

Department of Forest Sciences
Faculty of Agriculture and Forestry
University of Helsinki

BREEDING IN AN AGRICULTURAL LANDSCAPE:
THE IMPORTANCE OF HABITAT AND PREDATION
FOR THE COMMON PHEASANT
(*PHASIANUS COLCHICUS*)

Heidi Krüger

ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty of Agriculture and Forestry
of the University of Helsinki, for public examination in lecture room B1
(Latokartanonkaari 7) on May 20th 2022 at 13 o'clock.

Helsinki 2022

Title of dissertation

Breeding in an agricultural landscape: The importance of habitat and predation for the common pheasant (*Phasianus colchicus*)

Author

Heidi Krüger (formerly Kallioniemi)

Thesis supervisors

Dr Petri Nummi

Department of Forest Sciences, University of Helsinki, Helsinki, Finland

Dr Veli-Matti Väänänen

Department of Forest Sciences, University of Helsinki, Helsinki, Finland

Pre-examiners

Prof Henrik Andréén

Department of Ecology, Swedish University of Agricultural Sciences, Sweden

Dr Patrik Karell

Novia University of Applied Sciences, Bioeconomy research Team, Finland

Opponent

Dr Julie Ewald

Head of Geographical Information Sciences,

Game and Wildlife Conservation Trust, UK

Dissertationes Schola Doctoralis Scientiae Circumiectalis,
Alimentariae, Biologicae 7/2022

ISSN 2342-5431 (Online)

ISBN 978-951-51-8167-1 (PDF)

ISSN 2342-5432 (Print)

ISBN 978-951-51-8164-0 (Paperback)

Cover photo

Heidi Krüger

Unigrafia, Helsinki 2022

To my children Lotta, Emil and Ida

ABSTRACT

Agricultural intensification has significantly impacted the habitat structure of agricultural landscapes and is one of the main drivers of biodiversity decline on farmlands. Farmland bird populations in particular have declined, but similar patterns have been shown for other taxa, including mammals, arthropods, and flowering plants.

Farmland birds are strongly linked to other farmland biodiversity and are therefore considered good and easily monitored indicators of biodiversity in agricultural habitats, both in open farmland and edge areas. Thus, factors affecting the success of these birds may provide vital information on how to tackle the challenge of halting biodiversity loss on farmlands.

In this thesis, I studied common pheasant (*Phasianus colchicus* L.; hereafter pheasant) hens and broods as well as artificial pheasant nests during the breeding season to identify factors affecting the breeding success of pheasants in an agricultural environment in southern Finland.

I found that both bird quality, i.e. wild compared with hand-reared hens, and predator density affected pheasant survival. In my study, both wild and hand-reared birds were translocated to the study areas, so the wild birds had no advantage from previous knowledge of the study area e.g. in terms of food resources and predators. Introduced hand-reared birds survived well in the low predator density area throughout the study period, whereas they suffered high predation during the first two weeks in the high predator density area. Wild birds in the high predator density area survived similarly to birds in the low predator density area: both had a very steady death rate over the study period. The death rate of hand-reared birds in the high predator density area evened out after a few weeks. These results show that even hand-reared pheasants can breed successfully, especially if red fox (*Vulpes vulpes* L.) numbers are low, as they are the main predator of pheasant hens, and if weather conditions are not too averse.

Following the broods by radio-tracking revealed that field margins were an important and preferred habitat. Most observations were made in grain fields, but comparing habitat use to availability showed a significant preference for margins. Even proximity to field margins seemed to be preferred. This suggests that the combination of margin and grain field offers an ideal habitat for pheasant broods, which require high-quality arthropod prey and shelter from predation.

A study setup with wildlife camera traps and artificial pheasant nests revealed that an invasive alien species, the raccoon dog (*Nyctereutes procyonoides* Gray), may be a common predator of ground-nesting bird nests in agricultural landscapes in Finland. The raccoon dog was the most common primary predator at nests and also the most frequent predator visiting the signposts that measured the predator density index in the study areas.

Information gained from our study is useful for planning introductions of hand-reared birds, irrespective of whether they are reintroductions of endangered species or introductions of birds for game management purposes. The results show that introductions using hand-reared birds can be successful as long as predation risk is low and provided that other circumstances required for successful brood production are favorable.

Finally, despite the common pheasant having no conservation value per se, the information received from my thesis may guide game managers and farmers to put more effort into creating better brood-rearing environments for pheasants, which may then benefit other farmland wildlife. Margins along small grain fields may provide arthropod-rich habitats and controlling predators may enhance the nesting success and survival of ground-nesting farmland birds. My results support earlier findings that field margins should be appreciated as vital biodiversity-enhancing elements in agricultural landscapes. Including field margins as a conservation tool in the AES measures of the EU Common Agricultural Policy (CAP) would therefore be worthwhile, e.g. an edge-to-area ratio could be utilized.

Keywords: hand-reared, predator density, raccoon dog, habitat use, field margin, agriculture, biodiversity

ACKNOWLEDGEMENTS

My journey with pheasants and this dissertation began already in 1995 when I was practising at the University Farm in Suitia where Juha Virtanen had just started his experiments with radio tagged pheasants. I remember mowing take-off grounds for pheasants in the Castle Park when the grass and weeds had grown way too thick for them. We trainees had a few laughs with the farm workers over the enthusiastic researcher and his birds (or their remains) that we had to dig out from fox dens. Even the cow stalls' slurry pit had to be emptied to retrieve one of the expensive radio tags. But, little did I know, in 1998 I was the one holding the antenna and taking care of the field work for the research. By this time, I had realised that the best crew at the University was at the Department of Applied Zoology, and that Wildlife Biology and Entomology were far more interesting than Animal Husbandry. Thank you Juha, Veli-Matti, Petri, Jani, Pauliina, Gunnar, Ville, Fredrik, my former professor Kari Heliövaara, and everyone else at the department, for creating an enthusiastic atmosphere where everything from weevils to musk oxens was most interesting.

Studying wildlife biology allows one to take part in unforgettable field trips, such as skiing in Lapland (and seeing plenty of willow grouse and ptarmigans!), calling for hazel grouse at Evo (and staying awake all night singing with Petri, Suski & Pauliina!), visiting National parks with plenty of cacti and some volcanoes in Mexico, over four kilometre high mountains and buddhistic temples in China (to hear and see tibetan grouse and brown eared pheasants!), the Pyrenees in Spain (no rock ptarmigans detected, but a chamois and some ground hogs!), a little lower mountains in South France (wonderful heather hills!), some bogs in Lithuania (did we see some wildlife?) and roaring red stags on Hungarian hills. All these trips have included the company of friends with shared interest, thanks to all of you!

Being a PhD student makes it possible to travel with travel grants to scientific congresses even abroad (see above). There is one congress that really made me understand the importance of connecting face to face with new people. As a fresh PhD Student, I travelled to the IUGB congress in Barcelona in 2011 to present my pheasant studies. On that trip, I met the most wonderful people from the Game and Wildlife Conservancy Trust. My dearest thanks to Frances who invited me to join your dinner entourage! I have loved being in touch with the GWCT crew, visiting UK research fields with my daughter Ida, discussing predator problematics with Dave and Mike, and participating in the Perdix congresses. The recent Perdix tour in Hungary was fantastic. Thank you Peter Pal for inviting us all to your hometown!

Being a PhD Student means friends and colleagues that study wildlife biology. At some point in Viikki we all ended up sharing a room where the Wetland Ecology Group still holds its base. Sari, Mia, Stella, Milla, Antti P. and Elmo, thank you for the Wildlife afternoons, great lunch company, helping out

in all my major and minor problems and of course for laughing so much. You truly define positive attitude to work. Special thanks to Antti L. for patiently teaching me how to use QGIS!

In the spring of 2015 Veli-Matti and I came up with the idea of finding out who destroys pheasant nests in the wild. This needed plenty of wildlife cameras and hundreds of pheasant eggs. In a big hurry I lent 20 cameras, all different types, from 20 different friends (at that time wildlife camera trap studies were a novelty), as well as contacted all friends and acquaintances in order to have my studies carried out on their lands. Thanks to everyone who loaned their cameras, and thanks to Fredrik, Gus, Reinhard, Lasse A., Mika, Isabella and Markku for providing good research areas! Huge thanks to Heikki who also provided all the hundreds of pheasant eggs needed for the study!

I have become friends with so many of you, even though the first encounter hasn't always been so promising. For instance Kim. I met Kim for the first time at a statistics class. He was teaching and I tried to learn. This is still the set up. I am still trying to learn. Thank you so much! I hope I will not have to bother you again with my statistics problems. It's much nicer to see you with your family and dogs, or even discuss job related invasive alien species problematics, ideally in the archipelago!

Thanks to my instructors Petri and Veli-Matti, the heart and soul of Viikki's wildlife biology studies. We have had a long journey together, from the very basic studies to many kinds of field trips and now finally this dissertation project that has craved a never-ending patience from you. You two are among the kindest people I know. You have always supported me and gently guided me in the right direction. Words can't express the gratitude I have for you.

I present my warmest thanks to Patrik Karell and Henrik Andrén, who kindly reviewed my thesis. As well as to my responsible Professor Carita Lindstedt-Kareksela who helped me look at my subject outside of my own wildlife management bubble. Your comments really improved my work! Thanks Stella for checking the language!

I am very grateful for the grants that I have received during the years, for studying, writing, travelling and buying equipment. Thank you Niemi-Säätiö, Suomen Riistanhoito-Säätiö, Haavikko Säätiö, the Finnish Hunters Association, University of Helsinki and Waldemar von Frenckell's stiftelse. The help of my co-authors in writing articles has been amazing, thank you all for every detail you checked, all the comments you made, for your ideas and for the sheer work on analyses and writing, as well as addressing the scientific questions from the correct angle. I'd also like to thank all the people who collected the data before I started on the project and everyone who helped in this project in some way or other!

It took me a very long time to finish my master's thesis and it has taken almost as long to finish this next level. I thank all my friends who have stood beside me, believed in me and supported me. I have never heard you say one negative thing about me studying. Never have you expressed doubts or questioned the rationale behind my decisions. Thank you Kata, Suski and

Ritva, you have supported me in all the storms in my life, but also been there when the sun shines. I am eternally grateful for your support!

Scientific discussions, may they be of horses or wildlife, far or near, are always welcome. Maija and Janne, thank you!

Thank you Mimma for support and commenting on the Summary, definitely needed your educated opinion! Thanks to you and Jacki for hosting raccoon dog and mink control trips to the archipelago. The trip in May 2021 that ended up in me having a knee operation that tied me to the sofa for the whole summer was a key factor in ever being able to write my last article!

Thanks to my colleagues at work, especially Jussi, Sami, Janne and Vesa. You delayed my dissertation by employing me in March 2019 when I had just gotten a grant to finish. Thank you for that, it is a pleasure to work with you guys! You have shown me what life after the everlasting PhD student life looks like, and I like it.

Thanks to my sisters Anna and Mia! Our parents always let us choose our way, and never put pressure on what to study or when to finish studying. Sometimes I wonder if some pressure would have been beneficial. The death of our Mother in 2015 made many things more complicated, but having you super sister's by my side is a blessing.

My children are the most precious thing in my life. But they know of no other mother than a PhD student mother. Every single holiday has included me with a computer, thick books and printed scientific A4 papers flying around. I have been reading at the beach while the kids were at swimming school, at handball trainings and tournaments, at the judo dojo, at scout camp and in all kinds of hotel rooms and of course at home and summer cottage. My kids gave me the nickname "Doctor Mother" a few years ago and now they are worried about how they can make fun of me if I really graduate. Thank you Lotta, Emil and Ida, you are the light of my life!

Finally, thanks to Gus and Ukkonen, the men in my life. Ukkonen is a shorthaired Vizsla. A pointing dog, that loves pheasants. Ukkonen keeps me fit by taking me out on daily walks. He is a true companion, and will certainly appreciate me spending less screen time. Gus is my gunman, deeply adored by Ukkonen, since he provides him winged creatures to fetch. Thank you Gus for everything. Without you, I don't think I would have ever made it to this point. You have helped me financially and mentally. You have pushed me forward, given carrot and stick in a needed combination. You have rocked my dreamer's seat, but always shown appreciation for my work. I love that we share so many views, but I also love that I can argue with you on so many things. If I can convert you to loving birds and bog restoration, I can convert anyone. I promised you I wouldn't get any pheasants before I finish my PhD, but I think that obstacle is soon gone. I hope you let me guide you in creating good breeding environments for them on your fields. I think I might have some useful tips.

TABLE OF CONTENTS

LIST OF ORIGINAL PUBLICATIONS.....	10
1. INTRODUCTION.....	11
1.1. Agricultural intensification has triggered farmland bird declines	11
1.2. The habitat selection process acting on a farmland bird during breeding	13
1.3. Predation has an increasing impact on breeding farmland birds	14
1.4. Common pheasant, the world’s most common introduced bird.....	16
1.5. Why study common pheasants?	18
1.6. Thesis aims.....	19
2. MATERIAL AND METHODS	20
2.1. Studies I and III	20
2.2. Study II	22
2.3. Predators in the study areas.....	25
3. RESULTS AND DISCUSSION	27
3.1. Survival and breeding of introduced wild and hand-reared common pheasant hens.....	27
3.1.1. Hen survival.....	27
3.1.2. Breeding success	30
3.2. Who takes the nests? Depredation of artificial common pheasant nests	30
3.3. Common pheasant broods prefer field margins, farmland biodiversity hotspots	34
3.4. Forest as a landscape structure for common pheasant broods ...	37
4. CONCLUSIONS AND MANAGEMENT IMPLICATIONS.....	39
REFERENCES.....	42

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals. Articles I and II are reprinted with the kind permission of the publishers, while article III is the author's version of the submitted manuscript.

- I Kallioniemi, H., Väänänen, V-M., Nummi, P., Virtanen, J., 2015. Bird quality, origin and predation level affect survival and reproduction of translocated Common pheasants *Phasianus colchicus*. *Wildlife Biology* 21, 269–276. <https://doi.org/10.2981/wlb.00052>.
- II Krüger, H., Väänänen, V-M., Holopainen, S., Nummi, P., 2018. The new faces of nest predation on agricultural landscapes – a wildlife camera survey with artificial nests. *European Journal of Wildlife Research* 64, 76. <https://doi.org/10.1007/s10344-018-1233-7>.
- III Krüger, H., Jaatinen, K., Holopainen, S., Niemi, M., Vehkaoja, M., Virtanen, J., Väänänen, V-M., Nummi, P. 2022. Margins matter: the importance of field margins as avian brood-rearing habitat in an intensive agricultural landscape. *Manuscript, accepted, subject to revision*.

