111/j.1600-0587.1993.tb00063.x>.
- Nummi, P., Väänänen, VM., Pekkarinen, A. J., Eronen, V., Mikkola-Roos, M., Nurmi, J., Rautiainen, A. and Rusanen, P. 2019. “Alien Predation in Wetlands – The Raccoon Dog and Waterbird Breeding Success.” *Baltic Forestry* 25 (2): 228–37. <https://doi.org/10.46490/vol25iss2pp228>.
- Oehler, J. D. and Litvaitis, J. A. 1996. “The Role of Spatial Scale in Understanding Responses of Medium-Sized Carnivores to Forest Fragmentation.” *Canadian Journal of Zoology* 74 (11): 2070–79. <https://doi.org/10.1139/z96-235>.
- Oja, R., Pass, E., Soe, E., Ligi, K., Anijalg, P., Laurimaa, L., Saarma, U. and Lõhmus, A. 2018. “Increased Nest Predation near Protected Capercaillie Leks : A Caveat against Small Reserves.” *European journal of wildlife research*, 64(1), 1-8 <https://doi.org/10.1007/s10344-018-1165-2>.
- Pakkala, T., Pellikka, J. and Lindén, H. 2003. “Capercaillie *Tetrao Urogallus* - a Good Candidate for an Umbrella Species in Taiga Forests.” *Wildlife Biology* 9 (1): 309–16. <https://doi.org/10.2981/wlb.2003.019>.
- Pass, E., Lodjak, J., Mägi, M. and Lõhmus, A. 2019. “Complex Habitat Patterns Create Unpredictable Nest Predation Risk - an Artificial Nest Experiment.” *Ornis Fennica* 96 (4): 182–93.
- Pedersen, Å, Yoccoz, N. G. and Ims, R. A. 2009. “Spatial and Temporal Patterns of Artificial Nest Predation in Mountain Birch Forests Fragmented by Spruce Plantations.” *European Journal of Wildlife Research* 55 (4): 371–84. <https://doi.org/10.1007/s10344-009-0253-8>.
- Pellikka, J., Rita, H. and Lindén, H. 2005. “Monitoring Wildlife Richness — Finnish Applications Based on Wildlife Triangle Censuses” *Annales Zoologici Fennici* (pp. 123-134). Finnish Zoological and Botanical Publishing Board.
- QGIS.org. 2022. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org>.
- Ritchie, E. G. and Johnson, C. N. 2009 “Predator Interactions, Mesopredator Release and Biodiversity Conservation.” *Ecology Letters* 12 (9): 982–98. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>.
- Sachot, S., Perrin, N. and Neet, C. 2003. “Winter Habitat Selection by Two Sympatric Forest Grouse in Western Switzerland: Implications for Conservation.” *Biological Conservation* 112 (3): 373–82. [https://doi.org/10.1016/S0006-3207\(02\)00334-8](https://doi.org/10.1016/S0006-3207(02)00334-8).
- Šálek, M., Svobodová, J., Bejček, V. and Albrecht, T. 2004. “Predation on Artificial Nests in Relation to the Numbers of Small Mammals in the Krušné Hory Mts, the Czech Republic.”

Folia Zoologica 53 (3): 312–18.

