

ELIISA PASS

The effect of managed forest-wetland  
landscapes on forest grouse  
and nest predation



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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UNIVERSITY OF TARTU

Press

Department of Zoology, Institute of Ecology and Earth Sciences,  
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## LIST OF ORIGINAL PUBLICATIONS

This thesis is the summary of the following papers, which are referred to in the thesis by their Roman numerals I–IV. The author of the thesis is highlighted in bold type. All published papers are reprinted here with permission from the copyright owners.

- I** Oja, R., **Pass, E.**, Soe, E., Ligi, K., Anijalg, P., Laurimaa, L., Saarma, U., Lõhmus, A., & Valdmann, H. (2018). Increased nest predation near protected capercaillie leks: a caveat against small reserves. *European Journal of Wildlife Research*, 64, 6. <https://doi.org/10.1007/s10344-018-1165-2>
- II** **Pass, E.**, Lodjak, J., Mägi, M., & Lõhmus, A. (2019). Complex habitat patterns create unpredictable nest predation risk – an artificial nest experiment. *Ornis Fennica*, 96, 182–196.
- III** **Pass, E.**, Pensa, M., & Lõhmus, A. (2021). Short-term effects of predator removal and habitat restoration on ground-nesting birds in drained forests. *Wetlands Ecology and Management*, 30, 161–169. <https://doi.org/10.1007/s11273-021-09826-4>
- IV** Lõhmus, A., **Pass, E.**, Pensa, M. (2023). Distribution of grouse and their predators in peatland forest landscapes: A case for ecological integrity. *Forest Ecology and Management*, 546, 121332. <https://doi.org/10.1016/j.foreco.2023.121332>

AUTHOR’S CONTRIBUTION (\*’ denotes a moderate contribution, ‘\*\*’ denotes a high contribution, ‘\*\*\*’ denotes a leading role).

	<b>I</b>	<b>II</b>	<b>III</b>	<b>IV</b>
Original idea	*	**	**	*
Study design	*	***	**	
Data collection	**	***	**	**
Analysis and interpretation	**	**	***	*
Manuscript writing	**	***	**	**

# 1. INTRODUCTION

## 1.1. Nest predation as a limiting factor for bird populations in human-influenced forests

Most current predator-prey dynamics have a long evolutionary history in landscapes undisturbed by humans, where the top-down patterns regulated by predators have become established (Oksanen et al., 1981; Fretwell, 1987; Leroux & Loreau, 2015). In recent centuries, and especially in the last decades, ubiquitous human influence has been rapidly changing habitats as well as the predator-prey dynamics (Ryall & Fahrig, 2006). One of such “novel game-changers” in terrestrial landscapes is termed mesopredator release – a situation where an increase in distribution or abundance of middle-ranking predators (typically, mammalian predators) is a response to a human-caused decrease in the density or distribution of an apex predator (Soulé et al., 1988; Ritchie & Johnson, 2009; Pasanen-Mortensen et al., 2013; Jachowski et al., 2020). The ‘release’ can be mediated via anthropogenic landscape fragmentation (Soulé et al., 1988; Eagan et al., 2011) or caused directly by increased hunting on apex predators (Ritchie & Johnson, 2009; Russell et al., 2009; Wallach et al., 2015). However, a diverse predator fauna may mitigate high predation risk by intraguild predation – when predators species avoid or consume each other (Sergio & Hiraldo, 2008; Pahl et al., 2020).

A major consequence of mesopredator release is an increased risk of nest predation in birds (Soulé et al., 1988; Donovan et al., 1997; Crooks & Soulé, 1999). Across all species of birds, nest predation accounts for more than 80% of nest and brood losses, and affects around half of all nesting attempts (Newton, 1998; Fulton, 2018). Increased nesting failure is thus a major threat for bird population stability (Newton, 1998). However, the actual limiting role of nest predation in bird populations varies among species groups and habitats. Ground and shrub nesters, as well as single-brooded species generally suffer heavier losses than cavity and canopy nesters and multi-brooded species (Newton, 1998; Roos et al., 2018). Accordingly, there is no clear evidence that predation can limit populations of cavity-nesting and canopy-nesting bird species (e.g., woodpeckers and pigeons), while that is evidently possible in ground-nesting species (e.g., gamebirds, seabirds and waders) (Roos et al., 2018).

In theory, if at least a part of the predation-caused mortality is additive to other habitat-related mortality causes, then predation increases the total mortality on population level (Newton, 1998). In the case of mesopredator release, this is particularly likely when the predator-prey relationship is unprecedented and lacking strong negative feedback mechanisms. Historically, the introduction of invasive predators to oceanic islands has led some endemic bird populations to extinction (Newton, 1998). Such conditions may also appear when human activities reduce birds’ nesting habitat quality (Ibáñez-Álamo et al., 2015): many bird species are more vulnerable to nest predation in degraded and fragmented habitats, or after major changes in the habitat-surrounding matrix (Major & Kendal, 1996; Roos

et al., 2018; Kämmerle & Storch, 2019). For instance, nest aggregation to specific patches due to loss of suitable habitats can increase nest predation (Evans, 2004), and predation risk can increase not only through an increase of predator numbers, but also by alterations of landscape composition and configuration (Söderström et al., 1998; Reino et al., 2010; Ibáñez-Álamo et al., 2015; Roos et al., 2018).

In the northern temperate and boreal regions, most nest predation studies have been carried out in forest-farmland mosaics, while the extensive managed forest landscapes have been less studied. Woodlands cover roughly 60% of terrestrial area in these European regions (Baltic countries and Fennoscandia; Eurostat, 2023), whereas forest harvesting intensities significantly increased during the last decade (Ceccherini et al., 2020). A preliminary list of forestry activities that have been documented to affect nest predation risk is presented in **Table 1**. A general conclusion emerging from those studies is that nest predation can increase not just due to landscape transformation through deforestation (Hartley & Hunter, 1998), but also through the internal and dynamic fragmentation within the remaining forest (Small & Hunter, 1988).

However, in contrast to farmland mosaics, forest landscapes reveal no consistent relationships between the nest predation risk and the landscape structure and edges (Söderström et al., 1998; Lahti, 2001; Foggia et al., 2018), especially in coniferous forests (Bátáry & Báldi, 2004). This may be caused by the naturally complex landscape structure that comprises many different kinds of edges and multiple factor combinations. Even in naturally less diverse Northern Europe, most of the forested land consists of patches of intact forests, clearcuts and even-aged stands, whereas the landscapes are additionally dissected by wetlands, water bodies and human infrastructure, such as forest drainage networks and roads (Päivänen & Hännell, 2012; Roberge et al., 2018). Such landscapes create rather habitat gradients of varying nest predation risk rather than distinct edge areas. It is both a behavioural and ecological question of how animals respond to those landscape gradients, and a research methodological question of how to measure those gradients to study the animal responses.

## **1.2. Forest grouse as a focal group for sustaining birds in human-influenced forests**

Worldwide, 82 species in the grouse tribe (Tetraonini: Phasianidae) have been categorized as inhabitants of forests and 36 species as inhabitants of ‘forest edge’ (Storch, 2007). In Europe, the number of the species is low, but all the few forest-dwelling grouse have become model species in landscape conservation and planning studies (Angelstam, 2004; Angelstam et al., 2004; Löhmus et al., 2017). Here, ‘forest grouse’ refers to three habitat specialist species: the black grouse (*Lyrurus tetrix* (L.)), hazel grouse (*Tetrastes bonasia* (L.)) and western capercaillie (*Tetrao urogallus* L.).



**Table 1.** Overview of notable case studies on forestry impacts on nest predation and grouse populations.

<b>Forestry impact</b>	<b>Effect on nest predation</b>	<b>Effect on grouse population</b>	<b>Reference</b>
<b>Drainage</b>		Negative effect on all 3 forest grouse brood survival	Ludwig et al., 2008
	Negative effect on black grouse daily nest survival		Ludwig et al., 2010
<b>Partial cutting</b>	Hardwood removal/ prescribed fire has increasing effect on nest predation risk in artificial nests	Negative effect on all 3 forest grouse survival	Huhta et al., 2017
	High proportion of fragmented forest increases nest predation risk in ruffed grouse ( <i>Bonasa umbellus</i> )		Morris et al., 2016
<b>Forest fragmentation by clearcuts</b>		High proportion of fragmented forest and clearcut-caused low proportion of old forest increases nest predation in capercaillie and black grouse	Yahner & Scott, 1988
	Forest fragmentation and edges increase nest predation in Eurasian treecreeper ( <i>Certhia familiaris</i> )		Kurki et al., 2000
	Forest patch edge proximity increases nest predation risk in the brown creeper ( <i>Certhia Americana</i> )		Huhta et al., 2004
	Significantly higher nest predation risk of artificial nests in intensively managed forest landscape		Poulin et al., 2011
			Wegge et al., 2012

In northern Europe, the broad distribution of these three species overlaps (Lande et al., 2014); however, they prefer distinct stages of forest succession and site types in forest-wetland landscapes (Swenson & Angelstam, 1993; Angelstam et al., 2004; Elvesveen et al., 2023). In general, the black grouse mostly uses deciduous-rich pioneer successional stages and open bogs; hazel grouse inhabits mid-successional stages with some proportion of alders (*Alnus spp.*); and the capercaillie is most confined to mature or old-growth conifer stands, often dominated by Scots Pine (*Pinus sylvestris*) (Seiskari, 1962; Swenson, 1993; Swenson & Angelstam, 1993; Sjöberg, 1996; Wegge & Kastdalen, 2008).

