INLAND NORWAY
UNIVERSITY
OF APPLIED SCIENCES

Faculty of Applied Ecology and Agricultural Sciences

Torfinn Jahren

PhD-Thesis

The role of nest predation and nest predators in population declines of capercaillie and black grouse

PhD in Applied Ecology

2017

Preface & acknowledgements

This fall I had to make a choice. Hunting or delivering my thesis. Since you are reading this, you will not be enjoying a capercaillie dinner at my defence. I apologize. It was not really because of their gastronomical qualities I wanted to study capercaillie and black grouse. Ten years ago, I wanted to study hazel grouse for my bachelor thesis (they actually taste better). Very little was known about hazel grouse and all the known and unknown unknowns about them fascinated me. Almost anything you discovered would be new to science! Luckily, Torstein Storaas had some better ideas (Torstein is full of ideas). Soon enough, all grouse nests in Hedmark County were on the most wanted list and we were working with the most important issues of our time. The five Ws of nest predation.

Torstein, you are a true grouse aficionado. Your enthusiasm and positive energy is contagious and there was never a dull moment when discussing relevant or irrelevant [German wirehaired pointers --Ed.] topics. Formal tutor meetings in your office were never formal and usually complemented with jokes about stuffed hooded crows or good stories about historic battles, kings or gods. I am deeply grateful for having you as my academic mentor. The PhD-education is a ride and the ride would not have been the same without you.

My co-supervisor Tomas Willebrand, I am also very grateful to you. I have really learned a lot from the discussions we had. Your professional assurance has been reassuring in times of distress and it means a little extra when the comment “nice paragraph” comes from you. Sometimes, I think you like to play the devil’s advocate. Am I right? Time and again I had to reconsider my positions and even argue for the new ones although we agreed on them in the first place. That has been very valuable and you have certainly given me many new tools for my science toolbox.

I owe a great deal to Olivier Devineau. Before I met him, bar charts in Excel was my only friend. Olivier signs his e-mails with an O. I believe it stands for Oracle. He has an intimate relationship with R-code and it appears that he prefer to specify model components manually, in algebraic form. There are also rumours that his quantitative ecology textbooks are actually in binary code. With remarkable patience (considering the frequency of students in his office asking for help), he showed the way, often in directions I hoped to avoid but he always got me there in the end.

```
gratitude::thank_you()
```

I would also like to thank Pål and Bjørn Roar up there in Steinkjer. In 2010, we joined forces and soon enough, all grouse nests in Nord-Trøndelag County were on the most wanted list as well. Your contribution to the nest project has been invaluable and effectively doubled its size. Sometimes I have envied ecologists studying insects in a lab. Nesting capercaillie and black grouse hens do not

want to be found. Red fox and pine marten move in mysterious ways. Data are hard to collect. This thesis would not have been possible without help from all the volunteers. The list of people is long and their joint efforts consists of many hours in helping with nest observations, transect surveys and tracking of red fox and pine marten.

Thanks also to my parents. You have helped me out and supported me in all the ways you can. Finally, Madlaina, the girl of my life. Thank you for being you. You have made the process of writing this thesis so much easier than it would have been without your support and caring.

I guess I could have told a story analogous to the ups and downs of doing a PhD-thesis so people without a PhD could relate. All I can say is; it was difficult and I would not do it again. Come to think of it, maybe on hazel grouse though…

Torfinn Jahren. Rasta, November 2017.

Contents

Sammendrag

I det sammenhengende Fennoskandiske barskogbeltet har storfugl- (*Tetrao urogallus*) og orrfuglbestandene (*Lyrurus tetrix*) gått ned over tid, og toppene i de sykliske svingningene har blitt mer uregelmessige og lavere. At endringene har skjedd over hele Fennoskandia antyder at de samme stor-skala prosessene kan ligge bak. Endringer i menneskelig arealbruk, endringer til varmere og våtere klima og økt predasjonstrykk fra generalistpredatorer er tre komplementerende hypoteser fremsatt som mekaniske forklaringer bak den negative utviklingen. Den bakenforliggende årsaken eller årsakene har ført til et misforhold mellom demografiske rater. Nedgang i reproduksjonssuksess og voksenoverlevelse alene eller til sammen har forårsaket storskala nedgang i nivået bestandene har variert rundt. Den primære dødsårsaken i alle livsfaser hos fennoskandisk hønsefugl er predasjon, og reproduksjon er den viktigste driveren av kortsiktig populasjonsdynamikk. For å heve kunnskapsgrunnlaget om årsaksforhold bak den negative utviklingen i bestandstettheter og reduksjon i syklisk dynamikk, har jeg ved bruk av omfattende data på både bestands- og individnivå satt søkelyset på reproduksjon og predatorer som begrenser reproduksjon.

Helt konkret var mine mål som følger; 1) Fastslå langtids og storskala trender i reproduksjonssuksess hos storfugl og orrfugl samt å evaluere reproduksjonens rolle i bestandsnedgangene. 2) Identifisere og kvantifisere predatorer på reir av storfugl og orrfugl samt å utforske funksjonelle og numeriske responser til de viktigste predatorene. 3) Studere næringssøket hos rødrev (*Vulpes vulpes*) og mår (*Martes martes*) og 4) evaluere forholdet mellom menneskelig arealbruk og bestandsdynamikk hos rødrev.

Jeg fant bevis for at reiroverlevelse og kullfrekvens hos fennoskandisk storfugl og orrfugl har sunket over lang tid. Antall kyllinger per høne sank også, men over et kortere tidsrom. I samme periode, økte overlevelse på voksne høner. Oppgangen i overlevelse hos voksne høner var ikke tilstrekkelig for å kompensere for nedgangen i reproduksjon. I dag er rødrev og mår de to viktigste predatorene på orrfugl og storfuglreir. Bortsett fra ett tilfelle med predasjon fra kongeørn (Aquila chrysaetos), identifiserte vi bare pattedyr som reirrøvere. I motsetning til tidligere antakelser, basert på arbeid med kunstige reir, observerte vi hverken at kråke (*Corvus cornix*) eller ravn (*Corvus corax*) predaterte reir. Selv om det kan tenkes at kråkefugl predaterer skogsfuglreir, skjer dette fenomenet trolig langt sjeldnere enn tidligere antatt, og kunstige reir kan ikke brukes for å finne hvilke dyr som røver reir.

Hvor raskt orrfuglreir ble røvet (predasjonstakten) var avhengig av smågnager- og mårindeksen. Mye smågnagere gav mindre røving, og mye mår gav mer røving. Sammenhengen mellom predasjonstakt og smågnagere opphørte imidlertid når mårindeksen økte. Ved høy mårindeks spilte det ingen rolle for røvingstakten på orrfuglreir om det var mye smågnagere eller ikke. Predasjonen på storfuglreir

var hovedsakelig avhengig av smågnagersyklusen. Flest reir ble røvet i krasjfasen av smågnagersyklusen, men predasjonstakten sank suksessivt ettersom smågnagersyklusen utviklet seg til oppgangs- og toppfasen. Også sammenhengen mellom predasjonstakten på storfuglreir og smågnagere opphørte når mårindeksen økte og ved høy mårindeks overgikk predasjonstakten i oppgangsfasen den i toppfasen. Når det var lite mår, støttet mønsteret i predasjon på storfuglreir den alternative byttedyrhypotesen (ABH), i motsetning til hos orrfugl.