- Savola, S., Henttonen, H. and Lindén, H. 2013. “Vole Population Dynamics during the Succession of a Commercial Forest in Northern Finland.” *Annales Zoologici Fennici* 50 (1–2): 79–88. <https://doi.org/10.5735/086.050.0107>.
- Seibold, S., Hempel, A., Piehl, S., Bässler, C., Brandl, R., Rösner, S. and Müller, J. 2013. “Forest Vegetation Structure Has More Influence on Predation Risk of Artificial Ground Nests than Human Activities.” *Basic and Applied Ecology* 14 (8): 687–93. <https://doi.org/10.1016/j.baae.2013.09.003>.
- Shaffer, T. L. 2004. "A unified approach to analyzing nest success." *The Auk* 121(2): 526-540. <https://doi.org/10.1093/auk/121.2.526>.
- Sirkiä, S., Lindén, A., Helle, P., Nikula, A., Knape, J. and 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 (6): 1540–48. <https://doi.org/10.1016/j.biocon.2010.03.038>.
- Sjöberg, K. 1996. “Modern Forestry and the Capercaillie.” *Conservation of Faunal Diversity in Forested Landscapes*: 111–35. <https://doi.org/10.1007/978-94-009-1521-3>.
- Statdb.luke.fi. 2022. http://statdb.luke.fi/PXWeb/pxweb/en/LUKE/LUKE__06%20Kala%20ja%20riista__02%20Rakenne%20ja%20tuotanto__16%20Metsastys/5_Mets_saalis.px/ [retrieved on 01/05/2022]
- Storaas, T. 1988. “A Comparison of Losses in Artificial and Naturally Occurring Capercaillie Nests.” *Journal of Wildlife Management* 52 (1): 123–26. https://www.jstor.org/stable/3801071?seq=1#page_scan_tab_contents.
- Storaas, T., Kastdalen, L. and Wegge, P. 1999. “Detection of Forest Grouse by Mammalian Predators: A Possible Explanation for High Brood Losses in Fragmented Landscapes.” *Wildlife Biology* 5 (3): 187–92. <https://doi.org/10.2981/wlb.1999.016>.
- Storch, I. 1993. “Habitat Selection by Capercaillie in Summer and Autumn: Is Bilberry Important?” *Oecologia* 95 (2): 257–65. <https://doi.org/10.1007/BF00323498>.
- Storch, I. 2000. “Conservation Status and Threats to Grouse Worldwide: An Overview.” *Wildlife Biology* 6 (1): 195–204. <https://doi.org/10.2981/wlb.2000.016>.
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. and Hanski, I. 2004. “Large-Scale Spatial Dynamics of Vole Populations in Finland Revealed by the Breeding Success of Vole-Eating Avian Predators.” *Journal of Animal Ecology* 73 (1): 167–78. <https://doi.org/10.1111/j.1365-2656.2004.00795.x>.
- Svobodová, J., Albrecht, T. and Šálek, 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 (4): 421–27. <https://doi.org/10.1080/11956860.2004.11682851>.
- Swenson, J. E., Saari, L., & Bonczar, Z. 1994. “Effects of weather on hazel grouse reproduction: an allometric perspective.” *Journal of avian biology* 25: 8-14.
- Syke.fi. 2022. https://www.syke.fi/en-US/Open_information/Spatial_datasets/Downloadable_spatial_dataset [last retrieved on 02/05/2022]
- Tarroso, P., Carvalho, S. B. and Velo-Antón, G. 2019. “Phylin 2.0: Extending the Phylogeographical Interpolation Method to Include Uncertainty and User-Defined Distance Metrics.” *Molecular Ecology Resources* 19 (4): 1081–94. <https://doi.org/10.1111/1755-0998.13010>.
- Tornberg, R., Reif, V. and Korpimäki, E. 2012. “What Explains Forest Grouse Mortality: Predation Impacts of Raptors, Vole Abundance, or Weather Conditions?” *International Journal of Ecology* 2012. <https://doi.org/10.1155/2012/375260>.
- Towerton, A. L., Dickman, C. R., Kavanagh, R. P. and Penman, T. D.. 2016. “Control of the Red

- Fox in Remnant Forest Habitats.” *Wildlife Research* 43 (2): 169–77.
<https://doi.org/10.1071/WR15133>.
- Turunen, J. 2008. “Development of Finnish Peatland Area and Carbon Storage” *Boreal Environment Research* 13 (4): 319-334
- Uusihakala, Linda. 2021. *Metson Haasteet Nuuksiossa – Maiseman Vaikutus Pesäpredaatioon Ja Supikoiraan Pesäsaalistajana*. Master’s thesis. University of Helsinki, Faculty of Biological and Environmental Sciences
- Wegge, P. and Storaas, T. 1990. “Nest Loss in Capercaillie and Black Grouse in Relation to the Small Rodent Cycle in Southeast Norway.” *Oecologia* 82 (4): 527–30.
<https://doi.org/10.1007/BF00319796>.
- Wegge, P., Rølstad, J. and Gjerde, I. 1992. “Effects of boreal forest fragmentation on capercaillie grouse: empirical evidence and management implications.” *Wildlife 2001: populations* 738-749. Springer, Dordrecht.
- Wegge, P., and Kastdalen, L. 2007. “Pattern and Causes of Natural Mortality of Capercaillie, Tetrao Urogallus, Chicks in a Fragmented Boreal Forest.” *Annales Zoologici Fennici* 44 (2): 141–51.
- Wegge, P. and Kastdalen, L. 2008. “Habitat and Diet of Young Grouse Broods: Resource Partitioning between Capercaillie (*Tetrao Urogallus*) and Black Grouse (*Tetrao Tetrix*) in Boreal Forests.” *Journal of Ornithology* 149 (2): 237–44. <https://doi.org/10.1007/s10336-007-0265-7>.
- Willebrand, T. 1988. “On the Danger of Using Dummy Nests to Study Predation.” *The Auk* 105 (2): 378–79. <https://doi.org/10.2307/4087508>.
- Wolf, C. and Ripple, W. J. 2017. “Range Contractions of the World’s Large Carnivores.” *Royal Society Open Science* 4 (7). <https://doi.org/10.1098/rsos.170052>.
- Yahner, R. H. and Mahan, C. G. 1996. “Effects of Egg Type on Depredation of Artificial Ground Nests.” *The Wilson Bulletin* 108 (1): 129–36.