The capercaillie and black grouse are area-sensitive lekking species, which require at least 0.9 km<sup>2</sup> and 2.2 km<sup>2</sup> patches of their preferred habitat for a local breeding population, respectively (Angelstam, 2004). Since the most common capercaillie habitats (mature conifer forests) are the most challenging to preserve in timber-harvested landscapes (Sjöberg 1996; Elvesveen et al., 2023), capercaillie is considered as a focal species for sustainable forestry approaches (Löhmus et al., 2017) and an umbrella species for other old-growth forest specialists (Suter et al., 2002; Pakkala et al., 2003; Elvesveen et al., 2023).

### **1.3. Decline of the European forest grouse, and the role of nest predation**

Despite being well acknowledged targets in conservation, forest grouse populations in Europe have been declining for decades (Storch, 2000; 2007; Jahren et al., 2016, Klaus & Ludwig, 2021). Across Europe, the evidence shows that grouse population declines are mostly related to anthropogenic habitat transformations (Klaus, 1991; Kurki et al., 2000; Wegge et al., 1992; Jahren, 2012) (Table 1).

In Northern Europe (including the Baltic States), production forestry has been aiming for maximum economic output during the last decades (Roberge et al., 2018). This is being achieved through intensive management techniques such as clear-felling, thinning and large-scale landscape drainage. Over time, most natural forest-wetland landscape mosaics have been transformed into patchworks of even-aged stands, fragmented by clearcuts and dissected by networks of drainage ditches and forest roads (Sjöberg, 1996; Kuuluvainen et al, 2004). A majority of these forest-wetland landscapes were transformed in the whole region during a short period of time, mostly within a few decades in the mid-20<sup>th</sup> century (Päivänen & Hånell, 2012). The following population declines of forest grouse have been more or less parallel with the landscape transformations in all the three forest grouse species (Marcström, 1986; Lindström et al., 1997).

The research reveals that those forestry-related factors, which increase overall nest predation risk in birds, overlap with the factors that are related to the declines of the grouse populations (Table 1). Although forestry drainage has been one of the main drivers of landscape changes (Päivänen & Hånell, 2012), just a small proportion of studies have considered drainage together with other forestry

effects in grouse population studies. More importantly, the long-term forestry effects and landscape integrity to grouse populations are yet largely unknown.

The fact that the grouse are single-brooded ground nesters makes them highly vulnerable to increased predator abundance (Roos et al., 2018). In predation studies, it is crucial to consider predator species compositions and distributions in particular landscapes (Söderström et al., 1998; Ibáñez-Álamo et al., 2015; Chiavacci et al., 2018). In Northern Europe, grouse nests and broods can be depredated by most mustelid and canid species. On a broad scale, it is acknowledged that a typical grouse predator species among mammals in forest-farmland mosaics is the generalist red fox (*Vulpes vulpes L.*). In forest landscapes, a somewhat more management-sensitive pine marten (*Martes martes L.*) can play a major role along with the fox (Kurki et al., 1997; 1998; Baines et al., 2004; Summers et al., 2009). Among birds, corvids are the main predators in forest-farmland areas and forest landscapes, but the dominant corvid species are landscape type specific (Andrén, 1992). In forests, the main bird predator of grouse broods and eggs is probably the common raven (*Corvus corax*), followed by northern goshawk (*Accipiter gentilis*) in brood predation and Eurasian jay (*Garrulus glandarius*) in egg predation (Andrén, 1992; Merta et al., 2009).

During the recent decades, abundances of most of the above-named species (except the Northern Goshawk) have been rising across the Northern Europe, which generally corresponds with the decreasing numbers and reproductive success in forest grouse (Kurki et al., 1997; Kauhala & Helle., 2002; Jahren 2016). The grouse reductions are remarkably high in human-degraded landscapes and, vice versa – in their preferred habitats the losses are smaller (Kämmerle et al., 2017). As a temporary experimental remedy, removal of mesopredators from critical forest grouse habitats can be feasible (Summers et al., 2004; Kämmerle & Storch, 2019) but no long-term population effects on brood and nest losses in degraded habitats has been found.

Besides predator culling, various restoration activities have been tested in degraded grouse habitats. For example, thinning of woody vegetation with small clearfellings, and removal of shrub thickets (Broome et al., 2013; Straupe et al., 2019), as well as burning and mowing can increase the cover of grouse food plants (Hancock et al., 2011). Furthermore, re-establishment of hydrological regimes in degraded peatlands by ditch closing can reverse the loss of plant and shrub assemblages typical of natural forest grouse habitats (Rochefort & Lode, 2006). However, none of these studies aimed to detect changes in grouse populations nor nest predation, and were rather small-scale experiments. On a regional scale, small reserves specifically for capercaillie leks have been established all over the Baltic States, covering almost 1200 km<sup>2</sup>, so that 90% of all the capercaillie leks in the region are protected (Löhmus et al. 2017). Despite the massive effort, the numbers of capercaillie and black grouse have been declining.

## 1.4. Aims and objectives

The mission of my thesis is to build a case for the improvement of declining grouse populations in managed forested wetlands, which have become their dominant habitats in northern Europe. In such a landscape context, there have been no studies that integrate grouse (or any other bird species group) reproductive success, nest predation, predator abundance, and restoration methods. More specifically, I aim to distinguish the ecological mechanisms of nest predation by linking nest predation rates and predator abundance measurements across the same habitat gradients (see Ibáñez-Álamo et al., 2015). Considering that, I synthesize on how landscape could mediate predation risk in general and whether intraguild predation or apex predators could affect grouse reproductivity.

In my study setups, I considered an increased nest or brood predation as the likely *direct* cause of the grouse decline, and the man-made habitat alterations as a likely *mediating* cause. Given the target ecosystems, I focused on the combined habitat-altering consequences of dominant production forestry operations (logging, thinnings, and drainage). By linking habitat and grouse brood data, I detected where on my study landscapes the grouse populations are most vulnerable to nest predation, and in which parts predator removal could improve the nesting success. Since capercaillie is acknowledged as a focal species in conservation and its habitats are most affected by forestry-conservation conflicts, I focused on the habitats and active management for that species.

I posed two main research questions and searched for answers in a total of four case studies in priority habitats for the Estonian capercaillie population.