Analysen av predasjon fra rev og mår på storfuglreir antydet to mekanistiske regimer. Uavhengig av smågnagersituasjonen økte predasjonstakten fra mår med mårindeksen mens predasjonstakten fra rødrev, uavhengig av rødrevindeksen, minsket med mengde smågnagere gitt av smågnagersyklusen. Predasjonsmønsteret til måren sammenfalt ikke med predasjonsmønster for generalistpredatorer beskrevet av ABH, men antydet heller tilfeldig predasjon eller spesialistpredasjon mens predasjonsmønsteret til rødrev var i overensstemmelse med ABH.

Mår var mer effektiv enn rødrev under jakt og graving etter byttedyr. Frekvensen av jaktforsøk overlappet, men rødreven gravde relativt oftere etter mat. Generelt overlappet næringsnisjene til rødrev og mår lite. Rødrev jaktet hovedsakelig på smågnagere og hare (*Lepus timidus*) og gravde først og fremst etter smågnagere og åtsler av hjortedyr. Mår jaktet for det meste småfugler og gravde frem lagrede egg. Langtidslagring av egg samt frekvensen av graving etter egg vitner om at egg er en betydelig ressurs for måren. Tolkningen av mår som spesialist på eggpredasjon er derfor støttet av dens næringsadferd om vinteren mens rødreven er til sammenligning en generalist som foretrekker smågnagere.

Bestandsdynamikken til rødrev var både i tid og rom nærmere knyttet til menneskelig arealbruk enn til naturgitte gradienter i landskapet. Det var mer rødrev ved relativt høyere tetthet av bosetninger og slakteavfall etter elgjakt. Variasjonen i mengde av rødrev over tid var dominert av direkte tetthetsavhengige prosesser, og tetthetsavhengighetens styrke var negativt knyttet til jordbrukets dominans i landskapet. I områder dominert av jordbruk, fluktuerte bestanden av rødrev rundt et høyrere og mer stabilt likevektsnivå enn i marginale jordbruksområder.

Summary

Throughout the continuous boreal forests of Fennoscandia, long-term and synchronous declines in population density and cyclic amplitude of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) have been observed for decades. The extensive spatiotemporal scale involved, implies large-scale processes behind causal mechanisms. Changes in human land use, climatic perturbations and elevated predation from generalist predators are three complementing hypotheses suggested as mechanistic explanations underlying the negative trends in density and oscillatory dynamics. As the proximate cause of population declines and short-term dynamics is a mismatch in demographic rates, diminishing reproductive success and adult survival have separately or jointly, brought about widespread changes in equilibrium densities and annual variation. The predominant cause of mortality during all life-history stages of Fennoscandian woodland grouse is predation and the major factor driving short-term population dynamics is reproductive success. By the use of comprehensive data on both individual- and population level, I therefore focus on woodland grouse reproduction and the predators limiting reproductive success in order to improve detailed understanding of important mechanisms behind reductions in population densities and amplitude of population fluctuations.

Specifically, my objectives were as follows; 1) Assess long-term and large-scale trends in capercaillie and black grouse reproductive success and evaluate its contribution to the observed population decrease. 2) Identify and quantify predators of capercaillie and black grouse nests and explore the numerical and functional responses of the most important predators. 3) Investigate foraging patterns of red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) and 4) evaluate relationships of anthropogenic land-use to red fox population dynamics.

I found evidence supporting long-term declines in nest success and broods per hen for Fennoscandian capercaillie and black grouse. The number of chicks per hen also declined, but over a shorter time-span. In the same period, hen survival increased. Despite elevated survival rates of adult hens, reproduction was not equalized. Today, red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) were the principal predators identified to prey upon capercaillie and black grouse nests. Apart from one identification of golden eagle (*Aquila chrysaetos*) predation, mammals predated all monitored nests. In contrast to earlier beliefs derived from artificial nests, hooded crows (*Corvus cornix*) and common ravens (*Corvus corax*) were confronted by the incubating hen and did not predate active nests. Although corvid predation may occur, it is far less than earlier claims and artificial nests should therefore not be used as substitutes for real nests.

Predation rates on black grouse nests depended on vole and pine marten abundance. The relationship between predation of black grouse nests and vole abundance was negative whereas the relationship to pine marten abundance was positive. The relationship to voles weakened as pine martens became more abundant. Capercaillie nests however, were heavily preyed upon in the crash phase of the vole cycle. Predation rates then successively relaxed as the vole cycle progressed into the increase and peak phase. Again, elevated abundances of pine marten detached the relationship between nest predation and voles and predation in the peak phase of the vole cycle eventually increased above those in the increase phase when pine martens were abundant. In contrast to black grouse, nest predation in capercaillie agreed with the alternative hypothesis (APH), but not when pine martens were abundant.

Analysis of partitioned predation by red fox and pine marten on capercaillie nests suggested a dichotomy in mechanistic regimes. Regardless of the vole situation, pine marten predation increased with pine marten abundance whereas red fox predation, regardless of red fox abundance, was inversely related to the vole cycle. Predation by pine marten was thus inconsistent with APH and suggested specialist or incidental predation of eggs whereas red fox predated nests consistent with APH.

Pine martens were more successful than red foxes when hunting or digging for food. The frequencies of hunting attempts overlapped whereas red foxes dug more frequently. Overall, their foraging niche overlap was small. Red foxes mostly scavenged and dug for voles and ungulates but hunted for mountain hares (*Lepus timidus*) and voles. Pine marten mostly scavenged for cached eggs and hunted for small birds. Long-term caching of eggs by the pine marten as well as the frequency of eggs in scavenging events speak to the importance of eggs to the pine marten. The interpretation of pine marten predation as an egg-specialist was therefore supported by their foraging behavior in winter whereas red fox is more of a generalist with a wider niche and a preference for voles.

The spatiotemporal dynamics of red fox populations in the boreal forest was more closely interrelated with anthropogenic land use than natural-given landscape gradients, and relative density of settlements and offal were related to higher abundances of red fox. Direct density dependent processes dominated the structure of temporal variation in red fox abundance and the strength of density dependence was inversely related to the amount of agriculture in the landscape. In areas dominated by agriculture, the red fox population fluctuated around a higher, more stable equilibrium than in marginal agricultural areas.

List of papers

I base my thesis on the following original publications and manuscripts, which I refer to by their Roman numerals.

Paper I:
Jahren, T., Storaas, T., Willebrand, T., Fossland Moa, P., Hagen, B-R. 2016. Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years. Animal Biology, **66**: 363–400.

Paper II:
Jahren, T., Storaas, T., Willebrand, T., Fossland Moa, P., Hagen, B-R. Impacts of voles and predators on nest predation in European boreal forest grouse. (*Manuscript)*.

Paper III:
Willebrand, T., Willebrand, S., **Jahren, T.** & Marcström, V. (2017) Snow tracking reveals different foraging patterns of red foxes and pine martens. Mammal Research, **62**(4): 331-340.

Paper IV:
Jahren, T., Odden, M., Linnell, J.D.C, Panzacchi, P. The impact of human land use and landscape productivity on the abundance and dynamics of red fox in southeastern Norway. (*Manuscript*).

The original publications have been reproduced with the permission of the publisher.