Appendix

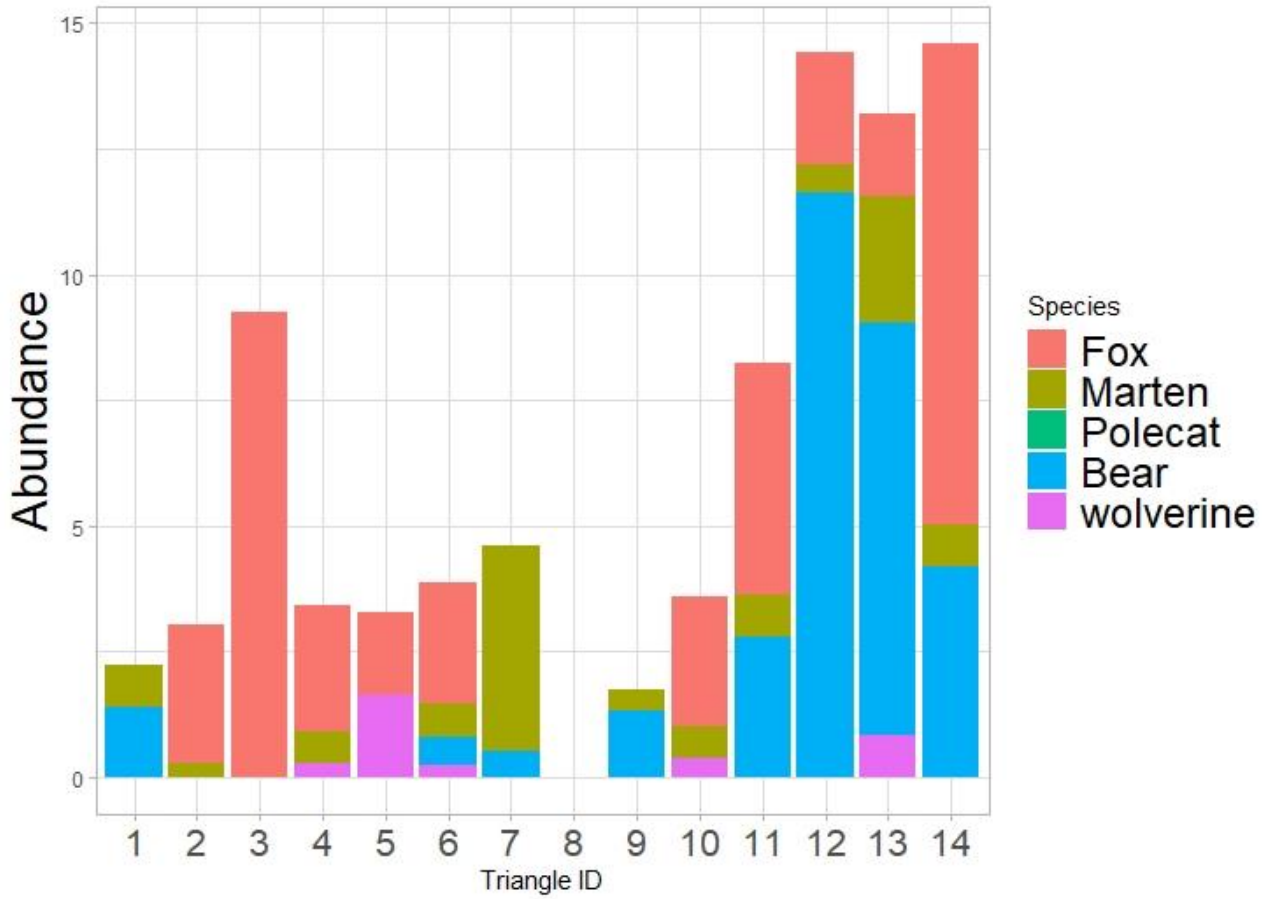


Figure 1. Relative abundance of different predator species according to the triangle data in the buffer around the triangles where I put nests. The triangle ID are from the northernmost