Author's contribution

The Author (Heidi Krüger, formerly Kallioniemi) contributed to the papers included in this thesis in the following manner: Heidi Krüger (HK) is fully responsible for the summary of this doctoral thesis, and she is the main author of all papers. Petri Nummi (PN), Veli-Matti Väänänen (VV), and Juha Virtanen (JV) were responsible for the original idea and the study plan of paper I. Data were collected over several years by VV, JV, and HK as well as some field assistants. VV and JV analyzed the data and HK was responsible for the writing. All co-authors commented on the manuscript. In study II, VV and HK were responsible for the original idea and planned the study protocol with Sari Holopainen (SH). The data were collected by HK and analyzed by SH. HK was responsible for the writing, and all co-authors commented on the manuscript. Study III was originally planned by PN, VV, and JV, as a part of study I. The final focus of the manuscript was formed by HK and Kim Jaatinen (KJ). Milla Niemi (MN) helped HK with data digitization and in the use of GIS programs. MN, SH, and Mia Vehkaoja (MV) helped in finding the correct methods for data analyses. KJ and HK analyzed the data, HK made the interpretations and the writing, with all co-authors commenting on the manuscript.

1 INTRODUCTION

Agricultural modernization advanced vastly in the Western world after the Second World War. Horses were replaced by tractors, and chemicals helped fight weeds and protect crops. Farm and field sizes increased, along with yields, and farmland concurrently began losing its heterogeneity. These changes are considered the major causes for farmland biodiversity loss (Altieri 1999; Chamberlain et al. 2000; Benton et al. 2003; Evans 2004; Powell 2015; Ponce et al. 2018).

Farmland birds have a strong connection to other farmland biodiversity and are therefore considered good and easily monitored indicators of biodiversity in agricultural habitats, both in open farmland and edge areas (Gregory et al. 2005). Thus, factors affecting the success of these birds may provide vital information on how to tackle the challenge of halting biodiversity loss on farmlands.

1.1 AGRICULTURAL INTENSIFICATION HAS TRIGGERED FARMLAND BIRD DECLINES

Agricultural intensification has significantly impacted the habitat structure of agricultural landscapes and caused a worldwide decline in biodiversity (e.g. Altieri 1999; Chamberlain et al. 2000; Benton et al. 2003; Evans 2004; Ponce et al. 2018). Intensification has caused many changes in land use that have had wide effects on the habitats of agricultural fauna and flora. Among these changes are the loss of heterogeneity and open parcel ditches, increases in field plot size, removal of landscape elements such as hedges and barns, increases in intense drainage and irrigation, increases in pesticide and fertilizer use, along with a shift in the timing of agricultural activities (Stoate et al. 2001; 2009; Hietala-Koivu 2002). Concurrently with these changes, many European farmland bird populations are facing severe, and ongoing, declines (BirdLife 2015; IUCN Red List 2021).

As birds are considered to reflect well the trends in other biodiversity elements (Gregory et al. 2005), the EU Farmland Bird Indicator (EFBI) uses multiple species to assess the biodiversity status of agricultural landscapes in Europe. One of these species is the native gray partridge (*Perdix perdix*, L. hereafter partridge) because of its tight habitat demands within the agricultural landscape (Potts 1986; European Council 2001; Gregory et al. 2005). During

the last 50 years, partridge populations have suffered an over 90% loss in Europe (EBCC 2017).

The reasons behind this decline have been identified with extensive studies across Europe. Increased herbicide use has caused a loss of the weedy vegetation that supports a diverse arthropod community, and insecticide use directly affects the arthropod fauna. These agricultural actions have jointly caused a lack of food for partridge chicks, which are dependent on a high-quality arthropod diet (Potts 1986; Potts and Aebischer 1995). Intensified land use has caused a loss of nesting habitats, such as hedges, small forest patches, and other semi-natural areas necessary for ground-nesting species (Aebischer and Ewald 2004). Predation by avian and mammalian predators has concurrently increased, leading to higher mortality of nesting females in particular (Panek and Bresiński 2002; Newton 2004; Langgemach and Bellebaum 2005; Ewald et al. 2010; Smith et al. 2010; Roos et al. 2018).

The common pheasant (*Phasianus colchicus*, hereafter pheasant), shares many habitat demands with the partridge during breeding time, so unsurprisingly the reasons suspected to be behind the decline of pheasants are similar to those causing the partridge decline in Europe: a lack of nesting places, loss of good brood-rearing habitat, and increased predation (e.g. Hill 1985; Potts 1986; Jorgensen et al. 2014; Ronnenberg et al. 2016; review by Taylor et al. 2018).

However, the changes in agricultural practices that have negatively impacted farmland birds are not solely caused by land use intensification. Many bird species currently inhabiting open farmlands are species that were able to adapt to human-modified landscapes when their original open habitats were turned into farmland. Today, these species are also threatened by extreme extensification, i.e. a loss of active agricultural measures that leads to abandoned fields and afforestation. This may be even more detrimental than intensification (Silva-Monteiro et al. 2021). Agricultural practices are therefore necessary for farmland biodiversity. The important question is what measures are best for enhancing biodiversity while simultaneously answering the global need for food security and economic viability of the agricultural enterprises (Tilman et al. 2011; Gabriel et al. 2013; Searchinger et al. 2018; Clough 2020).

1.2 THE HABITAT SELECTION PROCESS ACTING ON A FARMLAND BIRD DURING BREEDING

When trying to understand the process that leads to a bird species selecting a certain environment for breeding, it is essential to understand the hierarchical nature of the selection. It is necessary to view a landscape, a possible breeding ground, from a bird's view, thus from a different level and scale (Wiens 1989).

According to Wiens (1989), an individual of a species can be seen to possess an internal image or template (genetically and/or learned) of what constitutes a suitable habitat. This template sets the boundaries for a bird's habitat requirements. Habitats that fit the template provide various aspects that may lead an individual to settle in an area e.g. habitat structure, vegetation, food resources, edge area, microclimate, other individuals. The actual selection of a habitat based on these cues depends on various environmental factors that affect the optimal pattern determined by the template. Competition caused by population density or interaction with other species, even predators, may be crucial in decision making.

Habitat selection must not be confused with habitat use. Habitat use is the result of habitat selection, which is affected by many phenomena. When studying habitat selection, those phenomena and how they affect the choices made by individuals and the consequences of those choices must be examined (Jones 2001; Kristan et al. 2007). Habitat selection can be studied by comparing used habitat with unused habitat, but it is more informative to compare used habitat with habitat that is available to the focal species (Johnson 1980; Aebischer et al. 1993) while keeping in mind possible intolerances (stenotopicity) for certain unsuitable habitats or elements in otherwise suitable environments (Cunningham and Johnson 2019).

Wiens (1989) summed up a list of facts that can affect our understanding of a bird's habitat selection and that must be considered when studying bird - habitat interactions. The following apply to my study:

1. Responses by the species to predators, prey, parasites, or competitors
2. Sudden environmental factors such as weather
3. Incomplete sampling of environmental gradients
4. Using habitat measures that are inappropriate, incorrectly scaled, or too few, or using too many
5. Measuring habitats on an incorrect scale with reference to the question being asked

Johnson (1980) describes this selection process by dividing it into four orders. The first order is the selection of a landscape in which to settle. At least to a certain degree, the first-order selection in my study is performed by

researchers when selecting the area where the birds were translocated to. However, this was done by choosing a study area that is known from prior studies to be suitable for the studied species. The second-order selection is made by an individual bird within the first-order system, i.e. within the landscape. The released pheasant hen chooses a territorial cock that will provide good nesting and feeding areas on its territory along with offering safety from predators while the hen is feeding (Hill and Robertson 1988).

After chick hatching, the hen once again makes a second-order selection for a brood-rearing environment, which we refer to in this study as the brood home range. The third-order selection is made within this home range, where the hen makes decisions for choosing nutritious feeding habitats that are safe from predators. Even weather factors may affect this third-order selection, for example by making densely vegetated habitats too cold for a brood during a rainy day. Fourth-order selection occurs when the chicks select between different available food items, i.e. arthropods, and later on seeds and other vegetation.

To Johnson's four orders of selection, Wiens (1989) adds the importance of observing the system at the right scales in both space and time, when aiming for reliable predictions concerning a particular phenomenon. For example, the release timing of the birds is highly relevant in my study. Understanding the selection process that an individual, in my case a pheasant hen, is going through, requires thorough understanding of the behavioral and fitness contexts in which the selection is made (McGarigal 2016).

1.3 PREDATION HAS AN INCREASING IMPACT ON BREEDING FARMLAND BIRDS

By definition, predation means a relationship between two animal species in a community, in which one (the predator) hunts, kills, and eats the other (the prey) (Collins 2012). In recent decades, predation on farmland birds has increased, particularly affecting ground-nesting birds (Roos et al. 2018). Predators may affect breeding success by preying on adult birds or by depredating the nests, or even through disturbance leading to nest abandonment or no-nesting (Preisser et al. 2005; Koshev et al. 2020; Jaatinen et al. 2022). A myriad of studies explores various aspects of predation and its effects on both predator and prey species, and even on the effects on whole trophy chains, but nest predation is still considered one of the most important factors affecting the reproductive output of birds (Newton 1998). Especially in ground-nesting birds, such as ducks, waders, and Galliformes species, predation often impacts breeding numbers; nests on the ground are vulnerable

to many predators and some predators often kill the sitting female as well (e.g. Newton 1998; Bolton et al. 2007; Roos et al. 2018; Jaatinen et al. 2022).

One reason behind this increased predation is the multitude of factors destroying the breeding habitats as a result of agricultural intensification. According to Evans (2004), habitat deterioration may emphasize the effect of nest predation on breeding success in several ways:

1. Habitat change may cause an increase in predator numbers,
2. Loss of suitable nest-site habitats may result in increased nest densities and higher predation rates,
3. Habitat change may force birds to nest in more unsafe habitat types,
4. A reduction in the availability of alternative food sources may cause generalist predators to change their diets,
5. Habitat changes may lead to shortened breeding seasons and thus to less renesting opportunities, thereby increasing the sensitivity of breeding success to nest predation rates.

Besides habitat deterioration, evidence shows that the European populations of many predator species preying upon ground-nesting birds and their nests have grown considerably during recent decades (Panek and Bresiński 2002; Langgemach and Bellebaum 2005; Smith et al. 2010; Kauhala and Kowalczyk 2011). Europe has been going through major changes in its predator communities during recent years. These changes are caused by:

1. Shifts in attitudes towards predators, which have caused restrictions to the hunting, killing, and poisoning of both avian and mammalian predators, particularly affecting apex predators as well as mesopredators (Bern Convention 1979; EU 1992; Prugh and Sivy 2020).
2. Effective rabies control has increased the survival of canine predators, especially the red fox (*Vulpes vulpes*) (Chautan 2000)
3. Invasive alien predator species have spread to new areas and increased in numbers (Kauhala 1996; Kauhala and Kowalczyk 2011; Brzeziński et al. 2019).
4. Climate change is affecting the trophic cascades on many levels, changing the balance between species (Fuglei and Ims 2008; Weiskopf et al. 2020).

In concert with the increase in predator populations, the impact of predation on ground-nesting birds has increased (Brzeziński et al. 2010; 2019; Pöysä and Linkola 2021). Brzeziński et al. (2010) found a 25% increase in the overall predation rate over their 12-year study period in Poland, where the hunting bags of mammalian predators have increased, along with increasing corvid abundances.

Current nest predator communities in Europe include a variety of bird and mammal species (Langgemach and Bellebaum 2005). In addition to native species, several invasive alien predators are spreading across the continent, e.g. the raccoon (*Procyon lotor* L.), the raccoon dog (*Nyctereutes procyonoides*), and the American mink (*Neovison vison* Schreber). The mink and especially the raccoon dog (Fig. 1) have dramatically increased also in Finland during the last 50 years (LUKE 2021). The role of these new species as nest predators, along with their interactions with other predators, is not clear (Salo et al. 2007). The relationship between the removal of a certain predatory species and the survival of prey in the very variable predator communities has not been an easy task to show (Bolton et al. 2007; Salo et al. 2007; Ellis-Felege et al. 2012; Carpio et al. 2016; Nummi et al. 2019).

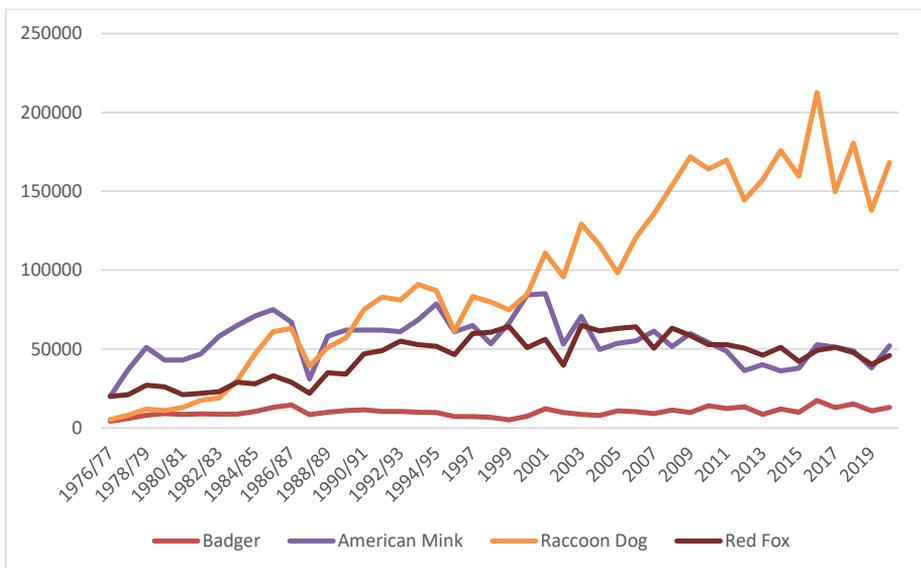


Figure 1. Annual game bag of the most important meso- and small predators in Finland by year (LUKE 2021).

1.4 COMMON PHEASANT, THE WORLD'S MOST COMMON INTRODUCED BIRD

The Common pheasant is a cosmopolitan species present in most of Europe and North America, due to extensive translocations begun already by the ancient Greeks (Robertson 1997). Its' native range is in East Asia, where a variety of subspecies still exist, many of them classified as threatened (Birdlife 2015). The common pheasant is a result of hundreds (or thousands) of years of breeding and mixing of various subspecies as well as mixing with the closely

related Japanese green pheasant (*P. versicolor* Vieillot), resulting in the highly varied appearance of the common pheasant: ranging from very dark, almost black, to nearly completely white pheasant cocks. As with many other Galliformes, common pheasant hens are more modest in their appearance compared with the showy cocks and have retained their simple brown plumage that helps them hide from predators (Pic. 1).