Supervisor:

Professor Torstein Storaas, Inland Norway University of Applied Sciences, Evenstad, NO-2480 Koppang, Norway

Co-Supervisor:

Professor Tomas Willebrand, Inland Norway University of Applied Sciences, Evenstad, NO-2480 Koppang, Norway

Introduction

Hypothetical mechanisms to long-term declines and short-term dynamics

Capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) are hallmark game birds of the Eurasian boreal forests. During the 1970s, several scientists reported decreasing capercaillie and black grouse population densities in the continuous boreal forests of Fennoscandia (Rajala 1974; Myrberget 1977; Wegge & Grasaas 1977; Lovel 1979) but long-term density estimates have been collected only in Finland from 1964 (Helle & Ikonen 2015). In Finland, estimates show nationwide declines from 1964 until populations stabilized during the 1990s. Snippets of data confirm this patterns for local Norwegian capercaillie and black grouse populations as well (Wegge & Grasaas 1977). There is no evidence that populations have recovered apart from a period of increase and subsequent decline in concert with an outbreak of Sarcoptic mange (*Sarcoptes scabiei*) in the Fennoscandian red fox population (Lindstrom *et al.* 1994; Smedshaug *et al.* 1999; Lindén & Helle 2003; Lakka & Kouki 2009; Wegge & Rolstad 2011). Despite universal declines in population densities, black grouse and capercaillie are of least concern globally (IUCN 2016), and both species are still hunted in Fennoscandia. During the previous decade, mean annual harvest in Finland was 38 000 and 155 000 (Naturresursinstitutet 2017), in Sweden 20 000 and 26 000 (Viltdata 2017) and in Norway 10 000 and 23 000 (Statistics Norway 2016) capercaillie and black grouse respectively.

Population declines in woodland grouse manifest in a mismatch in demographic rates. Decreasing adult, juvenile, chick or egg survival have in combination or alone caused capercaillie and black grouse declines from one equilibrium to another across an area of 1.2 million km^2. Under circumstances of stable reproductive success, a few studies investigating population dynamics in grouse have identified winter survival as the underlying driver of annual population fluctuations (e.g. Rajala 1974; Semenow Tjan Shanskiy 1979; Magnússon, Brynjarsdóttir & Nielsen 2004). The majority of studies have, however, identified reproduction as the important driver of short-term fluctuations (e.g. Lindström *et al.* 1997). To understand the mechanisms behind the long-term population declines in woodland grouse, a key characteristic of woodland grouse research has therefore been to understand limiting and regulating factors of reproductive success.

There are mainly three, possibly complementing hypothesis put forward to explain the universal and long-term declines in the Fennoscandian tetraonid reproductive success. Firstly, changes in anthropogenic land use, mainly by the industrialization of silviculture is believed to have deteriorated habitat quality (Sirkiä *et al.* 2010). One suggested mechanism is that intensified forest management have caused long-term reductions in bilberry (*Vaccinum myrtillus*) coverage (Ludwig 2007), and thereby also lepidopteran larvae which is staple chick food (Wegge & Kastdalen 2008; Baines, Richardson & Warren 2017). Secondly, climate change can limit reproductive success by limiting chick survival. Increased rainfall may for example reduce foraging time for chicks as they shelter underneath the hen during rainfall (Erikstad & Spidsø 1982; Moss 1986). Mortality caused by adverse weather or hunger happens occasionally but chicks are likely more susceptible to predation under such conditions (Wegge & Kastdalen 2007). Third and finally, elevated predation pressure from increased population densities of mammalian mesocarnivores can increase mortality rates for eggs and chicks. Aside from increased predation pressure caused by numerical responses in generalist predator populations (Helldin 2000a; Selås & Vik 2006), changes in land use and climatic perturbations may both interact with predators and modulate their functional responses (Storaas, Kastdalen & Wegge 1999; Wegge & Kastdalen 2007).

Historical changes in the boreal landscape

The boreal landscape of Fennoscandia is characterized by a long winter, short summer, and few species. Today, the landscape is a result of changing climate and anthropogenic land-use. The extent of land suitable for agriculture in Fennoscandia is small compared to further south in Europe and today, approximately 2.5, 4.9 and 7.8 % of Norway, Finland and Sweden is cropland. Since the 1930s, the extent of agricultural land on the Scandinavian peninsula has retracted by 14.3 % and most of this is attributable to Sweden as the extent of cultivated land in Norway increased by 9.6 % whereas cropland in Sweden decreased by 19.8 % (Li et al. 2013; Eurostat 2017).

During the period of decreasing grouse population densities, forestry practices and thereby forest structure have changed substantially. Until the 1950s, natural regeneration after selective felling was the principal process shaping the pre-mechanized forested landscape in Norway whereas particularly in Finland but also in Sweden, slash and burn practices were common (Östlund, Zackrisson & Axelsson 1997; Lindén & Helle 2003). Such practices generated landscapes wherein tree density and biomass was generally lower than today with continuous, open forest where single trees were selected and harvested. The composition of tree species, tree dimensions and age classes were therefore more heterogeneously dispersed across the landscape than today (Wegge & Rolstad 2011). Following the mechanisation of silviculture, widespread and intensive clearcutting practices resulted in extensive monocultures of even-aged conifer stands wherein the field layer was dominated by forbs and graminoids during parts of the stand rotation. The sudden superabundant graminoid habitats have been hypothesized to facilitate field voles (*Microtus agrestis*), and thereby also red fox (Christiansen 1979; Henttonen 1989) (Figure 1). Clearcutting may therefore also temporarily remove bilberry shrubs across entire stands during at least parts of the succession following timber harvest (Hansson 1992; Lakka & Kouki 2009; Hedwall & Brunet 2013; Tonteri *et al.* 2016).

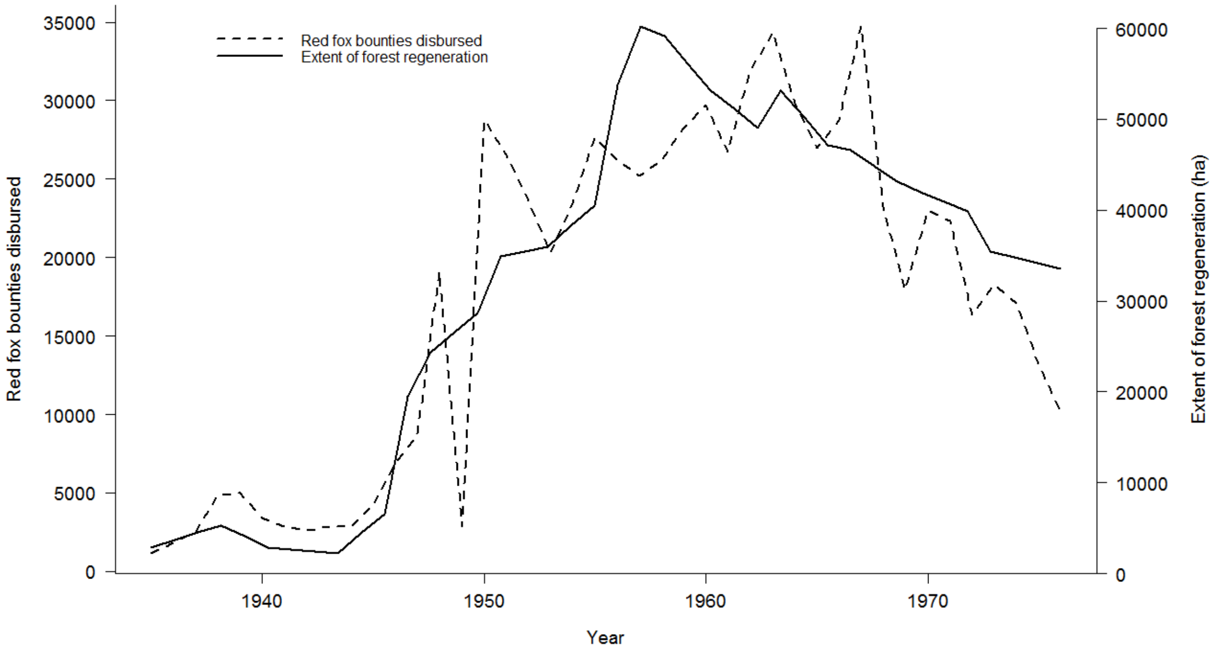

Figure 1 Annual number of governmental bounties disbursed for killed red foxes and the extent (hectares) of clearcuts produced annually in Norway from 1935 to 1976 after Christiansen (1979).