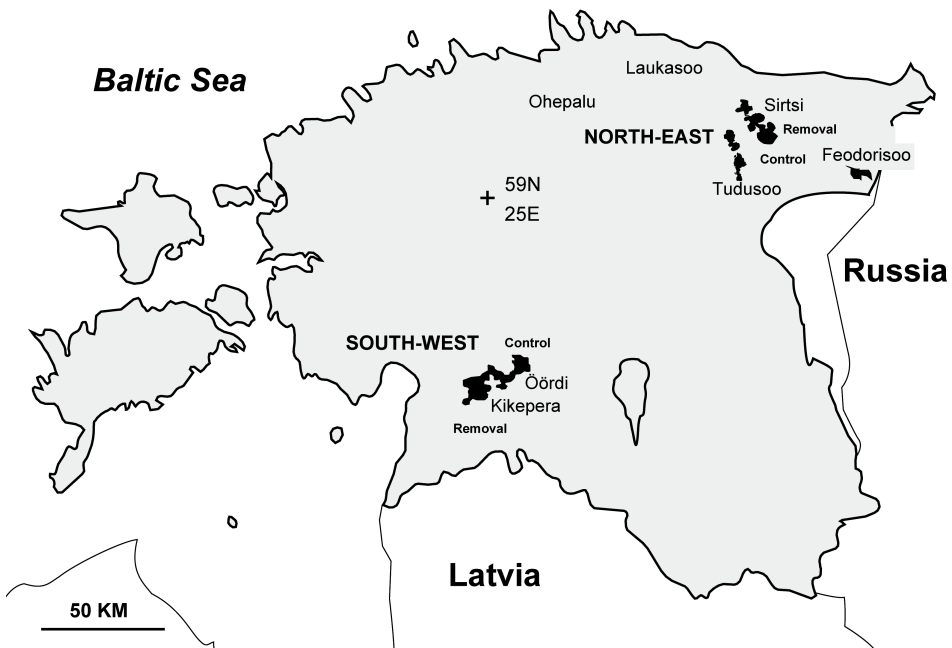
1. To understand whether, and to what extent, increased predation could result from habitat alteration, I explored which forestry operations or silvicultural systems are related to increased nest predation risk. I considered: (a) forest drainage (studies **II–III**); (b) even-aged (clear-cutting based) forestry (study **II**), (c) partial cuttings (thinning and selection logging; study **III**), (d) landscape context effect on remnant habitat patches (study **I**). Since the low densities of actual grouse nests pose a problem for ecological sampling designs and ethical problems for experimentation, I used artificial nest experiments for evaluating general predation risks in the grouse habitats. All the studies included both local and landscape scales, and study **II** additionally included tree nests for a comparison with ground nests to expand the treatment of location effects to alternative predators.
2. After establishing the forestry effects based on artificial nests, I explored brood and nest mortality hotspots for real grouse on drained landscapes. This included questions of the predictability of the predation risk for the breeding birds (study **II**) and of predator distributions on the landscapes (study **I–IV**). Both as an independent experimental evidence and potential conservation management approach, I also analysed preliminary data on experimental predator removal and drained habitat restoration as potential tools to relieve high nest and brood mortality of the birds (study **III**).

## 2. MATERIAL AND METHODS

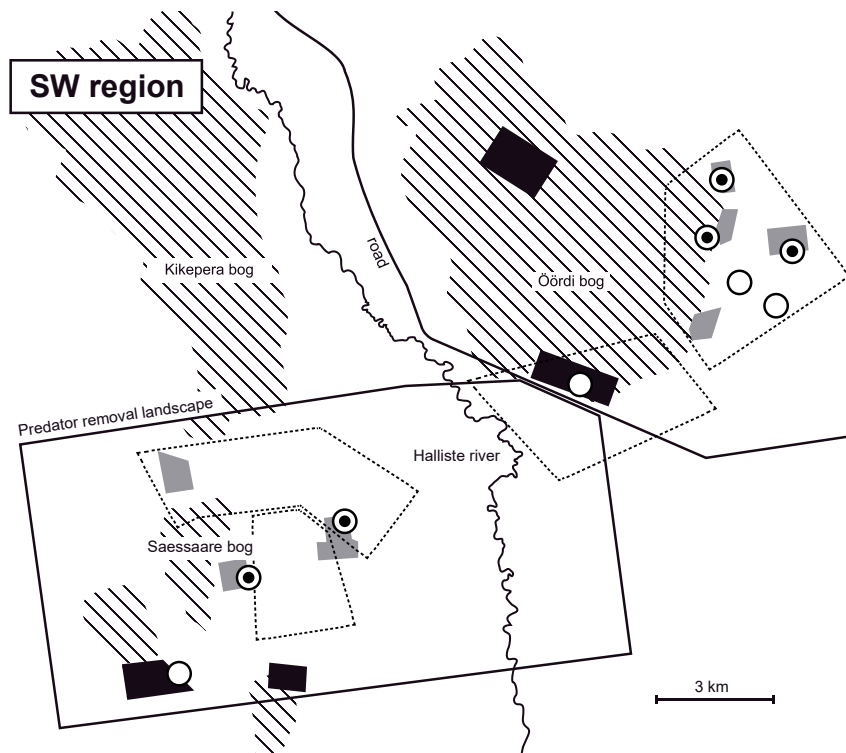
### 2.1. Study area and design

The research was conducted in 2014–2018 in two sparsely inhabited forest-wetland regions in the mainland of Estonia. Estonia belongs to the hemiboreal vegetation zone; mean temperatures are 17.8 °C in July and –3.1 °C in January; the mean annual precipitation is 661 mm.

Forests cover about half of the Estonian area and have a long history of mostly clearcutting-based (even-aged) management. Forty-six percent of the forests are managed by the State Forest Management Centre; the average stand age is 55 years (Raudsaar & Valgepea 2020). About quarter of the Estonian forests have been drained (550 000–560 000 ha) (Kaisel & Kohv, 2009), mostly in transitional bog and fen site types (Lõhmus, 1984). Although the establishment of new drainage networks is restricted, the draining impact is still continuing through the present ditch network. Currently, 14% of the total forested land is under strict protection and 11% has additional conservation-related restrictions to forest management (Raudsaar & Valgepea, 2020).



**Fig. 1.** The wetland landscapes studied in mainland Estonia. Studies I–II took place exclusively in the South-West region, study III included Sirtsii and Tudusoo landscapes, and study IV included all the landscapes. “Removal” (Kikepera and Sirtsii) and “Control” (Öördi and Tudusoo) mark the landscape design for the predator removal in study III.



**Fig. 2.** Locations of the artificial-nest experiments in the South-West (Soomaa) study landscape. Circles mark the sites of study **I**: filled circles – managed (drained) sites; empty circles – natural sites. Dashed lines delineate the sub-areas in study **II**. Black polygons are undrained natural sites and grey polygons are habitat restoration sites of the study **III**.

The studies were conducted in partially drained forest landscapes around bogs in two core regions of the Estonian capercaillie population: in South-West (‘SW landscapes’) and North-East (‘NE landscapes’) Estonia (Fig. 1). The SW landscapes comprised the surroundings of two bogs, Öördi (7154 ha) and Kikepera (3300 ha), in the Soomaa National Park. The NE study landscapes included the surroundings of Sirtsu, Tudu, Feodorisoo, Ohpalu and Laukasoo bogs (all >1000 ha). Across drained forest lands, densities of ditches were 55 m ha<sup>-1</sup> and 80 m ha<sup>-1</sup> in the NE and SW landscapes, respectively; most of the ditching dated back to the 1960s.

Studies **I** (in 2014) and **II** (in 2015–2016) were carried out solely in the SW landscapes; these included unmanaged and protected capercaillie lek surroundings and other intact natural areas, combined with variously managed forests (cf. study question 1). A part of study **III** (in 2014–2018) was also conducted in the SW landscapes, but the study plots consisted of drained and restored capercaillie habitats in addition to unmanaged (natural) capercaillie habitat plots. Another part of study **III** took place in and around Tudu and Sirtsu bogs. The study **IV** (in 2016) included all SW and NE landscapes; the study areas encompassed 8.9–35.8 km<sup>2</sup> in individual landscapes and 155.6 km<sup>2</sup> in total. Detailed view in Fig. 2.

## 2.2. Target species

The research focused mostly on the habitats of the capercaillie, but it also included hazel grouse and the black grouse. In the Baltic countries, all three species were abundant and intensively hunted game species until the beginning of the 20<sup>th</sup> century. Nowadays, these species are red-listed as Vulnerable in Estonia (Elts et al., 2019a) and their key breeding regions include Soomaa (here: SW study landscape), Lahemaa and Alutaguse National parks. (NE study landscapes).

According to the national Nature Conservation Act, the capercaillie belongs to the II protection category (requiring protection of at least 50% of its habitats). Nevertheless, its numbers have consistently declined: ca. 5500 males in the 1960s (Viht & Randla, 2001) vs 1300–1600 approximate breeding ‘pairs’ in 2017 (Elts et al., 2019b). Between the 1970s and 2000, 30% of the capercaillie lekking sites disappeared and the average lek size was reduced ca. 27%. Approximately 83% of the remaining capercaillie leks are situated on the state-owned land; 59% of lekking areas are parts of large nature reserves (e.g., national parks), 34% are small-scale reserves outside larger reserves, and 7% are unprotected (Randla et al., 2015).

The recent decline of the black grouse has been even more rapid in Estonia: 10 000–20 000 approximate breeding ‘pairs’ in the late 1990s (Elts et al., 2003) vs 4000–5000 in 2017 (Elts et al., 2019b). Since the local black grouse population breeds rather on (semi-)open wetlands than wooded areas (Kuus, 2016) and the study regions did not include the regionally most important breeding areas (Lõhmus, 2001; Kuus, 2016), the black grouse is the least targeted species in the study. The population decline of the most abundant species, the monogamous hazel grouse, is less clear: 20 000–40 000 breeding pairs in the late 1990s (Elts et al., 2003) vs. 20 000–25 000 breeding pairs in 2017 (Elts et al., 2019b). Both the black grouse and hazel grouse belong to III protection category, which requires at least 10% of their habitat being protected. An estimated 72% of known black grouse habitats are under protection (Kuus, 2016), but the species is still in decline.