Picture 1. A pheasant hen has a simple brown plumage while the cock is more colorful. (Photo Veli-Matti Väänänen).

The common pheasant is the most common introduced game bird in the world, and 35–57 million hand-reared pheasants are released each summer in Britain alone (Aebischer 2019; Hall 2020). The majority of hand-reared pheasants are released during summer and fall for commercial hunting. Adult pheasants are also released in late spring, in hope of establishing or supporting a permanent population.

Finland lies in the northernmost part of the pheasant's range. Even at these high latitudes, re-stocking using hand-reared birds is a common way to improve a shoot. As the populations of partridge, the only native non-migratory gallinaceous bird in Finland, have vanished and even the forest grouse populations in southernmost Finland are sparse and hunting is very restricted (Lehikoinen 2011), pheasant hunting provides the possibility of continuing sport hunting, particularly with pointing dogs (Väänänen and Nummi 2000). Pheasant hunting is very popular in the southern parts of the country, with a history of introductions dating to the 19th century (Nummi 1988). The natural population of wild pheasants is currently estimated at 20 000 birds (Lehikoinen 2011), the annual game bag being around 40 000 birds, consisting mainly of released birds (LUKE 2021).

However, the results of pheasant introductions have not always been encouraging. Earlier studies have shown that the survival of hand-reared birds is usually poor (Hessler et al. 1970; Hill and Robertson 1988a; b; Brittas et al. 1992; Musil and Connelly 2009). Pheasant and partridge introductions often fail, mainly due to high predation pressure and the quality of the birds, which may vary considerably (Krauss et al. 1987; Putaala 1997; Putaala and Hissa 1998). The pheasant is now the most common gallinaceous bird species in many agricultural areas previously inhabited by naturally occurring partridges. But even natural pheasant populations have been declining in recent decades. The ongoing large-scale introductions of pheasants, mainly for hunting purposes, have somewhat masked these population declines in the USA and Europe (Powell 2015; Robertson et al. 2017).

1.5 WHY STUDY COMMON PHEASANTS?

Even though the decline of an alien species, such as the pheasant, is not of biodiversity importance, the pheasant has economic value for countryside livelihoods. Because of decreasing natural populations, game managers are driven to increase the number of released birds. Understanding the reasons behind the pheasant's decline may help us reduce the need to release hand-reared birds and even understand the decline of other farmland ground-nesting birds.

Factors affecting the breeding success of pheasants are in many ways similar to those of the native partridge (Hill 1985; Potts 1986; Smith et al. 2015), which is considered an excellent indicator of open farmland biodiversity (e.g. Potts 1986; Aebischer and Ewald 2004; Brewin 2020). Pheasant and partridge broods both feed on the same foods in the same environments, to an extent to where a UK study showed their annual survival rates to significantly correlate (Hill & Robertson 1988).

Therefore, understanding how to manage arable landscapes in a manner that supports successful pheasant brood rearing could be beneficial to other farmland birds, along with farmland insect and plant biodiversity, bearing in mind the possibility that pheasants may compete with native birds e.g. through shared parasites (Tompkins et al. 2002; Rząd et al. 2021).

Pheasants are also very accessible birds for study purposes, as they are easy to rear, even wild birds can be caught quite easily, and translocation permits for wild birds are not very hard to obtain. Hand-reared birds are often considered to of lower quality regarding their ability to avoid predation or capability of finding or digesting food compared with wild birds, and even their capability

of producing offspring has been doubted (Hessler et al. 1970; Krauss et al. 1987; Hill and Robertson 1988a; b; Brittas et al. 1992; Putaala et al. 1997; Putaala and Hissa 1998; Musil and Connelly 2009). However, study setups have often been biased because the wild birds have not been translocated, i.e. they have had the advantage of being familiar with the environment and its predators and food resources, thereby potentially masking the true differences in bird quality. Many ongoing projects working on endangered Phasianidae still use hand-reared birds in their reintroduction programs (e.g. Collar 2020; IUCN 2020). Comparing the quality of wild and hand-reared birds originating from more equal starting points and facing different predation pressures may reveal important aspects that should be considered when planning reintroductions.

1.6 THESIS AIMS

The main aim of this thesis was to identify factors affecting the breeding success of a farmland bird, the pheasant, in an agricultural environment in southern Finland. I studied this from different aspects:

- 1) Investigating the impact of hen origin and quality on survival and breeding success
- 2) Revealing nest predation rate and nest predators with wildlife camera traps
- 3) Analyzing habitat use by radio-tracking broods

In my thesis, I evaluate factors that affect the success of pheasant reproduction. Earlier studies have investigated many aspects of pheasant survival and compared hand-reared birds with wild birds. However, in this thesis, I have tried to improve the methodology, to allow comparing the quality of birds of different origin. Both bird groups in my study are translocated, so that all individuals are naïve to the environment. Also, I compare bird success in a high and low predator density area, something not attempted in earlier studies. Increasing our understanding of the differences between and the effect that quality has on hand-reared and wild birds may even be helpful when planning the reintroductions of threatened Galliformes. Then, I use wildlife camera traps and artificial nests to examine the nest predator community depredate ground-nesting birds in the agricultural environment, focusing especially on alien predators. Finally, I look at the habitat selection of pheasant broods at various scales, with more precision than earlier studies have achieved. I attempt to uncover what the habitat use of pheasant broods indicates in our study environment and how this information could be used to enhance other farmland wildlife. Based on the results, I give suggestions for management.

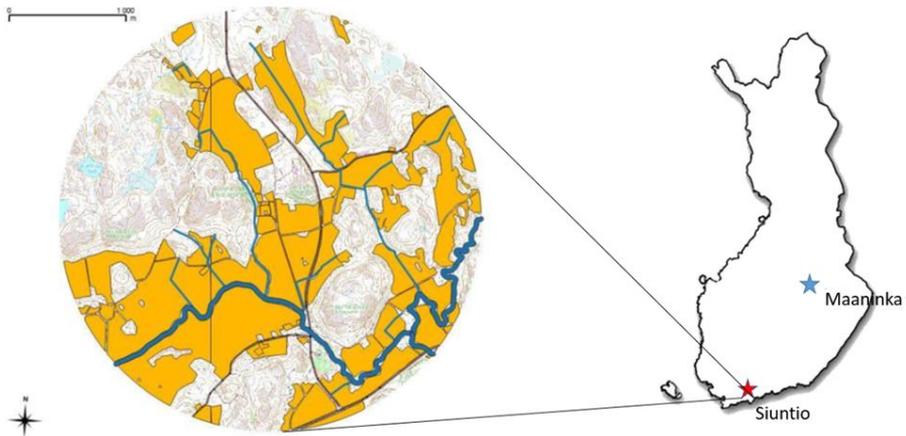
2 MATERIAL AND METHODS

2.1 STUDIES I AND III

We wanted to compare the survival, mortality factors, and reproduction of translocated hand-reared and wild pheasants in two study areas: in southern Finland where predator densities are high and in an area in central Finland where predator density is low (I). The work was conducted during 1995–2000 in Suitia in southern Finland (60°N, 24°E) and in Maaninka in central Finland (63°N, 27°E). We translocated hand-reared and wild pheasants to southern Finland and hand-reared pheasants to central Finland. Both areas consist of several hundred hectares of open agricultural landscape interspersed with small forest patches, wetlands and wastelands, and were thus suitable breeding habitats for pheasants. The distance between the two study areas is approximately 300 km in the north–south direction. The southern area has a maritime climate and usually less snow cover, so that the growing season begins earlier and lasts longer than in the northern area. This difference was accounted for in our study.

The Suitia area consisted of cultivated fields with a median field patch size of 1.9 hectares (Map 1). The patches were separated by open ditches. Cultivated crops were wheat, barley, oat, rye, rape, peas, and linseed. Several pastures and grasslands were also located in the area. Crops in Maaninka included the same species as Suitia, except for the pea. Maaninka also had small hemp fields that can offer good cover for pheasants after the brood phase. Similarly to Suitia, Maaninka had many pastures and grasslands, and small forest patches within the fields were typical.

We released a total of 77 (31 wild and 46 hand-reared) radio-marked pheasant hens in Suitia during the five study years, whereas we only released hand-reared pheasants in Maaninka, a total of 37 hens. The hand-reared hens in our study were reared from eggs originating from wild hens, so the hand-reared and wild hens were both of wild genetic origin. Study period length was determined at 13 weeks beginning on the day of the bird releases (I), or 31 days after the pheasant chicks hatched (III). All hens were marked with a leg ring and a necklace radio transmitter. The pheasants were monitored regularly during the study period. After brood hatching, the hens were tracked twice a day, for an average of 3–5 days per week. We compiled a habitat description of each observation from a 10 x 10-meter square. We collected information on habitat category, vegetation height in cm, vegetation density (1=very dense, 2=normal, 3= sparse), vegetation patchiness (1= even growth, 2= under 25% patches, 3= 25–50% patches, 4= over 50% patches), distance to forest and margin in meters, along with vegetation moisture (1= dry, 2= moist, 3=wet).



Map 1. Locations of the study areas on the map of Finland (I and III). The southern study area in Suitia (Siuntio county) was delineated as a circle with a radius of 1800 meters, equaling 1020 hectares. All yellow and dark blue areas were included in the study.

Habitats were classified into twelve categories: 1) grain fields 2) grasslands that are mowed twice during the summer 3) grain fields with undergrowth 4) pea fields 5) rape fields 6) other cultivated fields (potato, linseed, mustard, onions etc.) 7) pasture 8) field margin 9) garden 10) fallows (including meadows and set-a-sides) 11) forest 12) roads. To understand better the scale of habitat selection, we also collected a control sample with the same data but 50 meters in a random direction from the actual radio location of the brood.

When a pheasant was found dead, the cause of death was estimated by analyzing bite marks on the carcass or even on the transmitter. Brood size was estimated by counting the number of hatched eggs. Brood size was estimated again after two weeks by tracking the brood down with a visual sighting.

During the study years, we were able to collect sufficient data from 15 broods to conduct habitat analysis (III). We gathered a total of 458 observations. We counted home ranges with the minimum convex polygon estimate (Mohr 1947) (MCP95) for the broods for 10 and 31 days (Map 2). We divided the study area into the 12 habitat categories, removed those not used by pheasants, and counted the remaining surface areas for each habitat. Then we compared habitat use with availability at two levels. First, we examined home range selection within the entire study area by comparing the proportion of each habitat in the minimum convex polygon (MCP100) with that available in the study area. Secondly, we examined habitat use within home ranges by

comparing the proportion of radio locations in each habitat class with the availability of habitat classes within the home range (MCP100).



Map 2. Minimum convex polygons (MCP) for two broods for 10 days (purple polygons) and for 31 days (green polygons). Both polygons are MCP100, i.e. include all observations.

2.2 STUDY II

The fate of unsuccessful nesting attempts was often unclear in Study I, where we investigated the survival, mortality, and breeding success of adult hens, so we wanted to assess the threat faced by ground nests. We were interested in the species depredate eggs, along with how the landscape – i.e. distance to forest edge – affects the depredate rate of the nests.

Studies with artificial nests usually mimic the egg-laying period (nest uncovered), while data of real nests usually only cover the incubation period. This makes a comparison between real and artificial nests very challenging. Other sources of bias are also present in the comparison. For example, Willebrand and Marcström (1988) state that artificial nests lack the scent of the incubating hen and are therefore more difficult for mammalian predators to locate, which may then exaggerate the role of avian predators. Jahren (2017) showed that black grouse (*Lyrurus tetrix* L.) and capercaillie (*Tetrao urogallus* L.) defend their nests against corvids, and avian predation was therefore much less common in his study than earlier suggested in studies with artificial nests.

Nest predation studies with artificial nests show both less and more predation occurring on artificial than natural nests (Major and Kendal 1996; Thompson and Burhans 2003). Major and Kendal (1996) calculated an average nest success of 41% for artificial nests and 51% for natural nests. Predation rate was higher at artificial nests in 14 out of 20 studies. The authors also stated that different artificial nest setups may attract differing predator populations, and care should therefore be taken when interpreting the results. Artificial nests therefore cannot be used to estimate the predation rates of natural nests. However, they can provide data on nest predator species and insights to spatial and temporal trends in the predation of artificial nests that may bear some meaning for natural nests.

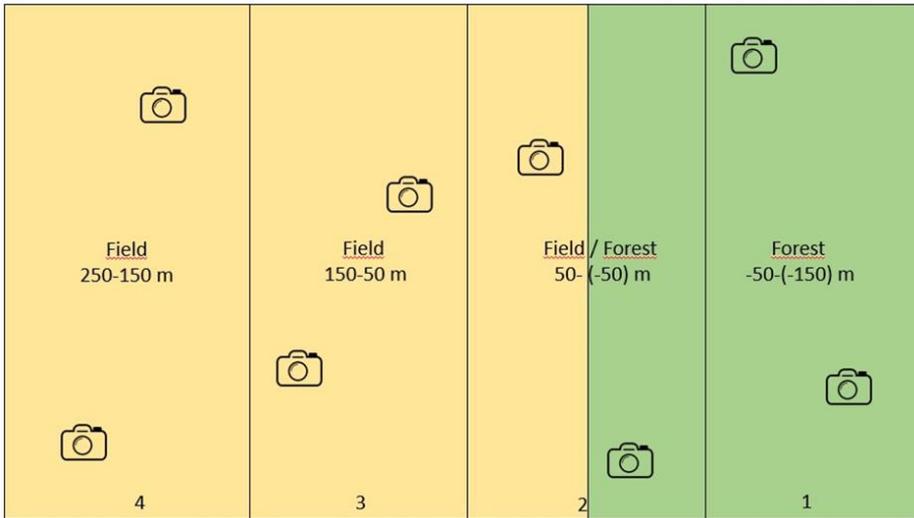
We wanted to develop methods for studying nest predation on a landscape level and for predator identification, which earlier studies have shown to be rather unreliable (e.g. Larivière 1999; Thompson and Burhans 2003). The use of artificial nests allowed us to build a study protocol where we could easily compare the effect of distance to forest edge with predation. We placed the nests on a fairly wide scale from the edge into the forest and into the open field, and we kept nest density low to avoid density-dependent nest predation (Gunnarsson and Elmberg 2008). Wildlife camera traps installed at the nests enabled predator identification and elucidated the fact that one nest can be visited by several predators during a short time. Identifying the initial nest predator would have been impossible without camera traps.