Clearcutting is still the dominating method of timber harvest in Fennoscandia but during the early 1990s, the forest industry implemented international certification standards. These certifications are instruments designed to reach ecological sustainable forestry practices and involves restrictions on interventions during the stand rotation (Spence 2001). Since the implementation of certification standards, deciduous species, buffer zones and areas of special consideration are to be left behind after thinning or final felling (Vanha-Majamaa & Jalonen 2001).

The small game community in the Fennoscandian boreal forest

In this thesis, I define the Fennoscandian small game community as capercaillie, black grouse, hazel grouse (*Bonasa bonasia*), mountain hare (*Lepus timidus*), red squirrel (*Sciurus vulgaris*), a guild of Arvicoline rodents (e.g. voles and lemmings), and their predators. The Arvicoline voles exhibit multiannual (3-5 year) population cycles (Hansson & Henttonen 1988). These cycles are considered the main driver of dynamics in the small game community as population size and predation pressure from red fox and other vole consumers fluctuate accordingly (Hornfeldt & Carlsson 1990; Henden, Ims & Yoccoz 2009; Sundell *et al.* 2013). Grouse, hares, red fox and pine marten are harvested annually during an open season of several months.

Capercaillie and black grouse exhibit population cycles with a periodicity of four to seven years, slightly longer than those of voles (Lindén 1988; Small, Marcström & Willebrand 1993). Some authors however, have demonstrated diminishing cyclicity in grouse (Cf. Ranta, Helle & Lindén 2004). Cyclic amplitude as well as periodicity increase with latitude (Lindén 1988) and fluctuations are synchronous across large areas (Ranta, Lindstrom & Linden 1995). These short-term cycles in population size are primarily driven by annual variation in hatching success and chick survival (Lindén 1981; Lindström *et al.* 1997). Both density dependent and density independent factors may cause these patterns. Apart from a few investigations (e.g. Dahl 1924; Brinchmann 1926) on grouse disease (e.g. density dependent), recent studies on mortality causes in capercaillie and black grouse point to predation as the predominant cause of mortality throughout all stages of the woodland grouse life-cycle (i.e. eggs, chicks and adults) (Paper II; Wegge & Kastdalen 2007; Åhlen *et al.* 2013).

Long- and short-term responses of mesocarnivores

Red fox and pine marten are the two most common generalist mesocarnivores preying upon woodland grouse eggs, chicks and adults in the forested areas of Fennoscandia (Marcström, Kenward & Engren 1988; Lindstrom *et al.* 1994; Smedshaug *et al.* 1999; Kauhala, Helle & Helle 2000; Paper II). Apart from bag statistics, reliable, long-term population estimates of red fox and pine marten are lacking, but there is a general consensus on increasing populations of both species during the past century (e.g. Krott & Lampio 1983; Helldin 2000; Selås & Vik 2006). Both species were previously valuable fur bearers (Figure 2) but compared to the red fox, the pine marten has been extremely difficult to farm (Statistics Norway 1934) and pine marten pelts could therefore only be obtained from wild animals. Subsequently, over-harvesting led to local extinctions and overall low population size during the 1930s, and pine martens became totally protected in both Sweden and Norway (Helldin 2000a).

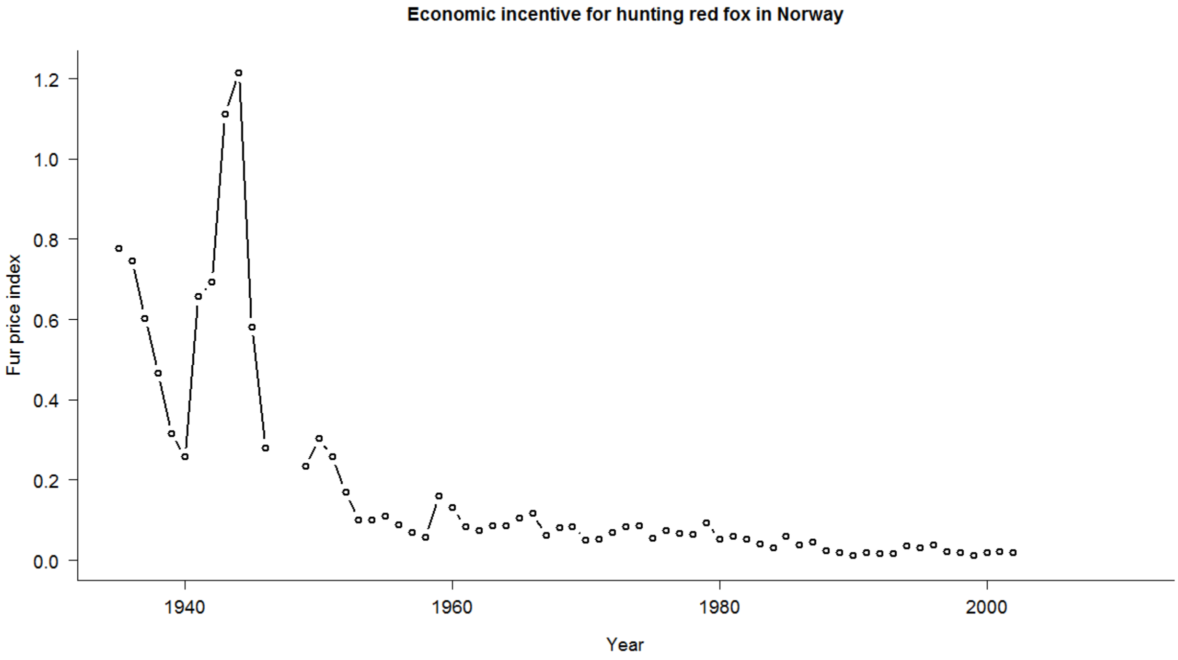

Figure 2 Red fox fur value relative to mean monthly wage from 1935 to 2011.

Despite periods with high fur prizes and public efforts to exterminate red foxes, populations persisted and probably increased until the outbreak of the epizootic sarcoptic mange. The mange was first detected in Finland in 1967, and by 1975 and 1976, the mange had spread to Sweden and Norway (Mörner 1992). Several explanations for the numerical increase in red fox have been suggested. Relaxed persecution from man (Hudson 1992), the mass creation of field vole (*Microtus agrestis*) habitat by modern forestry practices (Christiansen 1979; Henttonen 1989), an increase in scavenging opportunities from increasing herbivore populations (Selås & Vik 2006; Gomo *et al.* 2017), and a reduction in winter severity (Bartoń & Zalewski 2007) are proposed explanations. The disappearance of apex predators may additionally have caused trophic interactions via less intra-guild predation (i.e. mesopredator release) (Prugh *et al.* 2009), and some authors have argued for red fox increase due to mesopredator release (Pasanen-Mortensen, Pyykönen & Elmhagen 2013). In the time frame of this thesis however, large carnivore populations in Fennoscandia had already been decimated decades ago (e.g. Linnell *et al.* 2010).

The spatiotemporal variation in consumption rate by predators can be described by functional and numerical responses in the predator populations. These responses describe how the density of predator individuals and their consumption rate change according to varying prey density (Solomon 1949; Holling 1959). As such, functional and numerical responses are most prominent in unstable systems and the Fennoscandian boreal forest is therefore a good place to study them. Below I will explain their characteristics and contextual relevance.