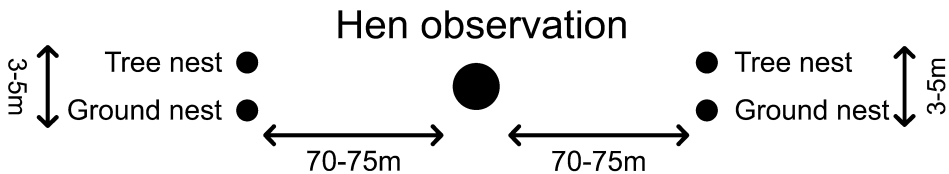
## 2.3. Data collection

### 2.3.1. Artificial nest experiments

Artificial nest experiments are widely used for relative assessments of bird nest predation risks and hatching success. In this approach, quail or hen eggs are placed in the field in a way that mimicks natural bird nests, and their survival over certain (standard) period is interpreted in terms of natural nest survival factors. By doing so, large samples can be systematically studied and nesting birds are not disturbed. The method is cost-effective and non-invasive; however, the results do not accurately reflect actual predation risk of bird nests (Major &

Kendal, 1996; Faaborg, 2004) or predator numbers (Villard & Pärt, 2004). Typically, the risk of nest predation is overestimated, e.g., due to a lack of parental defence or higher visibility of the nest (Major & Kendal, 1996; King et al., 1999; Burke et al., 2004).

Artificial nests were used in studies I–III and were the main indicator of potential nesting success in the whole research. In all the studies, the locations of artificial nests were planned in GIS prior to fieldwork. Capercaillie nests were mimicked in the studies I and III, by establishing shallow scoops into semi-concealed sites underneath or close to conifer trees. Each nest contained two brown medium-sized chicken eggs (ca  $48 \times 40$  mm, 50 g) and a wax egg (studies I, III) or a plasticine egg (study II) of similar colour and size. Distances between the nests were 50–150 m, depending on the site type. In study II, quail eggs (ca  $30 \times 22$  mm, 10 g) were chosen to compare ground nests with tree nests at 1.8–2 m height (study design in Fig. 3). The ring was filled with moss and leaves (Degraaf et al., 1999). In all the studies, the nests were exposed 20 days in the field, which is an approximate incubation period of forest grouse species. Nests were considered as depredated, if at least one egg was missing. The plasticine or wax eggs present were collected for identification of tooth/bill marks of predators by matching the marks with teeth marks of possible predator species taken from skulls.



**Fig. 3.** Design of the artificial nest experiment in study II: Two pairs of ground and tree nests were placed at a distance of 70–75 m from a place where a female grouse was observed last year (II).

### 2.3.2. Grouse and predator surveys

All four studies included systematic landscape-scale field observations of grouse and their predators, which were analysed after georepositioning.

In study I, the observations were recorded while conducting the artificial nest experiments. In studies II–IV, data on grouse nesting success were collected by systematic mapping of grouse individuals. The observations on potential predators of grouse or their nests were collected simultaneously. The surveys took place in June 2015–2018, at a time when grouse broods stay together and can be easily detected. Altogether, over 200 observers participated to cover each landscape. The landscapes were subdivided into plots (mean size 50 ha), each of which was searched by one observer during one day by placing the walking routes at approximately 50-m intervals. The observer recorded coordinates, numbers, sex, and brood incidence of the grouse individuals seen. Since most female forest



grouse obtain mates (Wittenberger, 1978), solitary hens were considered as having lost nest or brood, most likely due to predation (e.g. Wegge & Kastdalen, 2007). In hazel grouse, single adults of unidentified sex were counted as 0.5 females without brood (assuming 1:1 sex ratio in the adult population).

The predator abundances were estimated as relative indices. In studies **I–III**, the predator observations of each species were pooled within a plot at each visit (to reduce double-counting of the same individuals), then standardized across each landscape as observation densities per area. In study **I** with repeated visits to smaller areas, also the effort was accounted for (per-hour number of observations of potential nest predators). The study **III** also included data from licensed hunting (trapping) of mesopredators, which substantially increased in one landscape of both study regions in 2017–2018. The hunted species included pine marten, red fox and raccoon dog.

### 2.3.3. Habitat measurements

For distinguishing habitat factors that may affect nest predation risk, habitat characteristics were measured *in situ* and from GIS map layers. In studies **I–II**, the habitat structural measurements in the field included: canopy cover of overstorey trees (ca.  $\pm 5\%$  accuracy); evergreen shrub cover (estimated visually around each artificial nest within a 5 m radius); ground-level horizontal visibility (reverse of the visible proportion of a wooden pole). In studies **I** and **III**, distance between ditches and artificial nests was measured in GIS. During study **III**, before-and-after habitat restoration treatments were conducted in the SW study region (**Fig. 2**). The treatments included combinations of drainage ditch blockings and forest cuttings; untreated drained sites and undrained natural sites were used as control areas.

The remote habitat variables (e.g. nearest capercaillie lek; nearest clearcut or predator record to the artificial nest in study **II**; soil data and forest registry data in study **IV**) were obtained from digital forest and soil maps provided by the Estonian Land Board and the Estonian Environmental Agency, using MapInfo software.

## 2.4. Data processing

In studies **I–III**, proportions of depredated nests were compared among sites, and compared among different predator taxa, including specific contrasts comparisons to detect experimental effects of habitat restoration and predator removal in study **III**. To detect relationships between predator abundance indices and nest predation rates in studies **I–II**, Pearson correlations were used.

The effects of habitat variables on nest predation were studied using generalized mixed models (GLMM) in studies **I** and **II**. Nest predation was coded as a binary dependent variable (0, not predated; 1, predated). The independent variables included habitat characteristics, such as stand age, shrub and canopy cover

(study **II**), and spatial characteristics, such as the nearest capercaillie lek to a nest (study **I**) or nearest clear-cut or predator record (study **II**). In both studies, the sites were included as random factors. The final models were ranked according to the Akaike information criterion (AIC). For both analyses, R 3.0.1. and R 3.2.2. (R Core Team, 2013; 2015) were used, with package lme4 for mixed models (Bates et al., 2014) and packages “MuMin” (Barton, 2016) for the calculations of AIC and  $R^2$ .

In study **IV**, similar logistic models were applied to observational data of three grouse species. The approach was to compare habitat variables at the observation locations (1) and randomly distributed locations (0) for two main model sets: (i) across the landscapes (five soil type variables combined and general woodland variables); (ii) within woodlands (a more specific set of woody vegetation variables). An additional analysis compared the habitats where broods or nest were observed with other grouse observations in the breeding season.

To test for predator and grouse co-occurrence in study **IV**, their pseudo-correlations caused by observer abilities were first removed by randomly splitting plots and only considering those that had predator observations in one half. A  $\chi^2$ -test was then used to test whether the grouse were distributed randomly between the half-plots.

## 3. RESULTS

### 3.1. Artificial nest predation in variably managed forest-wetland landscapes (II, III)

In terms of local drainage effects, the distance from a drainage ditch had no effect on the predation rate of artificial ground nests (57% of 48 nests at 0–10 m from ditch and 59% of 32 nests at 30–50 from the ditch) in 2014. Furthermore, on the landscape scale, the nests in natural sites were depredated at higher rates (99% of 64 nests) than in drained sites (58% of 80 nests;  $\chi^2$  test:  $p < 0.001$ ) in that year (III).

However, in 2018, after the wetland restoration treatments, the results reversed on the landscape scale: 76% of 110 nests were depredated in natural sites vs. 93% of 108 nests in the drained/restored forest blocks ( $\chi^2$ -test:  $p < 0.001$ ). The three cutting treatments had 50–58% predation rates before partial cutting and 93–96% after cutting. Moreover, slight differences appeared on the local scale (98% of 62 nests farther from ditches vs. 90% of 63 nests near ditches,  $\chi^2$ -test:  $p = 0.054$ ). The rates in two unrestored drained plots were 65% and 96% in 2018 indicating substantial spatial variation (III).