The work was conducted in southern Finland at 12 locations during 2015–2016. The study areas are located south of the glacial esker running southwest to northeast through Finland in Länsi-Uusimaa (approximately 60° N, 24° E), except for one area located north of the esker. These areas are lowlands with hills, forest patches, small lakes, and rivers with smaller waterways. Because of the Finnish climate and high yearly precipitation, all fields are drained, and larger fields are usually separated by open ditches, creating narrow edge areas along field boundaries. Spring wheat, spring barley, spring oats, and rye are the most common crop types, along with oil seed crops, and peas. The majority of fields are ploughed during October and sown again in May. Grasslands are also common for feed production and grazing, as well as set-a-side land.

All areas consisted of fragmented agricultural landscapes. Having open field patches at least 500 m in width was one main criterion for choosing an area, as this allowed us to place a camera 250 m from the forest if necessary. In addition, the areas also required forest patches at least 300 m in width, allowing us to place cameras within the forest, 150 m from the forest edge.

We used artificial nests with four pheasant eggs in each. We received data from a total of 104 nests (eight nests/study site, one study site was used for two

consecutive years, hence 13 experiments). All nests were placed at sites where a pheasant hen could possibly lay a clutch (based on our own experience from earlier pheasant and duck studies (see Kallioniemi et al. 2015 (I) and Väänänen et al. 2016)). Our study protocol had four sample gradients in each of the areas that we randomly set nests in. To test the forest edge effect, the sample gradients were divided into four zones ranging from inside the forest to the open field: (1) (-150 to -50 m), (2) (-50 to +50 m), (3) (+50 to +150 m), and (4) (+150 to +250 m) (Pic. 2). The edge between forest and field was marked as 0 m.



Picture 2: The four distance zones from forest to field (1) (-150 to -50 m), (2) (-50 to +50 m), (3) (+50 to +150 m), and (4) (+150 to +250 m). Two artificial nests with wildlife cameras were placed in each zone, the exact nest location was randomized within the distance zone. The picture is figurative, in actual the nests were located over the whole study area and the minimum distance between nests was 150 m.

Each nest site was equipped with a light-triggered passive wildlife camera (Swann et al. 2011), approximately 1.5 m away from the nest. The experiment was carried out between the beginning of May and the end of July in 2015 and 2016, as this is the time span during which pheasants and many other ground-nesting birds tend to nest. The nests with cameras were kept in one place for eight days.

All predators visiting the nests were recorded. The first predator at the nest was classified as the primary predator and was included in our further analyses if it depredated at least one egg. Other predators were classified as second, third, and fourth predators, and so on. They were counted as predators if they depredated eggs that were left by the first predator or even if they just

scavenged or searched for egg remains at the nest sites. Repeated visits of the same species were counted as new visits with an interval of 24 h.

2.3 PREDATORS IN THE STUDY AREAS

Ground-nesting birds and their nests are popular prey items during the breeding season for many common species in Finland. Mammalian predators present in all the study areas (I, II, and III) were the red fox, raccoon dog, American mink, European pine marten (*Martes martes* L), stoat (*Mustela erminea* L.), European badger (*Meles meles* L), and the domestic cat (*Felis catus* L.). Avian predators included corvids, such as the hooded crow (*Corvus corone cornix* L.), raven (*C. corax* L.), Eurasian jackdaw (*C. monedula* L.), and Eurasian magpie (*Pica pica* L.), along with the Eurasian eagle owl (*Bubo bubo* L.) and western marsh harrier (*Circus aeruginosus* L.). Northern goshawks (*Accipiter gentilis* L.) were also present from August onwards. Two species of snakes were also present, the common European viper (*Vipera berus* L.) and the grass snake (*Natrix natrix* L.), both of which may be able to eat pheasant eggs. In addition, several deer species inhabit the areas, who are also known to predate bird eggs when given the opportunity: European roe deer (*Capreolus capreolus* L.), white-tailed deer (*Odocoileus virginianus* Zimmermann), and fallow deer (*Dama dama* L.; in five study areas (II)).

Of the listed predators, we focused on mammalian predators, which are common throughout southern Finland (Lindén 1996a). Most mammalian predators are hunted during species-specific hunting seasons in fall and winter. According to local hunters in Siuntio (Suitia study area), the hunting pressure on all listed predators was very low, as only a few raccoon dogs were reported killed annually. In Maaninka, the local hunters were very active in controlling mammalian predators, so the numbers of red fox and raccoon dog were low during the pheasant nesting season (Kauhala 1996). In studies I and III, the abundances of mammalian predators were estimated during the wintertime using the Finnish wildlife-triangle-scheme (WTS) (Lindén 1996a). Both areas had available wildlife-triangle data for the red fox, pine marten, and stoat (Lindén 1996b). We excluded the pine marten from our analyses and concentrated on the abundance differences of the red fox and stoat, as the pine marten is a forest species and does not inhabit cultivated fields in our study areas (Fig.2). The raccoon dog and badger are dormant over winter, so they are not included in the WTS. In study II, we used signposts (Kauhala 2004, Sálek et al. 2010) monitored with wildlife cameras to investigate the numbers and species of mammalian predators present in our study areas. Signposts do not attract avian predators. Signposts were placed after the artificial nest experiments on the same study sites using the same four distance zones in relation to forest edge. We placed four signposts per area, 52 cameras in total.

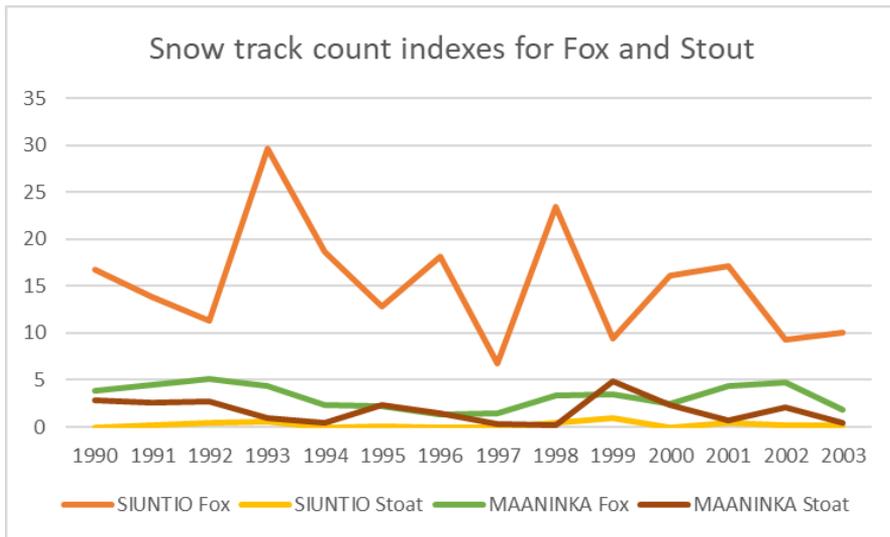


Figure 2. The Finnish wildlife-triangle-scheme (WTS) estimates for mammalian predator abundances during the wintertime through a snow track count index. There is a significant difference between our study areas in the fox snow track counts (Wilcoxon, $Z=-3.296$, $P=0.001$): the highest value for foxes in Maaninka (5.1) is lower than the lowest value in Siuntio (Siuntia study area) (6.8). The mean for all years shows that the fox track index for Siuntio is nearly five times higher than for Maaninka. The stoat was detected only very seldomly in Siuntio.

3 RESULTS AND DISCUSSION

Although the pheasant is an introduced alien species and therefore not of major conservation concern, it is recognized as being a part of the avifauna in our cultural landscape (Luonnontila 2021). The decline of the pheasant's natural population may not be considered a threat to biodiversity per se, but the fact that pheasant populations are declining along with other bird species should be taken seriously. The factors affecting pheasant success are similar to those of the very widely studied partridge, i.e. the loss of suitable habitats and increased predation (Hill 1985; Potts 1986; Jorgensen et al. 2014; Ronnenberg et al. 2016; Robertson et al. 2017; review by Taylor et al. 2018). The diets and nutritional requirements of pheasant and partridge chicks overlap markedly. Both species are dependent on a high-quality arthropod diet during the first 3-4 weeks of life. Both have been found to prefer Delphacidae, Heteroptera, Coleoptera, Symphyta, and Lepidoptera larvae, and do not prefer Araneae (Hill 1985; Itämies et al. 1996; Green 1984; Potts and Aebischer 1995). The quality of the diet is linked to chick development, especially to their feathers and body condition, which are linked to the ability to flee from predators and to withstand cold and rainy weather, in other words, survival. Pheasant brood success could thus be used as an indicator of a farmland providing high-quality arthropods as well as of a predator-safe environment, especially in areas where native partridges are absent.

3.1 SURVIVAL AND BREEDING OF INTRODUCED WILD AND HAND-REARED PHEASANT HENS

3.1.1 HEN SURVIVAL

We found that both bird origin, bird quality, and predator density affected pheasant survival. These findings are in concert with earlier studies (Hessler et al. 1970; Hill and Robertson 1988a; b; Krauss et al. 1987; Brittas et al. 1992; Leif 1994; Wilson et al. 1999; Musil and Connelly 2009). However, our comparisons (I) between the success of hand-reared and wild pheasants were performed in such a study setup that we could distinguish in more detail the differences in the chances of success between hand-reared and wild pheasants. The hand-reared birds in this study were of the same genetic origin as the wild birds, so they offered a nice pair for comparison between our two study areas with very different predator abundances, in this case the red fox. On the other hand, the wild translocated birds in Suitia provided a very good comparison

on the effect of bird quality versus predator abundance between the two areas, and on bird quality versus the effect of translocation on the birds. Earlier studies have often compared wild birds already familiar with the area with introduced hand-reared birds. In such studies, it is impossible to determine whether the fitness of the wild birds is caused by better adaptation to the environment regarding predators and nutrition or by the quality of the birds per se.

The introduced hand-reared birds survived well throughout the study period in Maaninka, whereas their Suitia counterparts suffered high predation during the first two weeks. The difference in depredation rate between the study areas was over threefold. The wild birds in Suitia survived similarly to the wild birds in Maaninka, both groups had a very steady death rate over the study period (Fig. 3). The death rate of the hand-reared birds in Suitia evened out after a few weeks. When excluding the first two weeks of our study, we could not find any statistically significant difference between survival of any of the bird groups. Many game bird studies have reported a high death rate for hand-reared birds during the first weeks after release (Potts 1980; Musil and Connelly 2009).

I note that survival does not necessarily solely concern the behavioral differences between hand-reared and wild pheasants. Putaala (1997) studied the differences between hand-reared and wild partridges and stated that released birds, lacking both behavioral and physiological preconditions to use natural food, may thus initially be forced to focus on maintaining a positive energy and nutrient balance at the cost of an increased predation risk. Hoodless et al. (1997) found that released pheasants that were given supplementary wheat spent proportionally less time actively foraging for food and more time being alert compared with pheasants without supplementary food. In our study, we tried to tackle this problem by keeping both groups of birds in the same pens under similar conditions for three months prior to release.

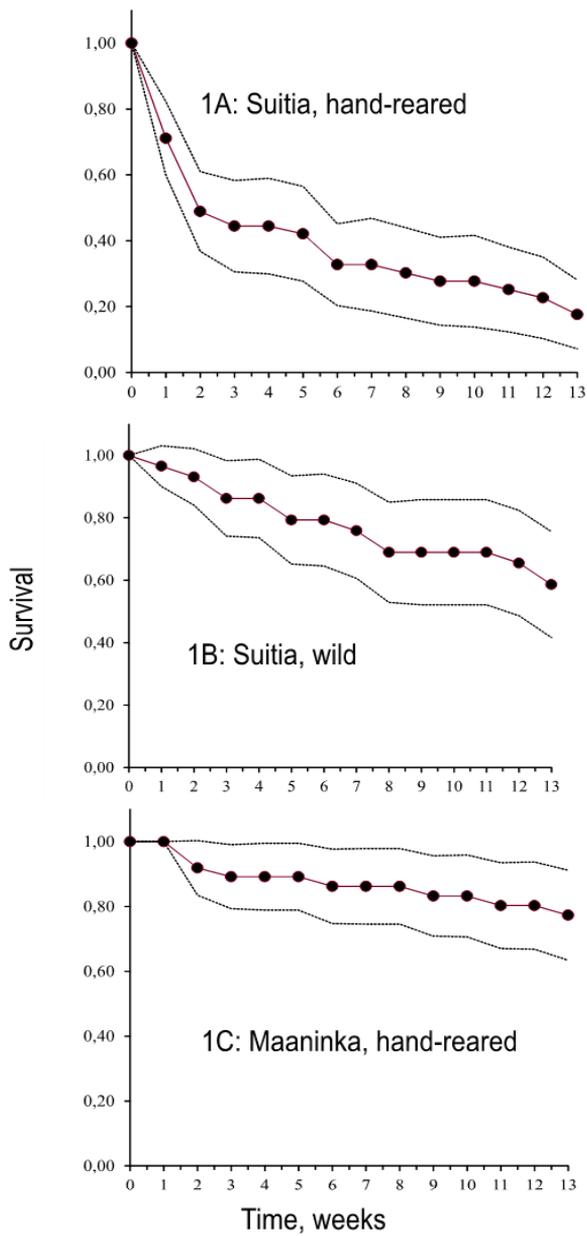


Figure 3. Pheasant hen survival during a 13-week period after release based on the Kaplan-Meyer method. Dotted lines represent the 95% confidence interval for survival, (A) represents the hand-reared hens in Suitia, (B) the wild hens in Suitia, and (C) the hand-reared hens in Maaninka (I).

3.1.2 BREEDING SUCCESS

Hens at both locations attempted to begin nesting within one week of release. No significant differences were observed in nesting success between the groups of birds that managed to begin nesting (I). Nesting was considered successful if the chicks survived to one day of age.

The hand-reared pheasants in Maaninka were significantly more successful at producing six-week-old chicks than the hand-reared birds in Suitia, but only when excluding the very rainy year 1998, when the Maaninka broods failed completely. In Suitia, three (38%) of the hand-reared birds that had managed to hatch a clutch managed to raise their broods to the age of six weeks. Of the wild birds in Suitia, 13 (81%) managed to raise a brood to the age of six weeks. A nearly significant difference was observed between brood survival to the age of six weeks in Suitia (hand-reared versus wild). No difference was observed between the hand-reared birds in Maaninka and the wild birds in Suitia (I).

The proportion of hens with chicks was rather high in Maaninka, especially if 1998 is left out (I). Summer 1998 was very rainy and cold, so the pheasants in Maaninka completely failed in their attempts to produce over six-week-old broods. In the following two study years, weather conditions were closer to average and the Maaninka birds managed to produce broods surprisingly well. It seems that weather played a more important role than predation in terms of brood survival in Maaninka.