Numerical response

The numerical response describes how predator density change according to prey density (Solomon 1949), and is typically separated in two sub-groups; an aggregational (i.e. spatially explicit) and a demographic (i.e. temporally explicit) response. Whereas the result of the two phenomena is similar, the mechanisms at work are different. Heterogeneous distribution of food supplies across the landscape can cause predator populations to aggregate where prey is abundant or otherwise vacate areas where prey is depleted (McKinnon *et al.* 2013; Henden, Stien & Bårdsen 2014). An archetypical example of such aggregation is the long-distance invasions of the spotted nutcracker (*Nucifraga caryocatactes*), probably triggered by a depletion in per capita food supply (Formosof 1933). Similarly, the demographic response also describe how the number of individual predators change but via changes in survival and reproduction over time rather than movement across space.

Functional response

There are three types of functional responses described and they explain how predation rates from a constant number of predators change with changing prey density (Holling 1959). In its simplest form (Type I), the per capita consumption rate increase linearly with increasing prey density. Type II and III differ from type I in that they incorporate saturation levels at certain prey densities (e.g. searching and processing food are mutually exclusive activities). Type III depicts a relationship between consumption rates and prey density that could involve prey switching.

Alternative prey hypothesis

A characteristic component in the Fennoscandian small game community dynamics is the synchronous fluctuations of small herbivores and their predators (Hagen 1952; Lack 1954; Small, Marcström & Willebrand 1993). This covariation across trophic levels materialise in synchronous population cycles of different lengths depending on the species involved and latitude (Lindén 1988). During a three-year population cycle of voles (i.e. increase, peak and crash), predation pressure from a generalist predator (e.g. red fox) on alternative prey (e.g. grouse) inversely relates to the abundance of voles. Whereas the numerical and functional response depicts predator numbers and consumption rates through an increase in prey density, the alternative prey hypothesis combines the two responses to explain the chain of events in multi-annual, synchronous population cycles in herbivores sharing a predator species (Angelstam, Lindström & Widén 1984).

A fundamental assumption of the alternative prey hypothesis is prey switching (i.e. type III functional response) among predators. The hypothesis therefore best explain predation on alternative prey by a generalist predator whose main food resource cycle in abundance (e.g. grouse, red fox and voles). Northern systems wherein red fox predation predominates are generally in accordance with this model (Hörnfeldt 1978; Danell & Hörnfeldt 1987; Angerbjörn 1989) whereas systems wherein pine marten predation predominates, the relationship is more uncertain (Pöysä, Jalava & Paasivaara 2016; Paper II).

The predation-concept in ecological research: from pest and garbage cans for a doomed surplus to the elephant in the room

The focus of the scientific community on the different mechanisms regulating and limiting woodland grouse reproduction has shifted since the first literature emerged some 90 years ago. The proportion of hits in scientific databases reflected lower interest in predation studies after 1960, but increasing to pre-1960 levels from 1990 (Moss, Storch & Müller 2010). The common view on the effect of predation on grouse has also changed. In 1845, the Norwegian parliament adopted a law to exterminate predators of small game; goshawk (*Accipiter gentilis*), golden eagle (*Aquila chrysaetos*), white-tailed eagle (*Haliaeetus albicilla*) and eagle owl (*Bubo bubo*). Red fox was discussed, but in the end regarded as an useful species due the valuable fur (Richardsen 2012). The Norwegian law was consistent with Charles Darwin (1859) writing that "*there seems to be little doubt that the stock of partridges, grouse, and hares on any large estate depends chiefly on the destruction of vermin*". Although the extirpation of vermin was not Darwin's message, eradicating vermin was the dominating mind set behind previous and emerging wildlife legislation for a century. In Norway, it was legal to poison red foxes until 1981. Anti-carnivore legislation caused extensive depression and extinction of larger and smaller carnivorous species that posed threats to livestock as well as traditional hunting on the Scandinavian peninsula (Helldin 2000a; Linnell, Swenson & Anderson 2001).

Prior to the turn of the 19th century, Henrik Ibsen and other Scandinavian bourgeoisie was heavily influenced by Darwin's views when discussing scientific approaches to wildlife management (Heiberg 1995). These discussions were probably also facilitated by economic growth and inspired by philosophical ideas of animal ethics and personal freedom to hunt (Andersen, Fagerheim & Solheim 2009). Following economic growth, sports hunting became a popular activity among the growing Norwegian middle-class and the Norwegian sport hunting association was founded in 1871. One of their main activities on the beginning of the 20th century was control of small game predators (Søilen 1995). The effect of this extermination programme seemed enormous; grouse populations skyrocketed, but collapsed in spite of continued predator control (Hjeljord 2015). As dead grouse were observed, researchers questioned the effects of predator control and initiated investigations into disease and parasites in general and coccidiosis in particular (Lesley & Shipley 1912; Brinchmann 1926). Nonetheless, carnivore conservationists were blamed for sentiment and weak theoretical reasoning (Brooks 1926). In Norway, Sweden and Finland, overharvest subsequently led pine marten to be among the first carnivore species to be fully protected in 1930 (Helldin 2000a).

In the years to follow, Aldo Leopold led the way with a more holistic approach to wildlife conservation. Nature was in a state of balance but the anthropocentric view was still dominating as the landscape was to be managed to produce yields for man (Leopold 1933). In his *"A Sand County Almanac"* from 1949, he has a famous chapter, *"Think like a mountain"* where he give a mythical value to wolves. In the same period, Errington (1946) reviewed population effects of predation across a variety of vertebrate taxa and he famously concluded that predators functioned as garbage cans that only removed the doomed surplus. In 1967 however, a paper testing the hypothesis that reproduction in blue grouse (*Dendragapus spp.*) was related to the nutritive state of the hen as mediated by variability in habitat quality was among the early empirical studies following individual grouse (Zwickel & Bendell 1967). This study was very much inspired by previous work from Finland (Siivonen 1957) in which synchrony among herbivores was explained by variations in food quality. Zwickel and Bendell identified predation as the dominant reason for mortality of eggs. Nonetheless, they concluded that annual predation contributed to a "normal loss". Similar reasoning is found in subsequent research on grouse population dynamics (Lovel 1979).

Hagen's (1952) and Lack's (1954) hypotheses on how unexplained crashes in small mammals caused their predators to shift diet and supress other species, including woodland grouse were refined into what we today know as the alternative prey hypothesis (e.g. Angelstam, Lindström & Widén 1984). In the 1980s, several papers on both limiting and regulating effects of predation were published. The most important in forming the tide was Erlinge *et al.* (1983) "*Can vertebrate predators regulate their prey?"*. They suggested that generalist predation prevented cyclic dynamics in small herbivores because alternative prey sustained numerical stability in the predator populations. This particular study was controversial and heated scientific discussions followed (Kidd & Lewis 1987; Erlinge *et al.* 1988). In Fennoscandia, observational studies as well as randomized and natural experimental research continued to highlight the role of predation as a natural process shaping the population dynamics of woodland grouse (Storaas & Wegge 1987; Marcström, Kenward & Engren 1988; Lindstrom *et al.* 1994; Smedshaug *et al.* 1999; Kauhala, Helle & Helle 2000).