to the southernmost sampled location of the study area

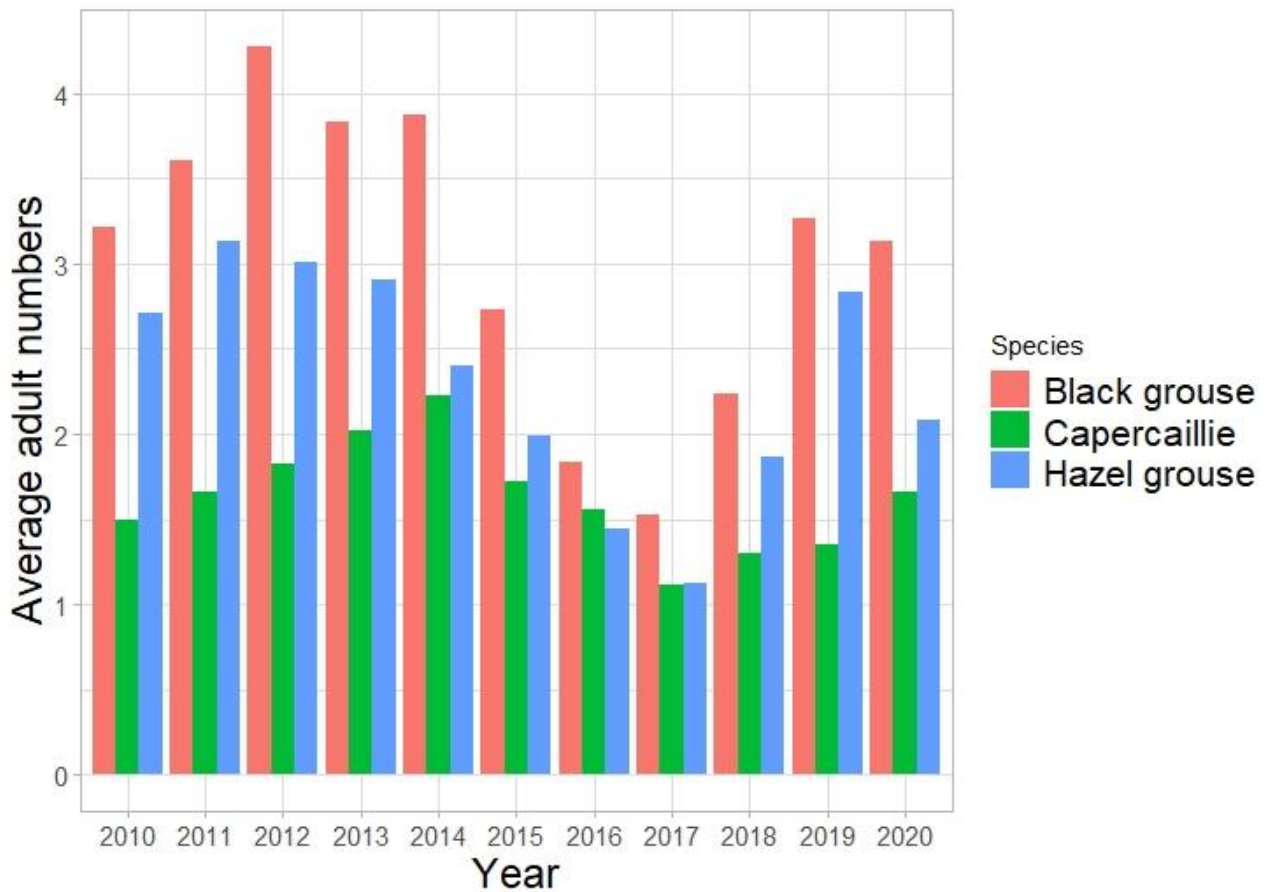


Figure 2. Average number of adults for each species of grouse over the whole study area (Kainuu and North Karelia) from 2010 to 2020.