Finally, we found no significant differences in brood production success between the groups of birds that managed to begin nesting (I). These results show that even hand-reared pheasants can breed successfully, especially if red fox numbers, the main predator of pheasant hens, are low and weather conditions are not too averse. Our findings are in concert with Leif (1994), who found that if a hen of hand-reared origin manages to hatch a clutch, it has almost as good of a chance of raising the brood as wild birds do.

3.2 WHO TAKES THE NESTS? DEPREDATION OF ARTIFICIAL COMMON PHEASANT NESTS

We found that nest predation was fairly equally distributed over the forest–field gradient (II) (Fig. 4). However, when testing bird and mammalian predation separately, we found that birds preyed on field nests further away from the forest (Fig. 5, II). Mammalian predation was not explained by the forest–field gradient, while, on average, their predation appeared to be more active closer to the edge, both in the field and forest. However, we did observe that nests closest to the forest edge had the highest survival rate.

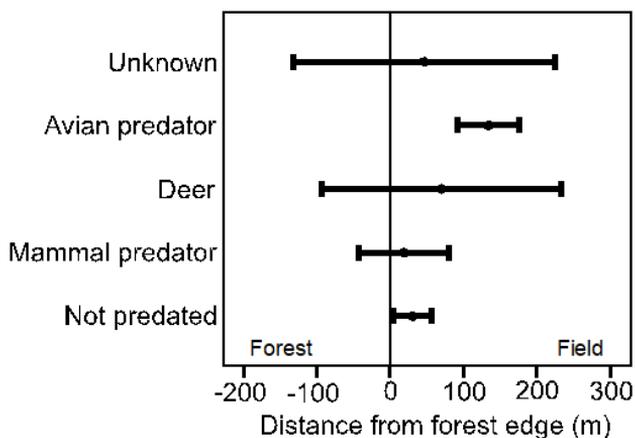


Figure 4. Mean distance from the forest edge for both predated and unpredated nests. Negative values indicate nests within the forest while positive values are from the field. The edge is presented as the zero line. Groups include observations as follows: unpredated n = 63, mammalian predators n = 12, roe deer n = 4, avian predators n = 21, unidentified n = 4. The circles represent the mean and the whiskers the 95% confidence intervals (II).

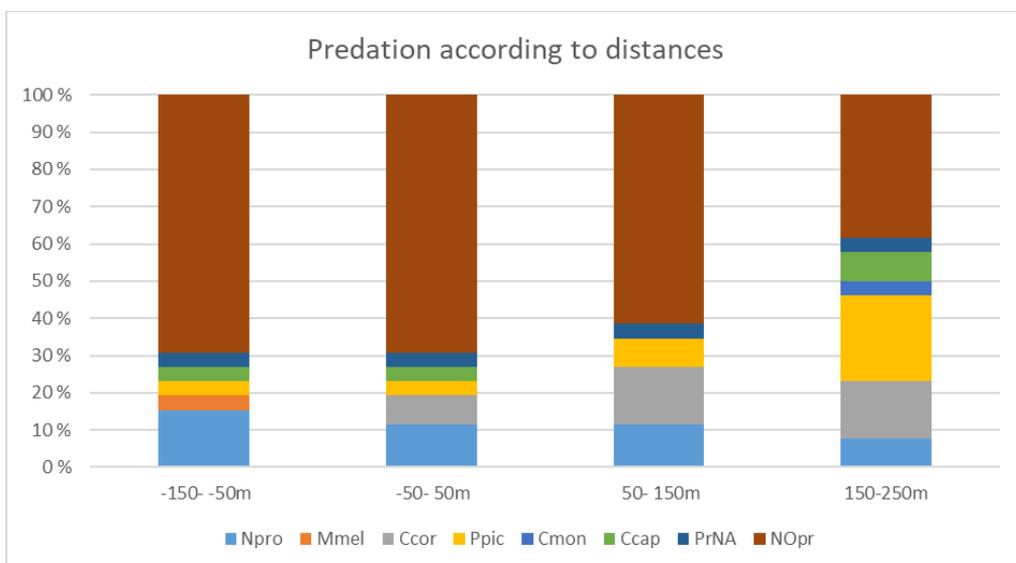


Figure 5: Predation of artificial nests (n=104) according to the distance classes. "Zero meter" distance indicates the edge between forest and field. Predators are indicated by abbreviations of their scientific names: Npro= Raccoon dog, Mmel= Badger, Ccor= Hooded crow, Ppic= Magpie, Cmon= Jackdaw, Ccap= Roedeer, PrNa= predator not identified, NOpr= Not predated.

Of the 104 artificial nests, almost 40% (n=41) were predated or destroyed during the eight-day study period. Of the 41 cameras, four failed to capture a single predator. Mammals were responsible for 39% (n=16) of the predated (or destroyed) nests, whereas corvids took 51% (n=21). This is in line with earlier and recent studies showing that corvids are effective nest predators (Andrén 1992; Holopainen et al. 2020a; 2020b). However, contrary to earlier studies (Kauhala et al. 1998; Kauhala 2004), our study with wildlife camera traps implies, for the first time, that the raccoon dog may be a common predator of ground-nesting bird nests in agricultural landscapes in Finland; raccoon dogs were responsible for 27% (n=11) of the total predation and 69% of mammalian predation. The raccoon dog population in Finland expanded in the 1980s to its current distribution range (Kauhala and Kowalczyk 2011), but the hunting bag has steadily increased since then (Fig. 1). Of course, it is important to bear in mind that my study used artificial nests that cannot be used to estimate the predation rates of natural nests (Major and Kendal 1996). However, artificial nests can provide data on possible nest predator species and may provide information of the spatial and temporal trends of predation, which may at least partly be applicable to natural nests.

The wildlife camera setup (II) allowed us to determine the exact date and time of predation, and we found that mammals and birds did not differ significantly in the time needed to locate a nest. Overall, we found evidence that the probability of daily survival increases with time; a response to this phenomenon has previously been shown experimentally by Gunnarsson and Elmberg (2008). Many authors have speculated on the reasons for the increase in nest survival with age. Davis (2005) suggests that increased concealment due to vegetation growth may be a positive factor for certain species. We also found a connection with visibility and predation. Hooded crows mainly preyed on open nests (predation rate = 0.9), whereas 40% of the nests depredated by magpies were covered. Nest visibility did not explain predation by mammals. Nest placement may also be a plausible explanation for the increase in nest survival with age, especially for artificial nests. Placing a nest close to paths used by predators may increase the early detection of a nest. Placing a nest in a place where other prey is plentiful, such as earthworms or rodents, may also increase early nest detection. And, vice versa, if a nest is not found during the first days, it may be placed outside the usual movement zone of predators. For example, field margins are preferred as movement corridors by predators compared with adjacent hay fields (Sálek et al. 2009). On the other hand, nest predation risk has been shown to decrease in field patches that are over 25 m wide (Gottschalk and Beeke 2014).

Half of the nests that were predated were visited more than once, often by several species (Fig. 6). The raccoon dog was the most common primary nest predator, and it was also the most common predator observed later on at the

nests. On many occasions, the predators were of the same species, in certain cases possibly even the same individuals returning to recheck the nest. This could be interpreted as the primary predator returning to the nest to see whether the female had laid new eggs. Nest predation may be compensatory in complex ecosystems, and the removal of one predator species may have no or even a negative effect on total annual nest survival (Bolton et al. 2007; Ellis-Felege et al. 2012). The abundance of nest visitors elucidates the importance of accounting for this when planning predator removals. On the other hand, the study by Holopainen et al. (2020b) on artificial duck nests shows that initial avian predators may facilitate secondary mammalian predation, which may elevate the mortality risk of incubating females.

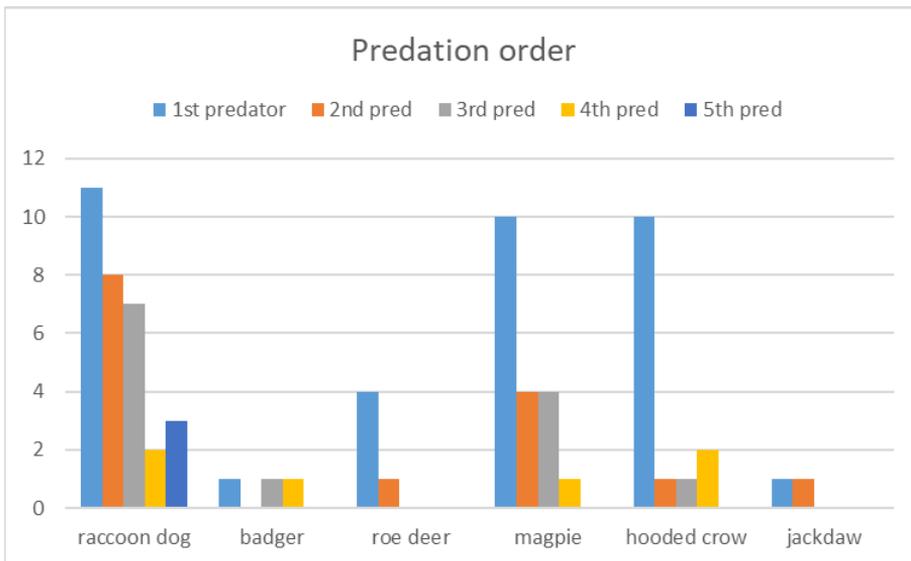


Figure 6. Order of predator visits (n=37).

We did not observe predation by red foxes and only one case of predation by badgers, despite these two species often being regarded as the main nest predators (Newton 1998; Draycott et al. 2008; Carpio et al. 2016). Signpost trapping verified the presence of red foxes in only four of our study areas, despite foxes being monitored in these areas through the annual WTS. The artificial nest and camera trap setup may be too suspicious for the wary red foxes and a study period of eight days too short a time for the foxes to become adjusted to the setup. The same applies to the signposts, which were only present for five days. On the other hand, recent studies have witnessed fox predation on similar camera trap setups in Denmark and also in Finland (Holopainen et al. 2021). Signpost trapping in our study showed that the raccoon dog was the most common predator on the signposts, and the signpost visits correlated with the predation rate of the area (II).

3.3 COMMON PHEASANT BROODS PREFER FIELD MARGINS, FARMLAND BIODIVERSITY HOTSPOTS

Many studies have demonstrated the value of field margins as biodiversity reservoirs (e.g. Chiverton and Sotherton 1991; Helenius et al. 1995; Meek 2002; Vickery et al. 2002; Ekroos et al. 2019; Martin et al. 2019). Our study showed field margins to be an important and preferred habitat for pheasant broods. When comparing habitat use to habitat availability (Fig. 7), field margins were the most preferred habitat, even though most observations were made in grain fields (n=199, 43.6% of the total observations).

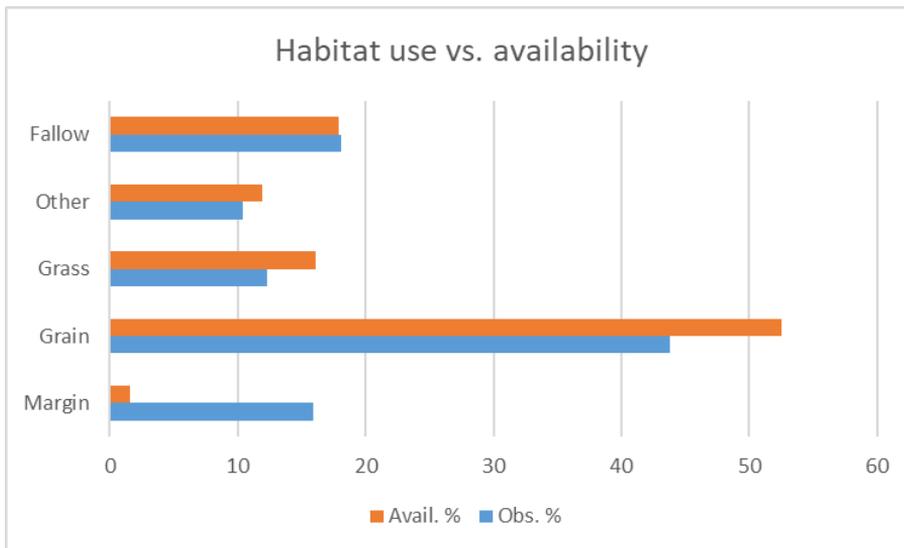
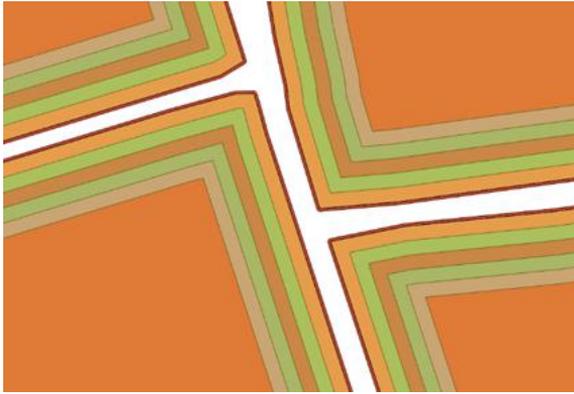


Figure 7. Brood observations divided into the following categories: "Grain", "Grass" (grasses, pastures), "Other" (pea, rape, linseed, and potato fields), "Margin" (field margins), "Fallow" (gardens, meadows, fallows), and their proportions of the total observations (n= 456) compared with the proportions of available habitat (430.6 ha) (III).

Besides field margins, we found that even proximity to field margins was preferred. Cumulative observations showed that 68% of the observations on grain fields were within a 25-m zone from the field margin (Pic.3), even though it only represents 40% of the available field area. Only 32% of the observations were over 25 m from the field margin, although this area represented 60% of the field area available (Fig. 8). This suggests that the combination of margin and grain field offers an ideal habitat for pheasant broods that require high-quality arthropods and shelter.



Picture 3. Field buffer zones from the field margin, white= road, dark red= field margin (1 m), other colors= buffer zones 0–25 m (5 m each) and inner area (>25m).

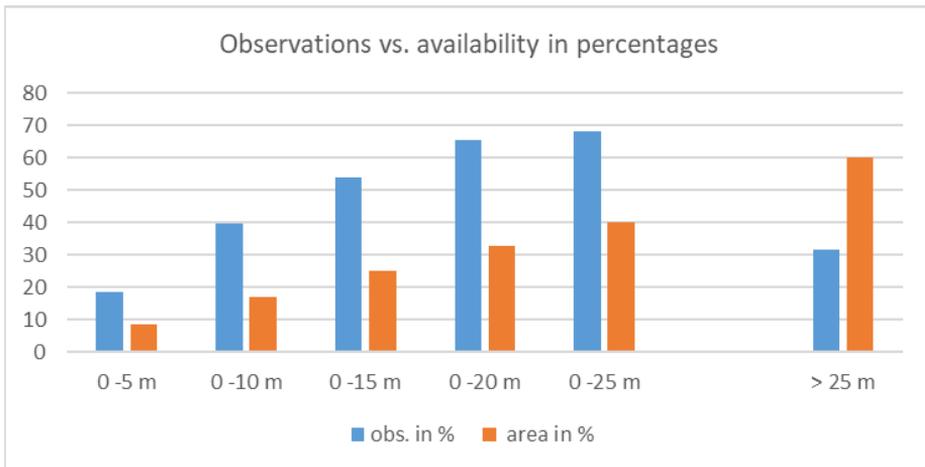


Figure 8. Cumulative number of observations in grain fields divided into distance zones from the field margin (0–25m) and the number of observations over 25 m from the field margin compared with the area over 25 m from the field margin.