Today, predation is considered as a limiting factor of grouse populations in Britain and central Europe (Storch 2007; Güthlin, Storch & Küchenhoff 2013; Baines, Aebischer & Macleod 2016). Currently, most scientific approaches attempting to understand grouse predators and predation rates, indirectly focus on the ultimate factors shaping predation pressure in landscapes dominated by various human land use practices (Güthlin, Storch & Küchenhoff 2013; Baines, Aebischer & Macleod 2016; Huhta *et al.* 2017; Kämmerle *et al.* 2017). The knowledge-vacuum concerning the fundamentals of predation-effects on grouse populations consist of detailed understanding of interspecies mechanisms like compensatory predation (e.g. Ellis-Felege *et al.* 2012), the importance of subsidization (e.g. Newsome *et al.* 2015) and mechanisms connecting habitat to woodland grouse mortality (Storch 2015). In many areas, predator removal is the only quick-fix to remnant grouse populations but it is a paradox that lethal control of predator species has generally low acceptance among the public (e.g. Messmer *et al.* 1999) despite strong evidence of the part played by humans in the numerical increase of generalist predators. This controversy is perhaps prolonging the time until more studies expand our knowledge of the elephant in the room.

Objectives

In the broadest sense, the perspective of this thesis is to improve detailed understanding of important mechanisms behind declines in population densities and reductions in cyclic amplitude of two small game species in Fennoscandia. The tenet has been that the proximate cause of mortality have been and still is predation, and that variation in reproductive success is the most important factor for short and long-term woodland grouse population dynamics. Specifically, the goals were:

I. Assess long-term and large-scale trends in capercaillie and black grouse reproductive success and evaluate its contribution to the observed population decrease.
II. Identify and quantify predators of capercaillie and black grouse nests and explore the numerical and functional responses of the most important predators.
III. Investigate foraging patterns of red fox and pine marten.
IV. Evaluate relationships of anthropogenic land-use to red fox population dynamics.

Material & methods

Study areas

This thesis is based on field-observations from southeast and central Norway (Paper I, II and IV) and northern Sweden (Paper III). Apart from Fennoscandian data in Paper I, I additionally included data from Andorra, Austria, England, Estonia, France, Germany, Italy, Poland, Scotland, Slovakia, Switzerland and Wales. Fennoscandia comprise mostly of intensively managed boreal forests dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Josefsson *et al.* 2010). Agricultural land and settlements are generally concentrated in the south and along the coast. Outside Fennoscandia, lowland capercaillie and black grouse habitats are mainly conifer plantations and scrublands whereas habitats of populations inhabiting the foothills of the alps are dominated by Norway spruce, fir (*Abies alba*) and beech (*Fagus sylvatica*) (Storch 1994; Saniga 2002) (Figure 3).

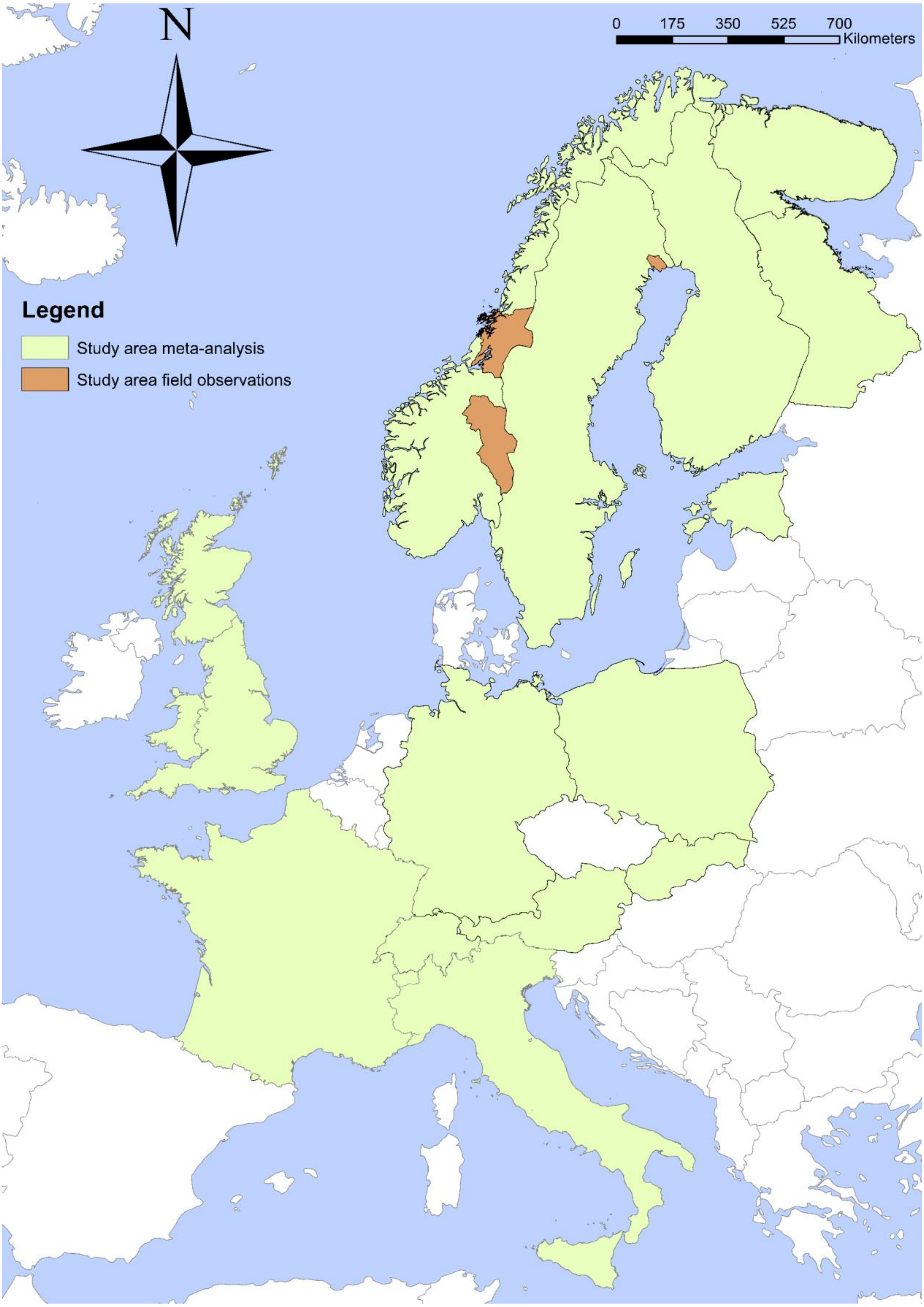

Figure 3 Map of study area used for field observations (dark) and meta-analysis of previously collected data (light).

Data collection and statistical analysis

Paper I

To conduct a meta-analysis of regional, long-term capercaillie and black grouse reproductive performance, I scanned online databases for publications reporting demographic data on reproduction parameters and adult survival throughout capercaillie and black grouse ranges. I also searched for data reported in grey literature like Grouse News, scientific monographs, institution reports, dissertations and conference proceedings. Additionally, I included nesting data collected for paper II between 2009 and 2012. In the end, the dataset spanned 80 years and originated from 16 countries in Fennoscandia, Great Britain and continental Europe. Nest success data was retrieved from 17 and 18 studies, brood data came from 16 and 24 whereas chick data originated from 29 and 33 studies of capercaillie and black grouse respectively. I evaluated trajectories of nest success, brood frequencies and chicks per hen by fitting additive binomial and Poisson mixed models (GAMM) (Wood 2006) with median year as independent variable. I fitted study and method used for collection (e.g. radio-marked, line transects etc.) as random intercepts. I weighed observations underlying nesting success models by sample size whereas model weights for brood and chick models were study duration. To illustrate the implications of changes in reproduction to capercaillie and black grouse populations, I estimated the survival adult females required to counterbalance the modelled production of chicks and compared these estimates to published survival rates.