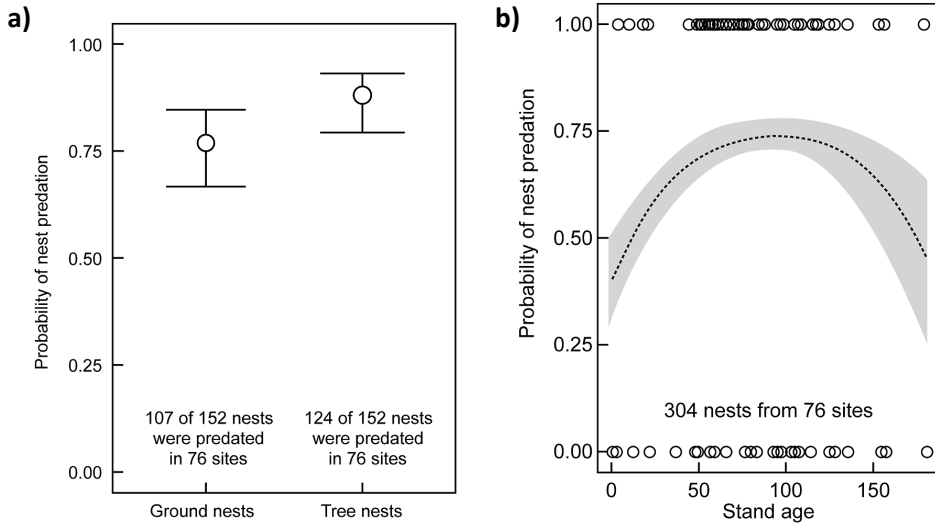
In the study on silvicultural factors (II), the best model explaining artificial nest predation through local factors incorporated forest stand age and nest location (ground vs tree) (Fig. 4). Tree nests had higher predation rates than ground nests (82% of 152 nests and 70% of 152 nests, respectively; Fig. 4a). The predation rates were lowest in the youngest and (arguably) in the oldest stands, and highest in mid-aged stands (Fig. 4b). The same model contained a marginally negative effect of shrub cover ( $p = 0.056$ ).

At the landscape scale, the predation rates matched with the local scale results: among four areas, predation rates varied from 67% to 83%; being the lowest in the area with the highest proportion of clearcuts, and highest in the area with fragmented mid-aged and old stands (II).

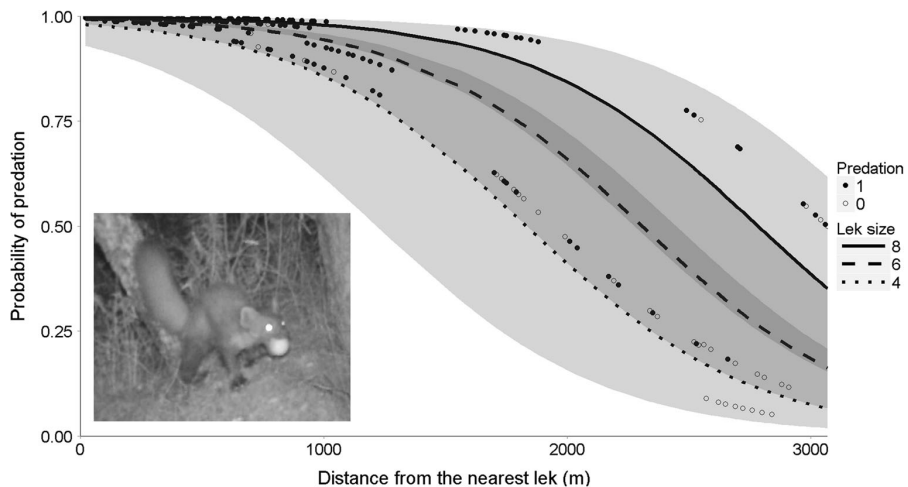
### 3.2. Predator aggregation patterns in relation to grouse and nests (I, II, IV)

On a landscape scale, the frequencies of predator observations matched well with the artificial nest predation risks. On landscape transects in I, there was a positive correlation in predator observations (per hour) and artificial nest predation rates ( $r = 0.85$ ;  $p = 0.016$ ; I). On a smaller scale, such relationships became blurred (e.g., in II, there were no significant relationships between distances between artificial nests and nearest predator observations). Likewise, in study IV, local distribution of grouse and predators was random: out of 111 observations, 58 grouse were in subplots (ca. 25-ha scale) without and 53 in subplots with small canids and/or *M. martes* records ( $\chi^2 = 0.23$ ;  $p = 0.64$ ). When considering all potential predators, grouse observations were equally divided.

In a transect setup with 303 artificial nests around capercaillie leks, the best models suggested an increased predation risk near the leks (**I**). In the best model ( $R^2_{\text{marginal}} = 0.48$ , Fig. 5), size of the nearest lek had a slight tendency ( $p = 0.12$ ) to contribute to the highly significant lek distance effect ( $p < 0.001$ ). Size of the second nearest lek, distance to the second nearest lek, and forest type had negligible contributions to the model.



**Fig. 4. (a)** Mean predation rates ( $\pm$  SE) of ground and tree nests. **(b)** Mean ( $\pm$  SE) relationship between nest predation probability (304 nests in 76 sites) and stand age (years). All values are back-transformed from logit models to linear scale (**II**).



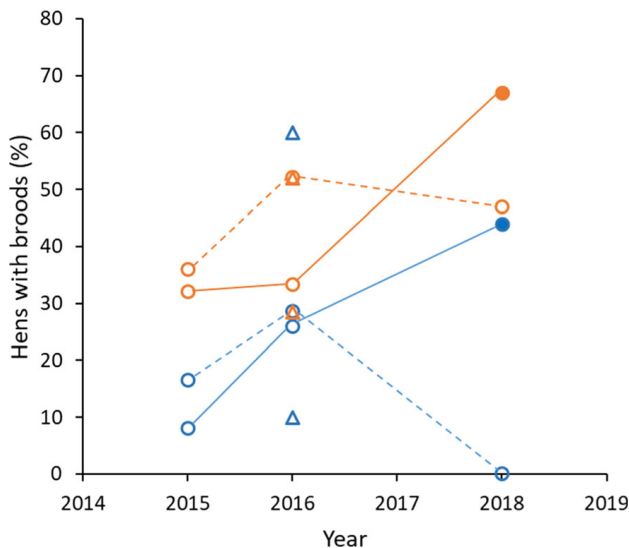
**Fig. 5.** The landscape model of predation risk in relation to distance from the nearest capercaillie lek and the lek size. The symbols show the empirical best linear unbiased predictors for the artificial nests. The grey area denotes  $\pm 1$  SE. Photograph: pine marten preying an artificial nest (recorded with UOVision UM565 camera) (**I**).

### 3.3. Grouse distributions and nesting across the landscapes (II–IV)

In the seven large landscapes, no grouse species showed a relationship between population density and ditch density (Pearson correlation,  $r < |0.3|$ ,  $p > 0.5$ ). The grouse loosely concentrated to a zone from ca. 0.2 to 1.5 km from bog edges. Most capercaillie were found in a radius of 2.5 km from the leks, but with a lower occurrence of broods within 0.5 km (IV).

Soil type had a clear segregative impact on all species along the bog-forest profile (Fig. 7). Capercaillie preferred transitional-bog Histosols ( $p = <0.001$ ); black grouse preferred bog Histosols ( $p = 0.042$ ) and avoided Gleysols ( $p = 0.003$ ); hazel grouse preferred fen Histosols ( $p = 0.014$ ) and avoided bog Histosols ( $p = 0.039$ ). Capercaillie preferred older stands, black grouse preferred semi-open areas and younger stands, and hazel grouse avoided pine stands. Notably, all three species avoided thinned stands, except that in capercaillie this effect was not significant on its preferred transitional-bog sites (IV).

In study II, the artificial nest predation probabilities did not differ in the sites where grouse with or without broods had been observed in the previous year (78% vs. 75%;  $\chi^2=0.2$ ;  $p = 0.65$ ). In both regions of study III (NE and SW of Estonia), both capercaillie and hazel grouse nesting success co-varied ( $r = 0.63$ ;  $p < 0.1$ ). In the SW landscape, between 2016 and 2018, nesting success increased in the areas where predators were removed; while nesting success dropped in the areas where predators were not removed (Fig. 6).



**Fig. 6.** Breeding success of the capercaillie (blue symbols) and hazel grouse (orange symbols) in the study landscapes, based on 7–19 capercaillie and 12–21 hazel grouse hens. Circles mark SW landscapes and triangles NE landscapes (only 2016). The lines refer to changes in the SW landscapes (solid line, filled circle – the predator removal landscape; dashed line – the control landscape)(III).

## 4. DISCUSSION

The dissertation integrated man-made habitat alterations in natural grouse habitats with their nest predation risk caused by co-occurring predators. As the habitat effects on nest predation corresponded well with grouse observations, I discuss nest predation risk together with grouse abundances on landscapes.