Comparison between the control points and actual observations showed that broods prefer vegetation that is not too dense but not completely open either (Fig. 9) (unpublished data). Broods may prefer patchy vegetation because openness in a cultivated field may indicate weed sprouts and a more suitable microclimate in the harsh boreal climate, i.e. warmer and dryer. Segetal vegetation is needed for arthropod habitat (Potts 1986), but bare ground offers movement corridors for young pheasants, where they can capture prey and avoid predators (Doxon and Carroll 2010). The concept of offering habitat containing both cover and open patches has proven effective when restoring partridge habitats in the North Sea Partridge Project (Brewin et al. 2020).

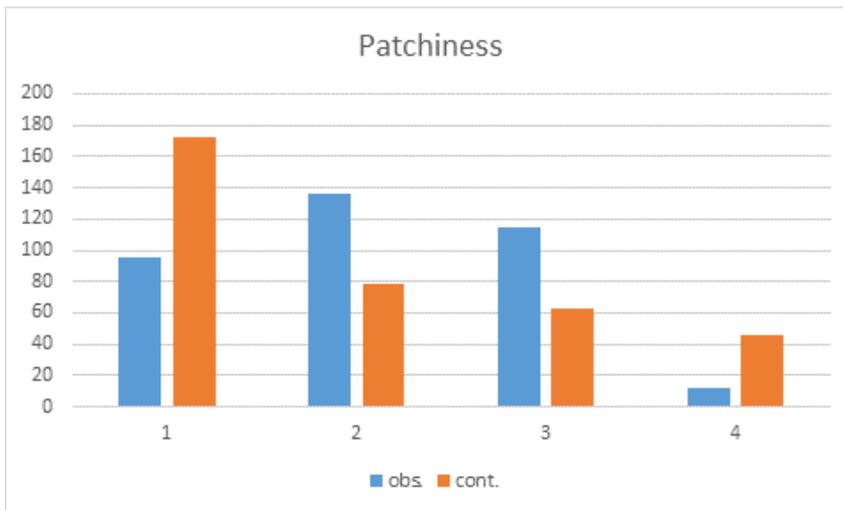


Figure 9: The vegetation patchiness data shows that the observations were gathered to vegetation with patches, i.e. classes 2 and 3 (Pearson's Chi-squared test, $\chi^2 = 77.026$, $p < 0.001$). Patchiness classes: 1= even growth, 2= under 25% patches, 3= 25–50% patches, 4= over 50% patches, y-axis indicates the number of observations.

A pheasant brood leaves the nest within one day after hatching. In our study (III), the broods quickly found good-quality home ranges. This was indicated by the rather small home ranges that the broods in our study occupied. Warner (1984) showed that brood movements were much greater, and home ranges larger, in broods feeding on large monoculture blocks, than in those feeding within a more diverse complex of farming, where insect densities would be expected to be higher. Habitats selected by broods largely reflect the levels of arthropod food that they contain (Hill 1985).

The broods reached their home ranges within two days on average, after moving an average 185 meters from the nest. The average distance from the nest to the home range centroid was 239 meters. It is possible that during the incubation period hens search for areas that offer good invertebrate supply and other suitable habitat characteristics for the brood, and then guide the chicks there as quickly as possible. Such behaviour has been shown in ducks (Casazza et al. 2020).

Larger home ranges have been connected to heavier chick mortality and have also correlated with fewer arthropods (Warner 1979; Hill 1985). Earlier studies have shown rather large home ranges for 10-day-old broods, spanning from ca. 5 to 11 hectares (Hanson and Progulské 1973; Warner 1979; Hill 1985). Even though our value of 1.4 ha (0.2–3.0 ha) for 10 days can be used as descriptive only because of the small number of observations, it seems that the

broods in our study quickly found good-quality home ranges. Warner (1979) showed that a brood's home range increases as the chicks grow. This could also be seen in our results. Home ranges at 31 days were larger in our study, 6.1 hectares on average (median 4.8 ha), but even then, they were rather small. Riley et al. (1998) observed broods for 28 days in the US on two row crop production areas for five years, and their results showed average home ranges of 66 and 76 hectares, (range 15–179 ha).

One explanation for the smaller home ranges in our study may be that pesticide use is not as intensive in Finland, according to FAO (2020), as in the US (five times more per ha) or in Europe (UK/France) (ten times more per ha), so arthropod communities are not as disturbed (Stoate et al. 2009). The small average field patch size in our study area increases the amount of margin area, 15 km/100 hectares in our study, which increases diversity per se. The edge-to-area ratio has been connected with high biodiversity value (Ekroos et al. 2019; Martin et al. 2019). The pheasant broods in our study showed a clear preference for margins, and the proximity of margins was preferred even in grain fields, indicating the high biodiversity value of margins supported by earlier studies (Meek et al. 2002; Vickery et al. 2002).

3.4 FOREST AS A LANDSCAPE STRUCTURE FOR COMMON PHEASANT BROODS

Spatial scale matters when investigating avian communities (Wiens 1989). We must scale out from the habitat requirements of individuals to observe processes that drive biodiversity and are governed by landscape composition. These processes are affected by the amount of semi-natural habitats in the landscape, and, on the other hand, by landscape configuration, such as the amount of field margins. Both factors affect ecological processes independently and interactively (Fahrig et al. 2011). Landscape structure may have more of an impact on the success of a certain species than suitable habitats, such as field margins, have on a smaller scale (Bennett 2006, Frei 2018). For instance, taxonomic richness and diversity of invertebrates in field edges has been observed to be positively related to large scale landscape complexity (Evans et al. 2016).

Sasaki et al. (2020) noted the importance of open land in maintaining farmland biodiversity in a forest-dominated landscape. Cunningham and Johnson (2019) showed the high intolerance (stenotopicity) of grassland birds for unsuitable habitat presence (tree cover) on a landscape level. Grassland-nesting birds appear to avoid woody edges and trees (Bakker 2003; Ellison 2013).

In my study, the mean distance from radio locations to “Forest” was 90.4 m (SD 82.16, Min 10, Max 500). Of the total study area, 54% was defined as “Forest”. Jorgensen et al. (2014) found that “Forest” habitat in a landscape was a limiting factor for pheasants, probably because of predators. Trees serve as perches for predators, e.g. for birds of prey and nest-predating corvids that can be important nest predators of ground-nesting birds, and tree-covered areas provide dens and travel corridors for mesopredators such as the red fox, badger, raccoon, and raccoon dog (Andrén 1992; Ellison 2013; Krüger et al. 2018; Holopainen et al. 2020a). It is therefore crucial to understand that despite such habitats potentially being suitable for brood rearing, predation pressure from the surrounding landscape elements may limit success.

4 CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our results (I) with hand-reared birds in a low-predator area show that introductions using hand-reared birds can be successful as long as the risk of predation is low and provided that other circumstances are favorable, such as nesting and brood-rearing habitats required for successful brood production. The two first weeks are the most vulnerable time for introduced birds. Effective predator control and supplementary feeding during the first weeks may provide hand-reared birds in particular time to adjust to the new environment and thereby enhance their possibility of surviving and reproducing.

The information gained by our study is useful for planning the introductions of hand-reared birds, whether they be reintroductions of endangered Galliformes or bird introductions for game management purposes. Minimizing bird mortality at the very beginning is crucially important, as we found no significant differences in brood production success between the groups of birds that managed to begin nesting; this indicated relatively good fitness of even the hand-reared birds. Besides predator control, other methods that improve the survival of farmland ground-nesting birds and their nest survival should be applied. These include training hand-reared birds to be more fearful and to seek cover (Krauss et al. 1987; Griffin et al. 2000) and landscape management methods providing safer nesting environments (Gottschalk and Beeke 2014). Recent studies have even attempted to teach mammals to avoid eating ground-nesting bird eggs (Tobajas et al. 2020; Norbury et al. 2021).

Predator communities change with time, and both alien and invading species may take their share of the prey community across Europe. Our results from the nest predation trials (II) indicate that, apart from the previously known mammalian nest predators (the red fox and badger), raccoon dogs are important nest predators in agricultural habitats. The raccoon dog is an alien species invading Europe; it is very opportunistic in its diet and difficult to eradicate (Genovesi et al. 2009; Kauhala and Kowalczyk 2011; DAISIE 2018). In 2017, the European Commission added the raccoon dog to the list of invasive alien species of Union concern (EU IAS 2017). However, minimizing its detrimental effects to ground-nesting birds is time-consuming and requires good trapping technics, along with specially trained dogs and very efficient and engaged hunters that are willing to invest time and effort into a long-term eradication project.

On the other hand, European Union countries currently face the return of all large mammalian apex predators, such as the gray wolves (*Canis lupus* L.) and Eurasian lynxes (*Lynx lynx* L.), as a result of the strict protection assigned to these species in accordance with the EU habitats directive (1992). In addition, even an expansion of the golden jackal (*Canis aureus* L.) range has been observed from the east. The increase of these predators may affect mesopredators and balance out the increased predation pressure on ground-nesting birds, at least to some extent (Prugh and Sivy 2020; Selonen et al. 2022). Simultaneously, the seriousness of the threat that invasive alien predators potentially pose on biodiversity has become clearer, and urgent actions to control their populations have begun across the continent (Brzeziński et al. 2019; Koshev et al. 2020; Holopainen et al. 2021; Pöysä and Linkola 2021). Because of the multitude of ongoing changes in the environment, in agricultural activities, and in species interactions, the future status of the predation pressure affecting birds breeding on farmlands is difficult to forecast. The threat of invasive predators must be taken seriously and necessary control methods applied.

Understanding how nest predation is related to habitat characteristics within a managed landscape, especially those characteristics that may affect predator abundance and behavior, provides useful information for determining how future management practices will affect the breeding success and survival of ground-nesting birds in agricultural landscapes. This information is also crucial in the objective of halting biodiversity loss by 2030, a target set by the EU (EU Publications Office 2020).

We found that pheasant broods preferred field margins over all other farmland habitats. On an area-for-area basis, field margins are effective at providing food for birds (Vickery et al. 2002) and could easily be integrated with whole-field management practices. Tews et al. (2004) define a “keystone structure” as a distinct spatial structure providing resources, shelter or ‘goods and services’ crucial for other species. Margins adjacent to croplands can be counted as such and may be a cost-efficient way to preserve biodiversity even under intensive farming practices, when integrated with low-intensity practices, such as methods that aim to minimize pesticide application near margins (Vickery et al. 2002). Agricultural areas, especially with small grain crop cultivation, which are considered to enhance pheasant success (Jorgensen 2014), may have great potential in providing more biodiversity. However, land use intensification methods that reduce the open-field ditch-bank habitat, such as subsurface drainage, (Helenius et al. 1995), must be compensated for with e.g. beetle banks and flower strips, and other biodiversity enhancing methods (Brewin et al. 2020).

The habitat preference of the pheasant broods in our study is closely related to the biodiversity loss agenda and to the success of many other farmland birds.

The need to begin appreciating field margins as vital biodiversity elements in agricultural landscapes is underlined by Ekroos et al. (2019), who found that field edge densities had a much stronger effect on farmland bird diversity than the agri-environmental scheme (AES) measures they studied. The analysis by Martin et al. (2019) connected edge density to higher functional biodiversity as well as to higher yield-enhancing ecosystem services in European landscapes. Reducing crop field sizes and thereby increasing the amount of margin and structural diversification instead of focusing on set-asides and organic farming is recommended as solution to halting the loss of biodiversity (Sirami 2019, Clough 2020, Salék 2021). Considering these results, changes in agricultural policy towards favoring the biodiversity-boosting effects of margins and their surroundings should be obvious.

REFERENCES

- Aebischer, N. J., 2019. Fifty-year trends in UK hunting bags of birds and mammals, and calibrated estimation of national bag size, using GWCT's National Gamebag Census. *European Journal of Wildlife Research* 65(4). <https://doi.org/10.1007/s10344-019-1299-x>.
- Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325. <https://doi.org/10.2307/1940062>.
- Aebischer, N.J., Ewald, J.A., 2004. Managing the UK grey partridge *Perdix perdix* recovery: population change, reproduction, habitat and shooting. *Ibis* 146, 181–191. <https://doi.org/10.1111/j.1474-919X.2004.00345.x>.
- Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. *Agriculture Ecosystems and Environment*. 74, 19–31. [https://doi.org/10.1016/S0167-8809\(99\)00028-6](https://doi.org/10.1016/S0167-8809(99)00028-6).
- Andrén, H., 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73, 794–804. <https://doi.org/10.2307/1940158>.
- Bakker, K.K., 2003. The effect of woody vegetation on grassland nesting birds: An annotated bibliography. *Proceedings of the South Dakota Academy of Science* 82: 119–41.
- Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation* 133:250–264. <https://doi.org/10.1016/j.biocon.2006.06.008>.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18, 182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9).
- Bern Convention 1979. <https://www.coe.int/en/web/bern-convention>.
- BirdLife International 2015. European List of Birds. Luxembourg: Office for Official Publications of the European Communities. <http://www.birdlife.org/datazone/info/euroredlist>. Accessed 3 May 2021.
- Bolton, M., Tyler, G., Smith, K., Bamford, R., 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology* 44, 534–544. <https://www.jstor.org/stable/4539271>.
- Brewin, J., Buner, F., Ewald, J., 2020. Farming with nature – promoting biodiversity across Europe through partridge conservation. The Game and Wildlife Conservation Trust, Fordingbridge, UK.
- Brittas, R., Marström, V., Kenward, R.E., Karlbom, M., 1992. Survival and breeding success of reared and wild ring-necked pheasants in Sweden. *The Journal of Wildlife Management* 56, 368–376. <https://doi.org/10.2307/3808836>.