Paper II

Paper II builds on monitoring of 267 capercaillie and 68 black grouse nests detected between 2009 and 2014 in Hedmark and Nord-Trøndelag counties in Norway. Because capturing and tagging numerous capercaillie and black grouse hens was not economically and logistically feasible, we called for nest observations during spring and early summer (May-July). We published calls in local newspapers and other media before the onset of nesting season. Rangers and forestry workers planting, thinning or logging forests reported additional nests. Initially, the main objective was to identify nest predators and we made efforts to monitor as many nests as possible with camera traps. We distributed cameras to volunteers responsible for organizing nest observations locally. Nest fates and nest site information was recorded at the end of incubation (> 30 days). To investigate relationships of nest predation to vole dynamics I had to utilize Tengmalm's owl reproductive data (Lehikoinen, Ranta & Pietiäinen 2011) at county resolution as a proxy of vole abundance and vole cycle phase. Expressing vole dynamics as both abundance and cycle phase allowed us to test for both cyclic amplitude and the temporal component in functional response in predator foraging behaviour (i.e. prey switching) during two complete vole cycles. Annual red fox and pine marten abundances were collected with the same method as in Paper IV and covered the entire forested areas in both Hedmark and Nord-Trøndelag counties. Grouse nests are most often detected when the hen flush from the nest due to the perceived threat by the approaching human. This means that nests where incubation is already completed or aborted have lower detectability. This bias is best accounted for by modelling daily probabilities of nest failure (Mayfield 1975) as opposed to crude nest failure (i.e. percentage of nests lost). Studies commonly treat nest fates as a binary variable, either hatched or predated. This is problematic when nests are predated by a guild of predators rather than a single species. Such pooling of different nest fates (e.g. different predator species) cloud mechanisms that are important in regulating nest loss due to e.g. inherent differences in predator ecology. I therefore modelled predation on capercaillie nests in both a binary and competing risks (Etterson *et al.* 2007) framework. I did not partition the few observed nest fates in black grouse. This way, I parametrized predation models to evaluate common hypotheses explaining predator-prey interactions and models were ranked in an information-theoretic framework (Burnham & Anderson 2002). I could not evaluate potential camera-effects on nest predation rates but I provide detailed information on camera trap efficiency. Finally, I regressed daily probabilities of predation against relative change in hunter bag size to visualize the importance of nest survival to annual population dynamics in capercaillie and black grouse.

Paper III

Red fox and pine marten snow track data that we utilized in paper III was collected during the winters of 1975-81 and 1985-87 in relation to a large-scale predator-removal experiment conducted in Northern Sweden (Cf. Marcström, Kenward & Engren 1988). A total of 2139 and 533 km of careful red fox and pine marten snow tracking was conducted by experienced trappers on mostly Bergön and Rånön islands off the coast in Kalix municipality. We observed 330 red fox and 107 pine marten tracking events and we used hunting attempts and snow-digging events to model their winter foraging behaviour and to evaluate their foraging niches in relation to snow-depth and temperature. We used frequencies of hunting attempts and dig events as well as their rate of success as dependent variables in a Bayesian regression model framework. We fitted year as random intercept and we considered four covariate sets for each model.

Paper IV

In paper IV I synthesize data on red fox tracks crossing 613 predefined transects. Data was collected during an extensive monitoring programme originally designed to monitor family groups of Eurasian lynx (*Lynx lynx*) in Hedmark County, Norway. In total 268-472 transects of 2.95 km length were repeatedly surveyed mid-winter each year from 2003 until 2014 yielding 21675 observations of crossing red fox tracks. In a Bayesian linear model framework I used red fox abundance (tracks km^{-1} 24hrs^{-1}) and the instantaneous rate of increase ($r_t = \ln(\frac{N_t}{N_{t-1}})$) as dependent variables. Because estimation of r_t requires complete time series with no gaps (e.g. no observations or years not surveyed), I pooled transects into 300 groups based on proximity. Transect groups thereby represented complete, spatially explicit time series used for estimating r_t. Abundance and growth (r_t) models were parameterized with predictors describing elevation, latitude, settlement density, agricultural density and the number of moose culled per hectare productive forest for each municipality. Moose culled was an index of available gut piles (i.e. offal). Each model of r_t was fitted with abundance as a consistent component of an interaction with each of the landscape predictors. This regressed r_t against abundance over e.g. varying elevation and thus allowed us to investigate direct density dependent growth across the landscape.

Results and discussion

Long-term changes in reproductive success

Reproduction success for both capercaillie and black grouse have universally declined in Fennoscandia between 1930 and 2012. Apparent nest success (i.e. proportion hatched) decreased from 0.89 to 0.35 for capercaillie whereas black grouse nest success decreased from 0.90 to 0.55. Overall, the proportion of capercaillie hens with a brood in late summer decreased from 0.90 to 0.37, with a halt in the decrease between 1977 and 2001. Similarly, the proportion of black grouse hens with a brood was reduced from 0.83 to 0.35. Declines in chicks per capercaillie hen were observed between 1958 and 1982, and the number of chicks reared per capercaillie hen decreased from 3.1 to 1.2 chicks whereas chicks per black grouse hens reduced from 3.5 to 1.6 between 1967 and 1987 (Figure 4). Despite an observed increase in survival for adult hens, the increase was not sufficient to counterbalance declines in reproduction (Figure 5).