Table I. Summary of artificial nest experiments investigating egg predation on European forest grouse

Article	Locality	Country	Year of data collection	Adjusted average predation rate over 14 days	Predator species
Pass <i>et al.</i> 2019	Soomaa region	Estonia	2016	49%	Unknown mammal (32%), pine marten (21%), unknown bird (15%), Eurasian jay (12%), small mustelid (9%), red squirrel (5%), raccoon dog (<i>Nyctereutes procyonoides</i>) (2.5%), large carnivore (1%) and red fox (1%)
Oja <i>et al.</i> 2018			2014	61.6%	Lynx, Marten (main predator), raccoon dogs (2 reported), red fox, squirrel, raven, jay
Svobodová <i>et al.</i> 2004			2002	11.8%	Foxes and martens were identified as the main nest predators
Svobodová <i>et al.</i> 2007			2003	50.6%	Not reported
Cukor <i>et al.</i> 2021			2020	26.13%	The stone marten was the main nest predator in Jeseníky (89% of predation events), the red fox was recorded in one case of nest predation (11%). In Ore Mts., the main nest predator was common raven with seven records (37%). The Eurasian jay was responsible for most predation attempts in Jeseníky (five records, i.e., 83%),

	Krušné hory mountains	Czech Republic			while in the Ore Mts., most predation attempts were done by red fox
Šálek <i>et al.</i> 2004			2002-2003	36.67%	From the 34 destroyed nests in 2002, only 8.8% (3 nests) was predated by an avian predator, while a medium-sized mammal predated in 64.7% of the cases (22 nests). The fox was proved to have predated nests three times more frequently than the marten (23.5% versus 8.8%)
Městková <i>et al.</i> 2012	Bohemian forest		2005	31.65%	Red foxes and martens were responsible for depredation of most of the nests from mammal
Seibold <i>et al.</i> 2013	Bohemian forest	Germany	2011	8.2%	Not reported
Storch 1991	Bavarian Alps		1988-1990	25.6%	Twenty (91%) of the nests [with an identified predator] had been robbed by mammals, and two by birds. Only in a few cases could the species of predator could be indentified (4 foxes, 6 martens)
Merta <i>et al.</i> 2009	Sudety Mountains	Poland	2006-2007	100%	Only ravens (93.9%) and foxes (6.1%)
Selva <i>et al.</i> 2014	Bieszczady Mountains		2011	46.67%	Not reported
Summers <i>et al.</i> 2004	Abernethy Forest	Scotland	1991-1999	34.3%	Mostly crows and martens
Angelstam 1986	Grimso Wildlife Research Area	Sweden	1981	26.13%	Jay and raven were the most important nest predators, followed by crow and badger and only little predations by marten and foxes
Pedersen <i>et al.</i> 2009	Nordland and Troms counties	Norway	2002-2003-2004	51.25%	The dominant predators were red fox and hooded crow, followed by raven and magpie. Mustelid predation was low, except in 2003.

Additional references

- Cukor, J., Linda, R., Andersen, O., Eriksen, L. F., Vacek, Z., Riegert, J. and Šálek, M. 2021. "Evaluation of spatio-temporal patterns of predation risk to forest grouse nests in the central European mountain regions." *Animals*, 11(2), 316.
- Městková, L., Romportl, D., Albrecht, T., Chuman, T. and Červený, J. 2012. "The effect of landscape fragmentation and habitat variables on nest predation of artificial ground nest in the Bohemian Forest." *Silva Gabreta* 18(2), 109-121.
- Selva, N., Berezowska-Cnota, T. and Elguero-Claramunt, I. 2014. "Unforeseen effects of supplementary feeding: ungulate baiting sites as hotspots for ground-nest predation." *PLoS One*, 9(3), e90740.
- Storch, I. 1991. "Habitat fragmentation, nest site selection, and nest predation risk in Capercaillie." *Ornis Scandinavica*, 213-217.
- Svobodova, J., Salek, M. and Albrecht, T. 2007. "Roads do not increase predation on experimental nests in a highly fragmented forest landscape". *Folia zoologica* 56(1), 84.