- Brzeziński, M., Zmihorski, M., Nieoczym, M., Wilniewicz, P., Zalewski, A., 2019. The expansion wave of an invasive predator leaves declining waterbird populations behind. *Diversity and Distributions* 26, 138–150. <https://doi.org/10.1111/ddi.13003>.
- Carpio, A.J., Hillström, L., Tortosa, F.S., 2016. Effects of wild boar predation on nests of wading birds in various Swedish habitats. *European Journal of Wildlife Research* 62, 423–430. <https://doi.org/10.1007/s10344-016-1016-y>.
- Casazza, M.L., McDuie, F., Lorenz, A.A., Keiter, D., Yee, J., Overton, C.T., Peterson, S.H., Feldheim, C.L., Ackerman, J.T., 2020. Good prospects: high-resolution telemetry data suggests novel brood site selection behaviour in waterfowl. *Animal Behavior* 164, 163–172. <http://dx.doi.org/10.1016/j.anbehav.2020.04.013>.
- Chamberlain, D.E., Fuller, R.J., Bunce, J.C., Duckworth, J.C., Shrubbs, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.* 37, 771–788. <https://doi.org/10.1046/j.1365-2664.2000.00548.x>.
- Chautan, M., Pontier, D., Artois, M., 2000. Role of rabies in recent demographic changes in Red fox (*Vulpes vulpes*) populations in Europe. *Mammalia* 64, 391–410. <https://doi.org/10.1515/mamm.2000.64.4.391>.
- Chiverton, P.A., Sotherton, N.W., 1991. The effects on beneficial arthropods of the exclusion of herbicides from cereal crops. *Journal of Applied Ecology* 28, 1027–1039. <https://doi.org/10.2307/2404223>.
- Clough, Y., Kirchweber, S., Kantelhardt, J., 2020. Field sizes and the future of farmland biodiversity in European landscapes. *Conservation Letters* 13:6, e12752. <https://doi.org/10.1111/conl.12752>.
- Collar, N. 2020. Preparing captive-bred birds for reintroduction: The case of the Vietnam Pheasant *Lophura edwardsi*. *Bird Conservation International* 30, 559–574. <https://doi.org/10.1017/S0959270920000039>.
- Collins 2012. Collins English Dictionary - Complete & Unabridged 2012 digital edition ©William Collins Sons & Co. Ltd. 1979, 1986 ©Harpercollins.
- Cunningham, M.A., Johnson, D.H., 2019. Narrowness of habitat selection in woodland and grassland birds. *Avian Conservation and Ecology* 14:14. <https://doi.org/10.5751/ACE-01372-140114>.
- DAISIE 2018. <http://www.europe-aliens.org>. Accessed 1 Mar 2018.
- Davis, S.K., 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor* 107, 605–616. <https://doi.org/10.1093/condor/107.3.605>.
- Doxon, E.D., Carroll, J.P., 2010. Feeding ecology of ring-necked pheasant and northern bobwhite chicks in conservation reserve program fields. *J. Wildl. Manage.* 74, 249–256. <http://dx.doi.org/10.2193/2008-522>.
- Draycott, R.A.H., Hoodless, A.N., Sage, R.B., 2008. Effects of pheasant management on vegetation and birds in lowland woodlands. *Journal of Applied Ecology* 45, 334–341. <https://doi.org/10.1111/j.1365-2664.2007.01379.x>.

References

- EFBI 2021. European Farmland bird index. https://agridata.ec.europa.eu/Qlik_Downloads/InfoSheetEnvironmental/infoC35.html. Accessed 1.4.2021.
- Ekroos, J., Tiainen, J., Seimola, T., Herzon, I., 2019. Weak effects of farming practices corresponding to agricultural greening measures on farmland bird diversity in boreal landscapes. *Landscape Ecology* 34, 389–402. <https://doi.org/10.1007/s10980-019-00779-x>.
- Ellis-Felege, S.N., Conroy, M.J., Palmer, W.E., Carroll, J.P. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. *Journal of Applied Ecology* 49, 661–669. <https://doi.org/10.1111/j.1365-2664.2012.02126.x>.
- Ellison, K.S., Ribic, C.A., Sample, D.W., Fawcett, M.J., Dadisman, J.D., 2013. Impacts of Tree Rows on Grassland Birds and Potential Nest Predators: A Removal Experiment. *PLOS ONE* 8(4): e59151. <https://doi.org/10.1371/journal.pone.0059151>.
- EBCC European Bird Census Council 2017. Trends of Common Birds in Europe, 2017 Update. <http://ebcc.birdlife.cz/trends-of-common-birds-in-europe-2017-update/>. Accessed 5.5.2021.
- European Council, 2001. Presidency conclusions, Gothenburg Council, 15 and 16 June 2001. SN/200/1/01 REV1, p. 8.
- EU Publications Office, 2020. EU biodiversity strategy for 2030. <https://eur-lex.europa.eu/legal-content/EN/LSU/?uri=CELEX:52020DC0380>. Accessed 15.6.2021.
- EU 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. <http://data.europa.eu/eli/dir/1992/43/oj>.
- EU IAS 2017. http://ec.europa.eu/environment/nature/pdf/IAS_brochure_species.pdf. Accessed 1 Apr 2018.
- Evans, K.L., 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* 46, 1–13. <http://dx.doi.org/10.1111/j.1474-919X.2004.00231.x>.
- Evans, T.R., Mahoney, M.J., Cashatt, E.D., Noordijk, J., de Snoo, G., Musters, C.J. 2016. The Impact of Landscape Complexity on Invertebrate Diversity in Edges and Fields in an Agricultural Area. *Insects* 7:7. <https://doi:10.3390/insects7010007>.
- Ewald, J.A., Aebischer, N.J., Richardson, S.M., Grice, P.V., Cooke, A.I., 2010. The effect of agri-environment schemes on grey partridges at the farm level in England. *Agriculture Ecosystems and Environments* 138, 55–63. <http://dx.doi.org/10.1016/j.agee.2010.03.018>.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* 14, 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>.

- FAO 2020. FAOSTAT, Agri-environmental Indicators / Pesticides. Available at <http://www.fao.org/faostat/en/#data/EP>. Accessed 14.5.2021.
- Frei, B., Bennett, E.M., Kerr, J.T. 2018. Cropland patchiness strongest agricultural predictor of bird diversity for multiple guilds in landscapes of Ontario, Canada. *Regional Environmental Change* 18: 2105–2115. <https://doi-org.libproxy.helsinki.fi/10.1007/s10113-018-1343-5>.
- Fuglei, E., Ims, R.A., 2008. Global warming and effects on the Arctic fox. *Science Progress* 91, 175–91. <https://doi.org/10.3184/003685008X327468>.
- Gabriel, D., Sait, S.M., Kunin, W.E., Benton, T.G., 2013. Food production vs. biodiversity: Comparing organic and conventional agriculture. *Journal of Applied Ecology* 50, 355–364. <http://dx.doi.org/10.1111/1365-2664.12035>.
- Genovesi, P., Bacher, S., Kobelt, M., Pascal, M., Scalera, R., 2009. Alien mammals of Europe. In: *Handbook of alien species in Europe, Invading nature—Springer series in invasion ecology* 3. https://doi.org/10.1007/978-1-4020-8280-1_9.
- Gottschalk, E., Beeke, W., 2014. How can the drastic decline in the grey partridge (*Perdix perdix*) be stopped? Lessons from ten years of the Grey Partridge Conservation Project in the district of Göttingen. *Berichte zum Vogelschutz* 51, 95–116.
- Green, R.E., 1984. The Feeding Ecology and Survival of Partridge Chicks (*Alectoris rufa* and *Perdix perdix*) on Arable Farmland in East Anglia. *Journal of Applied Ecology* 21, 817–830. <https://doi.org/10.2307/2405049>.
- Gregory, R.D., van Strien, A.J., Vorisek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B., Gibbons, D.W., 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B* 360, 269–288. <http://dx.doi.org/10.1098/rstb.2004.1602>.
- Griffin, A.S., Blumstein, D.T., Evans, C.S., 2000. Training Captive-Bred or Translocated Animals to Avoid Predators. *Conservation Biology* 14, 1317–1326. <https://doi.org/10.1046/j.1523-1739.2000.99326.x>.
- Gunnarsson, G., Elmberg, J., 2008. Density-dependent nest predation—an experiment with simulated Mallard nests in contrasting landscapes. *Ibis* 150, 259–269. <https://doi.org/10.1111/j.1474-919X.2007.00772.x>.
- Hall, A., 2020. Improving sustainability and monitoring within the UK pheasant release system. PhD thesis University of Exeter, UK.
- Hanson, L.E., Progulsk, D.R., 1973. Movements and cover preferences of pheasants in South Dakota. *The Journal of Wildlife Management* 37, 454–461. <https://doi.org/10.2307/3800308>.
- Helenius, J., Tuomola, S., Nummi, P., 1995. Food availability for the grey partridge in relation to changes in the arable environment. *Suomen Riista* 41, 42–52 (In Finnish with English summary).
- Hessler, E., Tester, J.R., Siniff, D.B., Nelson, M.M., 1970. A biotelemetry study of survival of pen-reared pheasants released in selected habitats. *The Journal of Wildlife Management* 34, 267–274.

- Hietala-Koivu, R., 2002. Landscape and modernizing agriculture: a case study of three areas in Finland in 1954–1998. *Agriculture Ecosystems and Environment* 91, 273–281. [http://dx.doi.org/10.1016/S0167-8809\(01\)00222-5](http://dx.doi.org/10.1016/S0167-8809(01)00222-5).
- Hill, D.A., 1985. The feeding ecology and survival of pheasant chicks on arable farmland. *Journal of Applied Ecology* 22, 645–654. <https://doi.org/10.2307/2403218>.
- Hill, D., Robertson, P., 1988. *The Pheasant: ecology, management and conservation*. BSP Professional Books.
- Hill, D., Robertson, P. 1988b. Breeding success of wild and hand-reared ring-necked pheasants. *The Journal of Wildlife Management* 52, 446–450. <https://www.jstor.org/stable/3801588>.
- Holopainen, S., Väänänen, V-M., Fox, A., 2020a. Landscape and habitat affects frequency of native but not alien predation of artificial duck nests. *Basic and Applied Ecology* 48, 52–60. <http://dx.doi.org/10.1016/j.baae.2020.07.004>.
- Holopainen, S., Väänänen, V-M., Fox, A., 2020b. Artificial nest experiment reveals inter-guild facilitation in duck nest predation. *Global Ecological Conservation* 24, e01305. <https://doi.org/10.1016/j.gecco.2020.e01305>.
- Holopainen, S., Väänänen, VM., Vehkaoja, M., Fox, A., 2021. Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. *Biological Invasions*. <https://doi.org/10.1007/s10530-021-02608-2>.
- Hoodless, A.N., Draycott, R.A.H., Ludiman, M.N., Robertson, P.A., 2001. Spring foraging behaviour and diet of released pheasants (*Phasianus colchicus*) in the United Kingdom. *Game and Wildlife Science* 18, 375–386.
- Itämies, J., Putaala, A., Pirinen, M., Hissa, R., 1996. The food composition of Grey Partridge chicks *Perdix perdix* in central Finland. *Ornis Fennica* 73:27-34.
- IUCN 2021. The IUCN Red List of Threatened Species. Version 2021-1. <https://www.iucnredlist.org> (accessed 14.3.2021).
- IUCN 2020. <https://www.iucn.org/news/india/202002/re-introduction-cheer-pheasant-wild-himachal-pradesh-india>. (accessed 9.2.2022).
- Jaatinen, K., Hermansson, I., Mohring, B., Steele, B. B., Öst, M. 2022. Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure. *Oecologia*. <https://doi.org/10.1007/s00442-021-05101-8>.
- Jahren, T., 2017. The role of nest predation and nest predators in population declines of Capercaillie and Black grouse. Dissertation, University of Inland. <http://hdl.handle.net/11250/2469015>.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71. <https://doi.org/10.2307/1937156>.
- Jones, J., 2001. Habitat selection studies in avian ecology: A critical review. *Auk*, 118, 557–562. <https://doi-org/10.1093/auk/118.2.557>.

- Jorgensen, C.F., Powell, L.A., Lusk, J.J., Bishop, A.A., Fontaine, J.J., 2014. Assessing Landscape Constraints on Species Abundance: Does the Neighborhood Limit Species Response to Local Habitat Conservation Programs? *PLoS ONE* 9, e99339. <https://doi.org/10.1371/journal.pone.0099339>.
- Kallioniemi, H., Väänänen, V-M., Nummi, P., Virtanen, J., 2015. Bird quality, origin and predation level affect survival and reproduction of translocated common pheasants *Phasianus colchicus*. *Wildl. Biol.* 21, 269–276. <https://doi.org/10.2981/wlb.00052>.
- Kauhala, K., Laukkanen, P., von Rége, I., 1998. Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. *Ecography* 21, 457–463. <https://doi.org/10.1111/j.1600-0587.1998.tb00436.x>.
- Kauhala, K., 1996. Introduced carnivores in Europe with special reference to central and northern Europe. *Wildlife Biology* 2, 197–204. <https://doi.org/10.2981/wlb.1996.019>.
- Kauhala K., 2004. Removal of medium-sized predators and the breeding success of ducks in Finland. *Folia Zoologica* 53, 367–378.
- Kauhala, K., 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, 584–598. <https://doi.org/10.1093/czoolo/57.5.584>.
- Koshev, Y.S., Petrov, M.M., Nedyalkov, N.P., Raykov, I.A., 2020. Invasive raccoon dog depredation on nests can have strong negative impact on the Dalmatian pelican's breeding population in Bulgaria. *European Journal of Wildlife Research* 66, 85. <https://doi.org/10.1007/s10344-020-01423-9>.
- Krauss, G.D., Graves, H.B., Zervanos, S.M., 1987. Survival of wild and game-farm cock pheasants released in Pennsylvania. *The Journal of Wildlife Management*, 555559. <https://doi.org/10.2307/3801268>.
- Kristan, W.B., Johnson, M.D. Rotenberry, J.T., 2007. Choices and Consequences of Habitat Selection for Birds, *The Condor*, Volume 109, Issue 3, 1 August 2007, Pages 485–488, <https://doi.org/10.1093/condor/109.3.485>.
- Krüger, H., Väänänen, V-M., Holopainen, S., Nummi, P., 2018. The new faces of nest predation on agricultural landscapes – a wildlife camera survey with artificial nests. *Eur. J. Wildl. Res.* 64, 76. <https://doi.org/10.1007/s10344-018-1233-7>.
- Krüger, H., Jaatinen, K., Holopainen, S., Niemi, M., Vehkaoja, M., Virtanen, J., Väänänen, V-M., Nummi, P. 2022. Margins matter: the importance of field margins as avian brood-rearing habitat in an intensive agricultural landscape. Manuscript.
- Langgemach, T., Bellebaum, J., 2005. Predation and the conservation of ground-breeding birds in Germany. *Vogelwelt* 126, 259–298.
- Larivière, S., 1999. Reasons why predators cannot be inferred from nest remains. *Condor* 101, 718–721. <https://doi.org/10.2307/1370209>.