### 4.1. Broad-scale presence of mesopredators in forest-wetland landscapes

All four case studies revealed a presence of diverse predator assemblages in each forest-wetland landscape: roughly 10–15 species in each region, including mammalian mesopredators, corvids, raptors, wild boar and large carnivores. Studies **I–III** demonstrated extremely high predation risk on artificial ground nests by mesopredators. Mammals seemed to destroy these nests more frequently than corvids. Given an even higher nest predation of tree nests in study **II**, I suspect that tree climbing Mustelidae species, especially the pine marten, were the most numerous predator species in the forest-wetland landscapes. The diverse predator fauna together with such a high nest predation risk does not support predation risk mitigation by intraguild predation by mesopredators (e.g. Lindström et al., 1995, see Introduction). Although apex predators were present in each region, the observations were too scarce for conclusions on their impacts.

On the other hand, diverse predator assemblages might explain continuously high nest predation risk – if nest predation from one species is excluded, other species compensate the predation risk (Beggs et al., 2019; Tobajas et al., 2020). Despite such possible compensatory mechanisms, predator culling in study **III** showed some positive short-term impacts on breeding grouse: the decrease in nest predation was simultaneous with actual bird reproductive success. Similar results have been obtained by in Kauhala et al. (2000), Summers et al. (2004) and Kämmerle and Storch (2019).

We found landscape-scale (**I, III**) correspondence between nest predation risk and predator densities, which became blurred at smaller scales (**II**). This is most likely related to a high mobility of mid-sized and large predators (incl. raptors and corvids) on the landscape, which makes their presence unpredictable for breeding birds in particular sites (studies **II, IV**). It implies that high predator densities have a potential to cause broad-scale population impacts on grouse and other birds, even though the predation risks on the landscape are not homogenous. Some habitat characteristics apparently provide safer breeding sites for the birds, and the loss of such sites can further contribute to, or perhaps mitigate, their population declines.

A co-occurrence pattern of potential population consequences was the aggregated nest predation around protected capercaillie leks in the production forest landscape (study **I**). A similar mechanism has been discussed by Angelstam (1986).

This result also corresponds to fewer capercaillie broods found within 0.5 km from lekking sites (IV). A small capercaillie lek reserve in a managed forest landscape can be seen as a “protected island”, favouring the aggregation of predators. Considering the nest predation risk differences between the areas in study II, we detected nest predation gradients in managed forest-wetland landscapes – a mechanism that is more commonly detected in forest-farmland mosaics.

## **4.2. Landscape alterations as predation mediators**

### **4.2.1. Forestry drainage**

Contrary to Fennoscandian studies (table 1) and also Pass (2015) thesis, the studies II–IV demonstrated that drainage ditches have little direct impact on nest predation risk or grouse presence. This is also in line with the result in study II where the shrub cover and ground visibility (enhanced by drainage) did not affect predation risk. However, grouse distribution was well explained by soil type (notably Histosols); with the soil type considered, grouse did not respond to ditch densities within 250 m (IV).

Hence, the areas with drained Histosols can host grouse populations, but the population demography in the drained ecosystem (and specifically long-term reproductive success) remains a question. In capercaillie and black grouse, some secondary succession impacts are apparently negative – increased vegetation growth degrades typical characteristics of lekking sites (Hotanen et al., 2006). As bilberry is crucial food plant for breeding capercaillie (Sjöberg, 1996; Gregersen & Gregersen, 2008), one positive mechanism could be the increased growth of bilberry on drained bog edges (Löhmus & Remm, 2017). As hazel grouse relies strongly on forest vertical heterogeneity, deciduous component and canopy cover (Åberg et al., 2003; Jansson et al., 2004), increased by drainage, the effects could be the least detrimental for the species.

### **4.2.2. Forest cuttings**

Some studies from the last two decades demonstrate low predation risk and capercaillie tolerance of younger managed forests (Borchtchevski et al., 2003; Sirkiä et al., 2010; 2011). The results in this thesis alert to place such findings into a wider picture. For instance, in study II, the smallest nest predation risk was found on clearcuts/young thickets. However, in the same study, the highest nest predation risk was found in middle-aged forests, indicating that post-clearcut succession might increase general nest predation. In study IV, capercaillie and hazel grouse avoided clearcuts explicitly – considering that, landscapes fragmented with clearcuts might enhance predation risk in remained middle-aged and mature habitat patches favoured by grouse (Yahner & Scott, 1988; Huhta et al., 2004; Poulin & Villard, 2011). In theory, habitat reduction-caused nest predation could caveat the entire grouse population. Secondly, clearcuts are detrimental for bilberry

(Lõhmus & Remm, 2017) that has the highest cover in mature uncut forests (Rodríguez and Kouki, 2015).

As for the black grouse, its preference for younger deciduous stands found in study **IV** is in line with the previous knowledge (see Introduction) and it could be assumed that the species can use clearcuts as a substitute habitat for drained bogs. However, given the growing proportions of clearcuts in Estonian forests (Ceccherini et al., 2020), black grouse habitat preferences and low nest predation risk in young forests (study **II**), it would then be plausible to expect a population increase in the black grouse. Instead, the population has been dropping continuously since the last decade (Eltis et al., 2019a, b). Therefore, forest age structure alone is insufficient to explain the population dynamics in this species and, possibly, in other grouse as well (Lõhmus, 2022).

The most novel findings were negative effects of thinning on nest predation and grouse abundance. Study **III** demonstrated increased nest predation risk on artificial nests in recently thinned stands. In contrast to other studies (Delong et al, 1995; Seibold et al., 2013; Bellamy et al., 2018), study **II** did not find an increased predation risk along with the ground visibility and reduced shrub cover (as caused by thinning). Thus, the effect in study **III** could be attributed to cleared ditch edges that probably offer predators better access to the area and might help to detect breeding hens more easily from the distance.

Importantly, during the brood season, all three forest grouse species avoided stands that had been thinned during the last 10 years (**IV**). One reason for that might be a temporary decrease of food plants after the forest management, or widespread post-thinning wooden slash that suppresses grouse mobility. Thinning has often been used and recommended for grouse habitat improvement (Moss & Picozzi, 1994; Broome et al., 2013). Considering the results in the thesis and a lack of actual before-and-after evidence of increased nesting success in the capercaillie, this method cannot be recommended in Estonia without specific supporting evidence. In the hazel grouse, thinning is in contrary with its main habitat requirements (Åberg et al., 2003; Jansson et al., 2004). Hence, while managing landscapes with sympatric grouse populations, large-scale thinnings should be avoided.

### **4.3. Methodological limitations and future advancements of the studies**

The studies included in this dissertation reached a point where advanced methods would be needed to describe, specifically, the predator behaviour in (managed) forest-wetland landscapes. My studies involved mostly point observations (including interpreting marks on dummy eggs), which is likely to include also some misidentification of scats (Mumma et al., 2016; Jõesuu 2023), and limited experimental culling. As a result, the knowledge of predator habitat use in relation to breeding birds remained rather superficial. As predators are more mobile than breeding grouse, radio-tracking and retrospective analyses based on wildlife



winter track counts would help to model continuous predation risk functions across the landscapes. In turn, since mesopredator distribution can be influenced by large carnivores (Ritchie & Johnson, 2009; Sergio et al., 2008; Wallach et al., 2015), top-down influences in predator guilds in the same study landscapes would be of high applied interest. Neither of these applications were possible with the current sparse datasets.

Three of the four studies were based on artificial nests – the most common method for evaluating *relative* nest predation risk in bird species with low densities on the landscape (Villard & Pärt, 2004). Even so, the method has been criticised due to high local density of replicates and conflicting results (Faaborg, 2004). To avoid pseudoreplication, I considered a pilot study in the SW study region, which confirmed that, at the densities used, the probabilities of nest predation were not higher near closest predated nests (Pass, 2015). Hence, I considered artificial nests in studies I–III as sufficiently independent replicates. Yet, the fact that none of the studies measured actual grouse nest predation (due to small sample size) is an obvious limitation particularly in terms of absolute estimates. On the other hand, artificial nest experiment results might be applicable to other ground-nesting bird species that are sharing habitat with grouse and are similar in size – e.g. ducks (*Anatidae*), Eurasian nightjar (*Caprimulgus europaeus*), and Eurasian woodcock (*Scolopax rusticola*). Through study II, which involved tree nests, the results can be further applied to measuring e.g. *Turdus sp.* nest predation risks in similar habitats.