References

- Lehikoinen, A., 2011. Population estimates of Finnish gallinaceous birds. – In: Valkama, J., Vepsäläinen, V., Lehikoinen, A., (eds.), The Third Finnish Breeding Bird Atlas. – Finnish Museum of Natural History and Ministry of Environment. - <http://atlas3.lintuatlas.fi/english!> (cited 7.9.2021) ISBN 978-952-10-6918-5.
- Leif, A. P., 1994. Survival and reproduction of wild and pen-reared ring-necked pheasant hens. *Journal of Wildlife Management* 58, 501–506. <https://doi.org/10.2307/3809322>.
- Lindén, H. (ed.), 1996a. Wildlife triangle scheme – the Finnish monitoring program of game animal populations. *Finnish Game Research* 49, 1–43.
- Lindén, H., 1996b. Kärppä. In: Lindén, H. et al. (eds), Riistan jäljille. Riista- ja kalatalouden tutkimuslaitos, Edita, Helsinki, pp. 9–10 (in Finnish).
- LUKE 2021. Natural resources institute Finland, game bag statistics. http://statdb.luke.fi/PXWeb/pxweb/fi/LUKE/LUKE__06%20Kala%20ja%20riista__02%20Rakenne%20ja%20tuotanto__16%20Metsastys/5_Mets_saalis.px/table/tableViewLayout2/).
- Luonnontila 2021. <https://www.luonnontila.fi/fi/elinymparistot/rakennetut-ymparistot/rk3-kulttuurimaan-linnut>. (Accessed 23.8.2021).
- Major, R.E., Kendal, C.E., 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138, 298–307. <https://doi.org/10.1111/j.1474-919X.1996.tb04342.x>.
- Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V. et al., 2019. The interplay of landscape composition and configuration new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters* 22, 1083–1094. <https://doi.org/10.1111/ele.13265>.
- McGarigal, K., Wan, H., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat modeling: A review and outlook. *Landscape Ecology* 31, 1161–1175. <https://doi.org/10.1007/s10980-016-0374-x>.
- Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation* 106, 259–271. [https://doi.org/10.1016/S0006-3207\(01\)00252-X](https://doi.org/10.1016/S0006-3207(01)00252-X).
- Mohr, C.O., 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37, 223–249. <https://doi.org/10.2307/2421652>.
- Musil, D.D., Connelly, J.W., 2009. Survival and reproduction of pen-reared vs translocated wild pheasants *Phasianus colchicus*. *Wildlife Biology* 15, 80–88. <https://doi.org/10.2981/07-049>.
- Newton, I., 1998. Population limitation in birds. Academic Press Ltd, London.
- Newton, I., 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146, 579–600. <https://doi.org/10.1111/j.1474-919X.2004.00375.x>.
- Norbury G.L., Price C.J., Latham M.C., Brown S.J., Latham A.D.M., Brownstein G.E., Ricardo H.C., McArthur, N.J., Banks, P.B., 2021. Misinformation tactics protect

- rare birds from problem predators. *Science Advances*, 7, eabe4164. <https://doi.org/10.1126/sciadv.abe4164>.
- Nummi, P., 1988. Suomeen istutetut riistaeläimet, s. 6–9. Helsingin yliopisto, Maatalous- ja Metsäeläintieteen Laitos, 1988. ISBN 951-45-4760-8.
- Nummi, P., Väänänen, V-M., Pekkarinen, A-J., Eronen, V., Mikkola-Roos, M., Nurmi, J., Rautiainen, A., Rusanen, P., 2019. Alien predation in wetlands - raccoon dog and waterbird breeding success. *Baltic Forestry* 25, 228–237. <https://doi.org/10.46490/vol25iss2pp228>.
- Panek, M., Bresiński, W., 2002. Red fox *Vulpes vulpes* density and habitat use in a rural area of western Poland in the end of the 1990s, compared with the turn of the 1970s. *Acta Theriologica* 47, 433–442. <https://doi.org/10.1007/BF03192468>.
- Ponce, C., Bravo, C., Alonso, J.C., 2014. Effects of agri-environmental schemes on farmland birds: do food availability measurements improve patterns obtained from simple habitat models? *Ecology and Evolution* 4, 2834–2847. <https://doi.org/10.1002/ece3.1125>.
- Potts, G.R. 1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research* 11, 1–79. [https://doi.org/10.1016/S0065-2504\(08\)60266-4](https://doi.org/10.1016/S0065-2504(08)60266-4).
- Potts, G.R., 1986. *The Partridge. Pesticides, Predation and Conservation*. Collins. London.
- Potts, G.R., Aebischer, N.J., 1995. Population dynamics of the grey partridge *Perdix perdix* 1793–1993: monitoring, modelling and management. *Ibis*, 137, 29–37. <https://doi.org/10.1111/j.1474-919X.1995.tb08454.x>.
- Powell, L., 2015. Hitler’s Effect on Wildlife in Nebraska: World War II and Farmed Landscapes. *Great Plains Quarterly* 35, 1–26. Project MUSE. <http://dx.doi.org/10.1353/gpq.2015.0003>.
- Preisser, E.L., Bolnick, D.I. and Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, 86, 501–509. <https://doi.org/10.1890/04-0719>.
- Prugh, L.R., Sivy, K.J., 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. *Ecology Letters* 23, 902–918. <https://doi.org/10.1111/ele.13489>.
- Putaala, A., 1997. Survival and breeding success of wild and released grey partridges (*Perdix perdix*): an ecophysiological approach. PhD thesis, Univ. of Oulu, Finland.
- Putaala, A., Hissa, R., 1998. Breeding dispersal and demography of wild and hand-reared grey partridges *Perdix perdix* in Finland. *Wildlife Biology* 4, 137–145. <https://doi.org/10.2981/wlb.1998.016>.
- Pöysä, H., Linkola, P., 2021. Extending temporal baseline increases understanding of biodiversity change in European boreal waterbird communities. *Biological Conservation* 257, 109139. <https://doi.org/10.1016/j.biocon.2021.109139>.

References

- Riley, T.Z., Clark, W.R., Ewing, D.E., Vohs, P.A., 1998. Survival of ring-necked pheasant chicks during brood rearing. *The Journal of Wildlife Management* 62, 37–44. <https://doi.org/10.2307/3802262>.
- Robertson, P.A., 1997. *A Natural History of the Pheasant*. Swan Hill Press, Shrewsbury, UK.
- Robertson, P.A., Mill, A.C., Rushton, S.P., McKenzie, A.J., Sage, R.B., Aebischer, N.J., 2017. Pheasant release in Great Britain: long-term and large-scale changes in the survival of a managed bird. *European Journal of Wildlife Research* 63, 100. <https://doi.org/10.1007/s10344-017-1157-7>.
- Ronnenberg, K., Strauß, E., Siebert, U., 2016. Crop diversity loss as a primary cause of grey partridge and common pheasant decline in Lower Saxony, Germany. *BMC Ecology and Evolution* 16, 39. <https://doi.org/10.1186/s12898-016-0093-9>.
- Roos, S., Smart, J., Gibbons, D.W., Wilson, J.D., 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: A case study of the UK. *Biological Reviews of the Cambridge Philosophical Society* 93, 1915–1937. <https://doi.org/10.1111/brv.12426>.
- Rząd, I., Stapf, A., Kornaś, S.A., Dzika, E., Sałamatin, R., Kaczmarek, A., Kowal, J., Wajdzik, M., Zalewski, K. 2021. Intestinal Helminth Communities of Grey Partridge *Perdix perdix* and Common Pheasant *Phasianus colchicus* in Poland. *Animals* 11, 3396. <https://doi.org/10.3390/ani11123396>.
- Sage, R. B., Hoodless, A. N., Woodburn, M. I., Draycott, R. A., Madden, J. R., Sotherton, N. W. 2020. Summary review and synthesis: effects on habitats and wildlife of the release and management of pheasants and red-legged partridges on UK lowland shoots. *Wildlife Biology*, 4. <https://doi.org/10.2981/wlb.00766>.
- Šálek, M., Kreisinger, J., Sedláček, F., Albrecht, T., 2009. Corridor versus hayfield matrix use by mammalian predators in an agricultural landscape. *Agriculture Ecosystems and Environment* 134, 8–13. <https://doi.org/10.1016/j.agee.2009.06.018>.
- Šálek, M., Kreisinger, J., Sedláček, F., Albrecht, T., 2010. Do foraging opportunities determine preferences of mammalian predators for habitat edges in an agricultural landscape? *Landscape and Urban Planning* 98, 86–91. <https://doi.org/10.1016/j.landurbplan.2010.07.013>.
- Šálek, M., Kalinová, K., Daňková, R., Grill, S., Žmihorski, M., 2021. Reduced diversity of farmland birds in homogenized agricultural landscape: A cross-border comparison over the former Iron Curtain. *Agriculture Ecosystems and Environment* 321:107628. <https://doi.org/10.1016/j.agee.2021.107628>
- Salo, P., Korpimäki, E., Banks, P.B., Nordström, M., Dickman, C.R., 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B* 274, 1237–1243. <https://doi.org/10.1098/rspb.2006.0444>.
- Sasaki, K., Hotes, S., Kadoya, T., Yoshioka, A., Wolters, V., 2020. Landscape associations of farmland bird diversity in Germany and Japan. *Glob. Ecol. Conserv.* 21, e00891. <https://doi.org/10.1016/j.gecco.2019.e00891>.

- Searchinger, T., Waite, R., Hanson, C., Ranganathan, J., 2018. Creating a Sustainable Food Future: A Menu of Solutions to Feed Nearly 10 Billion People by 2050 (Synthesis Report). World Resources Institute.
- Selonen, V., Brommer, J.E., Holopainen, S., Kauhala, K., Krüger, H., Poutanen, J., Väänänen, V.-M., Laaksonen, T., 2022. Invasive species control with apex predators: increasing presence of wolves is associated with reduced occurrence of the alien raccoon dog in the boreal predator community. Manuscript.
- Silva-Monteiro, M., Pehlak, H., Fokker, C., Kingma, D., Kleijn, D., 2021. Habitats supporting wader communities in Europe and relations between agricultural land use and breeding densities: A review. *Global Ecology and Conservation* 28, e01657. <https://doi.org/10.1016/j.gecco.2021.e01657>.
- Sirami, C., Gross, N., Baillo, A.B., Bertrand, C., Carrie, R., Hass, A., Henckel, L. et al. 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *PNAS* 116 (33), 16442–16447. <https://doi.org/10.1016/j.apgeog.2013.12.006>.
- Smith, R.K., Pullin, A.S., Stewart, G.B., Sutherland, W.J., 2010. Effectiveness of predator removal for enhancing bird populations. *Conservation Biology* 24, 820–829. <http://dx.doi.org/10.1111/j.1523-1739.2009.01421.x>.
- Smith, J.A., Matthews, T.W., Holcomb, E.D., Negus, L.P., Davis, C.A., Brown, M.B., Powell, L.A., Taylor, J.S., 2015. Invertebrate prey selection by ring-necked pheasant *Phasianus colchicus* broods in Nebraska. *American Midland Naturalist* 173, 318–325. <http://dx.doi.org/10.1674/amid-173-02-318-325.1>.
- Stoate, C., Boatman, N.D., Borralho, R.J., Rio Carvalho, C., de Snoo, G.R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. *Journal of Environment Management* 63, 337–365. <https://doi.org/10.1006/jema.2001.0473>.
- Stoate, C., Baldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., (...), Ramwell, C., 2009. Ecological impact of early 21st century agricultural change in Europe—a review. *Journal of Environmental Management* 91, 22–46. <http://dx.doi.org/10.1016/j.jenvman.2009.07.005>.
- Swann, D.E., Kawanishi, K., Palmer, J., 2011. Evaluating types and features of camera traps in ecological studies: a guide for researchers. In: O’Connell AF, Nichols JD, Karanth KU (eds.) *Camera traps in animal ecology*. Springer, Tokyo.
- Taylor, J.S., Bogenschutz, T.D., Clark, W.R., 2018. Pheasant Responses to U.S. Cropland Conversion Programs: A Review and Recommendations. *Wildlife Society Bulletin* 42, 184–194. <https://doi.org/10.1002/wsb.882>.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31, 79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>.
- Thompson, F.R.III, Burhans, D.E., 2003. Predation of songbird nests differs by predator and between field and forest habitats. *The Journal of Wildlife Management* 67, 408–416.

References

- Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Science of the USA* 108, 20260–20264. <http://dx.doi.org/10.1073/pnas.1116437108>.
- Tobajas, J., Descalzo, E., Mateo, R., Ferreras, P., 2020. Reducing nest predation of ground-nesting birds through conditioned food aversion. *Biological Conservation* 242. <https://doi.org/10.1016/j.biocon.2020.108405>.
- Tompkins, D., Draycott, R. and Hudson, P. 2000. Field evidence for apparent competition mediated via the shared parasites of two gamebird species. *Ecology Letters* 3: 10–14. <https://doi.org/10.1046/j.1461-0248.2000.00117.x>.
- Vickery, J.A., Carter, N., Fuller, R.J., 2002. The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. *Agriculture Ecosystems and Environment* 89, 41–52. [https://doi.org/10.1016/S0167-8809\(01\)00317-6](https://doi.org/10.1016/S0167-8809(01)00317-6).
- Väänänen, V.-M., Pöysä, H., Runko, P., 2016. Nest and brood stage association between ducks and small colonial gulls in boreal wetlands. *Ornis Fennica* 93, 55–66.
- Warner, R.E., 1979. Use of cover by pheasant broods in east-central Illinois. *The Journal of Wildlife Management* 43, 334–346. <https://doi.org/10.2307/3800342>.
- Warner, R.E., 1984. Effects of Changing Agriculture on Ring-Necked Pheasant Brood Movements in Illinois. *The Journal of Wildlife Management* 48, 1014–1018. <https://doi.org/10.2307/3801459>.
- Wiens, J., 1989. *The Ecology of Bird communities* (Cambridge Studies in Ecology). Vol. 2 Processes and variations. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511608568>.
- Willebrand, T., Marcström, V., 1988. On the danger of using dummy nests to study predation. *The Auk* 105, 378–379. <https://doi.org/10.2307/4087508>.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B., 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture Ecosystems and Environment* 75, 13–30. [https://doi.org/10.1016/S0167-8809\(99\)00064-X](https://doi.org/10.1016/S0167-8809(99)00064-X).
- Weiskopf, S.R., Rubenstein, M.A., Crozier, L.G., Gaichas, S., Griffis, R., Halofsky, J.E., Hyde, K.J.W., (...), Whyte K.P., 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. <https://doi.org/10.1016/j.scitotenv.2020.137782>.