Artificial nests can be considered as an imprecise, but cheap, method, while systematic collection of grouse and predator observations requires much effort. Although in Estonia, wintertime wildlife track squares (including grouse tracks) are being surveyed annually, simultaneous predator and grouse mapping during the breeding period had not been carried out before. Considering the detailed landscape-scale datasets collected (described in study IV) and the plausible results in studies II–IV, the method could be valid for some long-term grouse reproduction studies in selected landscapes. It has been already taken into use for before-after designs in large wetland-restoration projects in Estonia. As a broader impact, engaging volunteers while coaching them is an excellent tool for raising social awareness about the habitats and ecology of declining bird species. Predator counts provide adequate side-data; however, predator mobility on forest-wetland landscapes needs to be studied with more comprehensive methods as explained above.

#### **4.4. Grouse populations in forest-wetland landscapes: future perspectives**

Synthesizing the results, the most unfavourable wetland-forest landscape transformation for all three species is a landscape where (too) small refuge patches become interspersed with middle-aged fragmented stands, recently thinned areas, and peatlands that are rapidly overgrowing due to drainage. In many cases, this

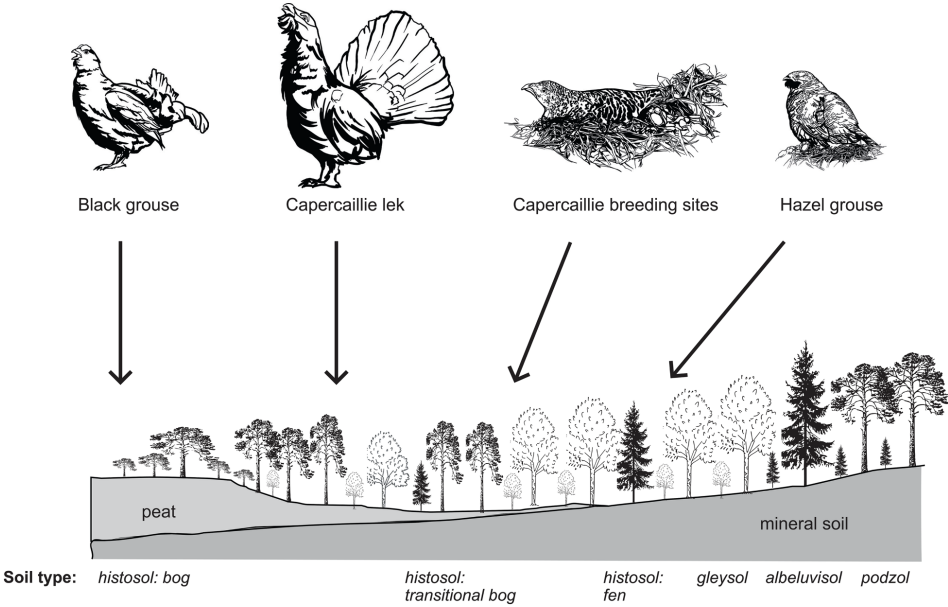
is what a typical even-aged silvicultural system produces as a contemporary production forest landscape (Kuuluvainen et al., 2004).

In contrast, a grouse-friendly landscape could be conceptualized as a forest-wetland mosaic with soft natural edges, various tree age-classes and all types of intact Histosols (Fig. 7). As the description refers to a typical pristine forest-wetland landscape, one must emphasize the importance of preserving such remained habitats. As all three grouse species act as focal species (Angelstam et al., 2004), good-quality habitat maintenance would benefit in sustaining the populations of other forest-wetland specialists. In Estonia, a few described and protected landscapes do exist as large reserves, and some local capercaillie populations show even slight increases in such landscapes (Lõhmus et al., 2017). However, maintenance of such landscapes is pressured by the limited management zones that surround the strictly protected core areas. In practice, the limited management zones include also intensive forestry practices that impact negatively near-natural or even intact areas inhabited by viable grouse populations (National Audit Office of Estonia, 2023).

At the European scale, the key question for a future perspective of forest grouse is how to improve their reproductive success in unfavourable landscapes as described above. Study III, alongside with others (Kauhala et al., 2002; Summers et al. 2004; Moreno-Opo et al. 2015), demonstrated predator culling as a potential short-term solution for improving grouse productivity. However, predator culling requires long-term planning to sustain the grouse reproduction, and possibly to optimize it (for instance by targeting mesopredator hunting pressures around small capercaillie reserves; I). Even so, protection areas need to be supported by reducing management pressures at least 200 ha around capercaillie lek centre and at least 90 ha from a black grouse lek centre (see Angelstam, 2004). For reducing grouse predation, habitat supporting mechanisms require avoiding fragmented forest patches, as well as large-scale forest thinnings alongside with sustaining the existing drainage systems. In addition, preserving various unthinned age-classes would benefit sympatric grouse populations. The effectiveness of proposed remedies could be measured through before-and-after studies in small protected grouse habitats in production forestry landscapes – perhaps also including some kind of predator culling.

Study III raised the question about the effectiveness of habitat restoration on grouse. Although in the study, forest cuttings and hydrological modifications were planned considering capercaillie habitat requirements, nest predation rose significantly in the restoration areas. In the same years, capercaillie only bred unsuccessfully in the restoration sites (Lõhmus, unpublished data). Although this could be a short-term mechanism before the recovery of pre-drainage vegetation, the study indicates that large-scale restoration actions might negatively affect local capercaillie populations in the short term. To avoid that, wetland restoration projects need to consider creating restoration sites patch-wise and avoid large-scale thinnings at sites where breeding grouse have been detected in the pilot studies. For continuance, grouse reproductive success and nest predation need to be measured periodically, as the post-restoration succession develops. However,

given that grouse-friendly landscapes do exist, it is more cost-effective to preserve existing functional forest-wetland landscapes, especially in the limited management zones, than to degrade the habitats with harvests and drainage, and establish costly restoration systems after degradation.



**Fig. 7.** Forest grouse habitat preferences along Histosol gradients in forested peatlands (IV).

## 5. CONCLUSIONS

1. Artificial nest experiments were successfully combined with actual grouse and predator observations to provide broad scale insights into nest predation across landscapes. This would not have been possible with any of those methods alone. The main limits to such combined observational approaches are set by predator mobility, and advanced research could include radio-tracking and between-predator behaviour, notably including top predators.
2. Diverse and dynamic predator fauna makes nest predation unpredictable for breeding birds in forest-wetland landscapes. It also makes it difficult for managers to mitigate an increased abundance of predators. Nevertheless, nest predation and grouse reproductive success do vary across and between landscapes; thus the habitat characteristics providing safe breeding conditions need further clarification and, potentially, protection.
3. In addition to predator abundance and forest stand age, habitat quality of grouse populations needs to be evaluated by integrating multiple forest management factors (incl. drainage, thinning, soil characteristics).
4. Among forestry effects, clearcuts caused by production forestry are the most unfavourable grouse habitats and pose persistent problems in terms of nest predation. First, capercaillie and hazel grouse avoid clearcuts. Secondly, although lowest nest predation was detected on clearcuts, the fragmented landscape can aggregate predation risk into remaining patches, including mid-aged production forests and old forest fragments protected for the birds.
5. For sustaining viable grouse populations, large natural forest-wetland landscapes are crucial habitats, and the habitat quality needs to be sustained also in the limited-management zones. Around small reserves surrounded by production forestry, clearcuts, large-scale thinnings and drainage-system maintenance are detrimental.
6. Habitat restoration projects can locally reduce grouse productivity at least shortly after the habitat manipulations. Large-scale thinnings are specifically likely to have negative impact. To mitigate such impacts, patch-wise restoration should be considered, possibly with temporary predator control measures.

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## SUMMARY IN ESTONIAN

### Majandatud metsa-märgalamaastike mõju metsakanalistele ja pesarüüstele

Inimtegevuse tõttu on viimaste aastakümnete jooksul kiskja-saaklooma suhted muutunud. Selle üks väljunditest on „väikekiskjate levimise hüpotees”, mille puhul tippkiskjate kadumisel ökosüsteemist suureneb väikekiskjate arvukus sedavõrd, et see hakkab vähendama saaklooma arvukust.

Väikekiskjate levimise üks tagajärjedest on suurenenud röövlusohht lindudele, eriti nende kurnadele ja poegadele. Kui väikekiskjate mõju lisandub teistele looduslikku suremust põhjustavatele teguritele, võib kogu linnupopulatsioon ohtu sattuda. Sarnane olukord võib tekkida ka siis, kui lindude looduslikud elupaigad killustatakse või nende kvaliteet järsult halveneb. Oludes, kus kiskjad ja saaklinnud koonduvad samadesse killustunud elupaigalaikudesse, võib pesarüüste suureneda märgatavalt isegi siis, kui kiskjate arvukus maastikul ei tõuse.

Pesarüüste suhtes on kõige tundlikumad maaspesitsejad, näiteks kanalised. Euroopa metsa-märgalamaastikes on nendest esindatud metsis (*Tetrao urogallus*), teder (*Lyrurus tetrix*) ja laanepüü (*Tetrastes bonasia*) – nende liikide arvukus on viimastel aastakümnetel langenud kogu Euroopas. Maastiku lõikes nende liikide elupaigad kattuvad, kuid iga liik eelistab erinevat ja erivanuselist puistut. Seejuures vajab metsis sigimiseks vähemalt 2,2 km<sup>2</sup> ja teder vähemalt 0,9 km<sup>2</sup> suurust pesitsusala. Metsisele sobilikud elupaigad (suured vanad männikud) on neist kolmest kõige majandamistundlikumad, mistõttu peetakse metsist ka jätkusuutliku metsamajandamise suuniliigiks ja vanade metsade katusliigiks.

Metsakanaliste arvukus Põhja- ja Baltimaades on langenud samaaegselt metsamajanduse intensiivistumisega 20. sajandil. Ulatuslike lageraiete ja kuivendussüsteemide rajamisega on muudetud enamik looduslikest metsa-märgalamaastikest killustatuks ja struktuurilt lihtsustunuks, ning seal on palju vähem vanu metsi. Ka viimasel aastakümnel on metsaraie pindala kasvanud, eriti just Põhja- ja Baltimaades. Kuna lageraiepõhine metsandus soodustab ka pesarüüsteriski, on põhjust arvata, et kanaliste vähenemine on vähemalt osaliselt põhjustatud pesarüüste suurenemisest. Siiski on metsandusvõtete ja nende pikaajaline koosmõju kanaliste sigimisedukusele teadmata, ning vaid üksikutes uuringutes on arvestatud kuivenduse mõju.

Kanaliste arvukust on üritatud tõsta eksperimentidega, millest üks levinumaid on väikekiskjate sihipärane küttimine. Sobimatuteks muutunud elupaikades on harvendatud ka puistu ja põõsastiku struktuuri, et parandada kanaliste toidutaimede (näiteks mustika (*Vaccinium myrtillus*)) kasvutingimusi. Balti riikide majandusmetsadesse on metsise ja tedre kaitseks rajatud spetsiaalsed kaitsealad; samuti on nendes riikides 90% metsisemängudest kaitse all. Sellele vaatama on metsise ja tedre arvukus vähenemistrendis.

Töö eesmärk oli uurida kaitsemeetmete tõhusust kolme metsakanalise (eriti metsise) sigimisedukuse parandamiseks majandatud metsa-märgalamaastikes.

Varem ei ole tehtud uuringuid, mis ühendaksid kanaliste (ja ka mõne teise linnuliigi) sigimisedukust, pesarüüset, röövlust ning metsamajandusvõtteid. Oletasin, et suurenenud röövlus on kanaliste sigimisedukuse vähenemise otsene põhjus ning maastikumuutused (lage- ja harvendusraied, kuivendus) on selle vahendajaks.

Esmalt uurisin, kuidas metsamajandusvõtted metsise, tedre ja laanepüü pesarüüset ja sigimisedukust mõjutavad (uuringud **I–III**). Selleks tegin tehispesaeksperimente erineva intensiivsusega majandatud metsades. Teine eesmärk oli teada saada, millistes maastikuosades on kanaliste kurnad ja pesakonnad kõige röövlusaltimad. Selleks uurisin, kas kanalised valivad pesitsemiseks suure röövlusohuga piirkondi (**II**) ning millistes maastikuosades liigub rohkem kiskjaid (**I–IV**). Kaardistasin 2015–2018 kanaliste, nende pesakondade ja kiskjate paiknemise maastikul. Uurisin ka kuivendatud elupaikade taastamise ja kiskjate küttimise mõju nii pesarüüsetele kui ka kanaliste sigimisedukusele (**III**). Uuringuladeks olid erineva majandamisintensiivsustega maastikud Öördi ja Kikepera rabade ümbruses Soomaal, ning Tudu- ja Sirtsisoo ümbruses Kirde-Eestis.

Ehkki pesarüüsete oli erinevate majandusvõtetega maastikes varieeruv, oli üldine rüüsterisk väga kõrge (**I–III**). Mõningast leevendust pakuks kiskjate küttimine, ent selle mõju on lühiajaline ja lokaalne (**III**). Väikesel ruumiskaalal oli kiskjate paiknemine juhuslik (**II**), ent maastiku mastaabis võis täheldada koondumist: metsisemängude vahetus ümbruses oli pesarüüsterisk suurem (**I**) ja seal oli vähem pesakondi (**IV**), mis viitab kiskjate koondumisele väikeste metsise mängualade ümbruses keset majandusmetsa (**I**). Erinev rüüsetase tuvastati ka **II** uuringu maastikel – see näitab, et pesarüüsete varieerub erinevalt majandatud maastikuosades, kuid rüüsete mehhanismi selgitamiseks on tarvis täpsemaid uuringuid. Lokaalses mastaabis oli aga kiskjate esinemissagedus juhuslik, mis näitab kiskjate dünaamilist liikumist maastikul – see võib olla ka põhjus, miks kanalised ei suuda pesitsemiseks valida alasid, kus tuvastati väiksem röövusoht (**II**). Kuna tehispesade uuringud on võrdlemisi ebatäpsed ning kiskjate liikumine maastikus laiamastaabline ja muutlik, on vaja kiskjauuringutes lisaks kaardistamisele kasutada täiendavaid meetodeid (raadiosaatjad, rajakaamerad, jäljeloendused).

Metsandusvõtete analüüsist selgus, et ehkki kuivenduskraavide olemasolul puudus otsene mõju nii pesarüüsetele kui ka kanaliste esinemissagedusele (**II, IV**), seostus lindude esinemine (kuivendamata) soomuldade mitmekesisusega. Tedre esinemine koondus rabamuldadele, metsisel siirdesoomuldadele ning laanepüül madalsoomuldadele. Lageraie mõju nõuab tulemuste võrdlust suures plaanis: ehkki puistu vanuseklasside lõikes oli lageraielankidel ja noortes puistutes pesarüüsterisk madalaim (**II**), vältisid selliseid alasid nii metsis kui ka laanepüü (**IV**). Kõrgeim oli aga pesarüüsete keskealistes puistutes. Kui metsamaastikke killustada ulatuslike raielankidega, võivad nii linnud kui ka kiskjad koonduda säilinud keskealise ja vana metsaga elupaigalaikudesse, mis halvendaks lindude sigimisedukust veelgi. Tugev negatiivne mõju oli ka harvendusraietel: **III** uuringus selgus hüppeliselt suurenenud pesarüüsterisk elupaiga taastamise käigus tehtud kujundusraiate tagajärjel, samuti vältisid kõik kolm liiki alasid, mida viimase 10 aasta jooksul on harvendatud (**IV**).

Tulemuste põhjal on kanalitele kõige sobimatud maastikud, kus väikesed kaitsealused elupaigalaigud on killustatud lageraiete, keskealiste puistute, harvendusraiate ning tugevasti degradeerunud kuivendusalaadega. Nende tegurite koosinemine iseloomustab tüüpilist kaasaegset majandusmetsamaastikku. Kanaliste populatsioon aitab sellistes elupaikades säilitada suureskaalaliste lageraie- ja harvendusraiate vältimine, mitmekesiste puistute säilitamine ning maaparandussüsteemide rekonstrueerimise lõpetamine. Kaitsealuste metsise- ja tedremängude ümbruses tuleks aga peatada metsamaastiku killustamine lageraietega. Nende võtete efektiivsust saaks kontrollida enne-pärast eksperimentidega. Teisalt näitavad tulemused, et kanalitele sobilikum on mitmekesiste soomuldadega ning looduslike eriliigiliste ja -vanuseliste puistutega metsa-märgalamaastik. Kanalisi saaks sellistes loodusmassiivides ökosüsteemides kasutada suunisliikidena, kelle käekäik näitab ökosüsteemide üldist seisundit elurikkuse jaoks.

vahetult pärast taastamistõid mõjuvad elupaigamuutused kanaliste sigimisedukusele negatiivselt, mistap on elupaikade kujundusraiate mõju väiksem, kui neid teha pikema perioodi jooksul väikeste pindalade kaupa (III). Elupaiga taastamisele järgnevat negatiivset mõju on võimalik leevendada ka vahetult pärast taastamistõid väikekiskjate väljapüügiga taastatud aladel ja lähiümbruses. Kulu-efektiivsem oleks siiski säilitada toimivaid elujõulisi märgalamaastikke, vältides intensiivset majandamistegevust piiranguvõõndites.

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The dissertation is dedicated to Estonian nature and landscapes.



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