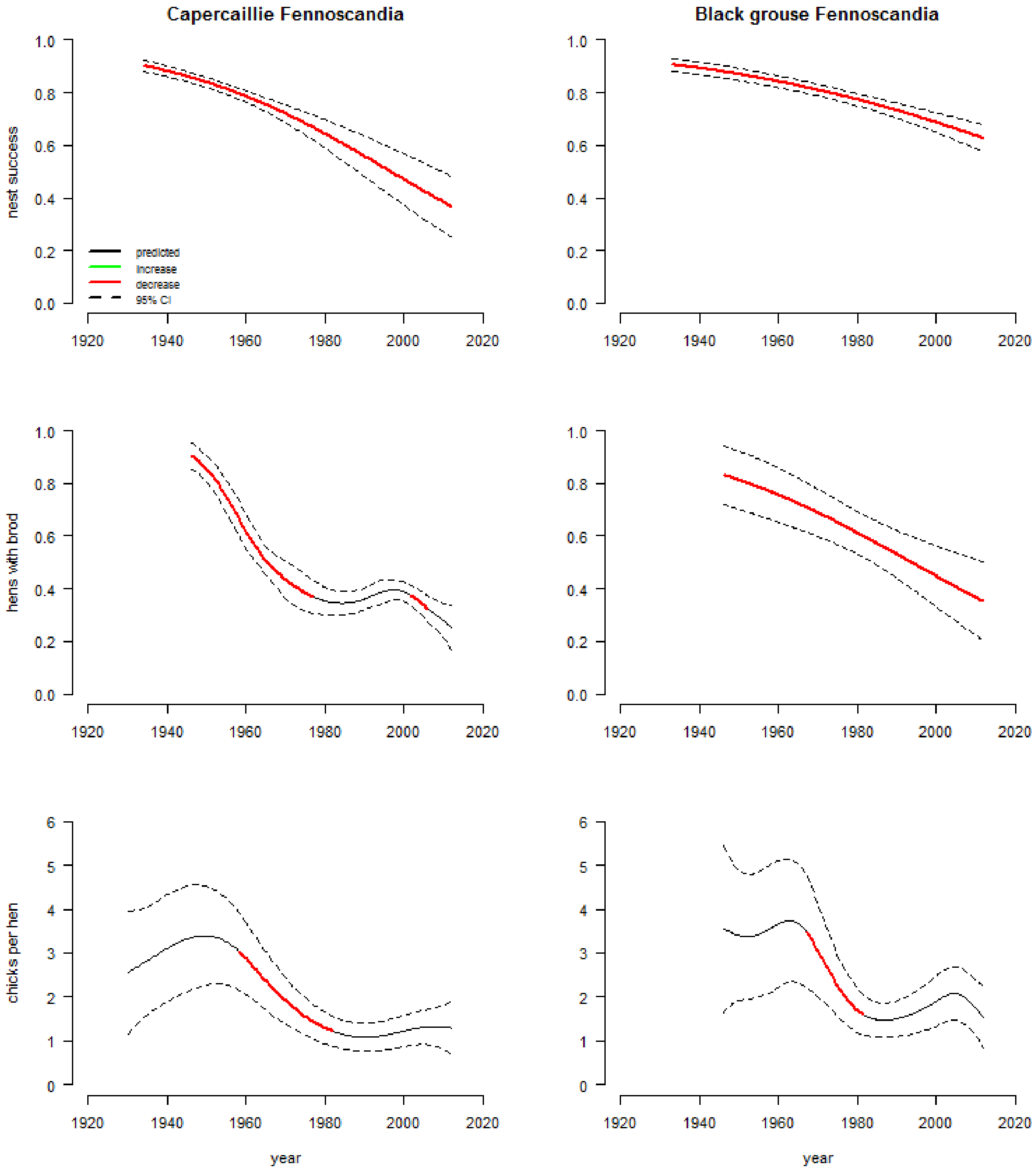

Figure 4 From top to bottom: Fitted trajectories from GAMM models of nest success, proportion of hens with brood and chicks per hen for Fennoscandian capercaillie (left) and black grouse (right) between 1930 and 2012.

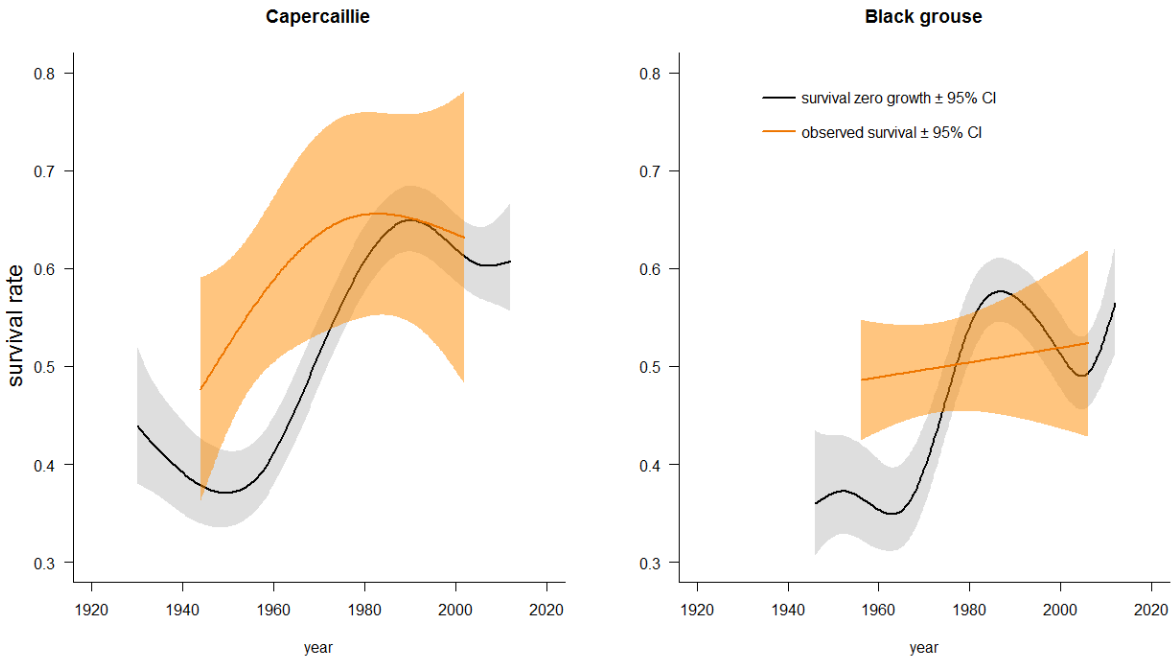

Figure 5 Annual survival rate for adult capercaillie (left) and black grouse (right) hens required to offset the modelled chicks per hen (black) and observed annual survival rates (orange).

Although the dominant cause of nest failure in most studies is predation, the relative proportion of other nest fates appears to have changed through time. In earlier studies, nest failures due to; desertions, embryo mortality and human disturbance occurred relatively frequently (Höglund 1953; Siivonen 1953; Myrberget & Hagen 1974). Later however, these types of nest fates have continuously receded on the account of predation. This may suggest that some nest predation is compensatory, and that predation occurs earlier than before. This further suggest that nest loss due to predation alone is represented by a steeper curve than the one showed here (Figure 4).

Despite few accounts of identified mortality-causes in capercaillie and black grouse chicks, fates are normally partitioned into predation or weather-related causes (Wegge & Kastdalen 2007). Indirect evidence also point to the importance of nutrition to chick survival (Picozzi, Moss & Kortland 1999; Baines, Richardson & Warren 2017), but the causal relationships of variations in chick survival to the nutritional conditions are unknown. Nevertheless, apart from incidental mortality directly caused by adverse weather or lack of food, chicks are more susceptible to predation under such conditions (Wegge & Kastdalen 2007). As such, weather and nutrition are likely agents shaping predation rates. Precipitation during incubation and chick-rearing have also been related to lower reproductive success in woodland grouse (Marcström 1960; Semenow Tjan Shanskiy 1979; Moss 1986). Predation rates on chicks and eggs can increase immediately after precipitation events (e.g. Herman-Brunson *et al.* 2009). Such moisture-facilitated predation can occur both due to increased bacterial growth on wet feathers as well as the increase in evaporation of scent molecules under wet conditions and thereby facilitating olfactory predators (Conover 2007).

There is no clear explanation for the increase in hen survival. Goshawks (*Accipiter gentilis*), an important predator on adult birds have increased (Kjellén & Roos 2000). Increased hen survival may originate from black grouse and capercaillie today, only surviving in landscapes where adult survival counterbalance poor breeding success. Similar mechanisms have been discussed for rock ptarmigan in Europe (Novoa *et al.* 2011). Alternatively, reproduction comes at a cost. Capercaillie hens loose about 20 % of their body weight between mating and hatching of the eggs (Storaas, Wegge & Kastdalen 2000) and studies of both altricial and precocial bird species, have linked successful reproduction to reduced survival of the female due to energetic stress of incubation and brood rearing (Nur 1984; Flint & Grand 1997).

Predation by red fox and pine marten on capercaillie and black grouse nests

Red fox and pine marten were the most frequent predators on nests from capercaillie and black grouse nests. Of identified predators, red foxes predated 42.4 % and 55.6 % whereas pine martens predated 41.0 % and 33.3 % of capercaillie and black grouse nests respectively. Corresponding predation from the European badger (*Meles meles*) was 12.1 and 11.1%. We observed one occasion of wolverine (*Gulo gulo*), domestic dog (*Canis familiaris*) and golden eagle (*Aquila chrysaetos*) predating capercaillie nests (Figure 6). We observed corvid species (common raven and hooded crow) at nest sites but the incubating hen constantly confronted them and no predation from corvids was observed at active nest sites (Figure 7).

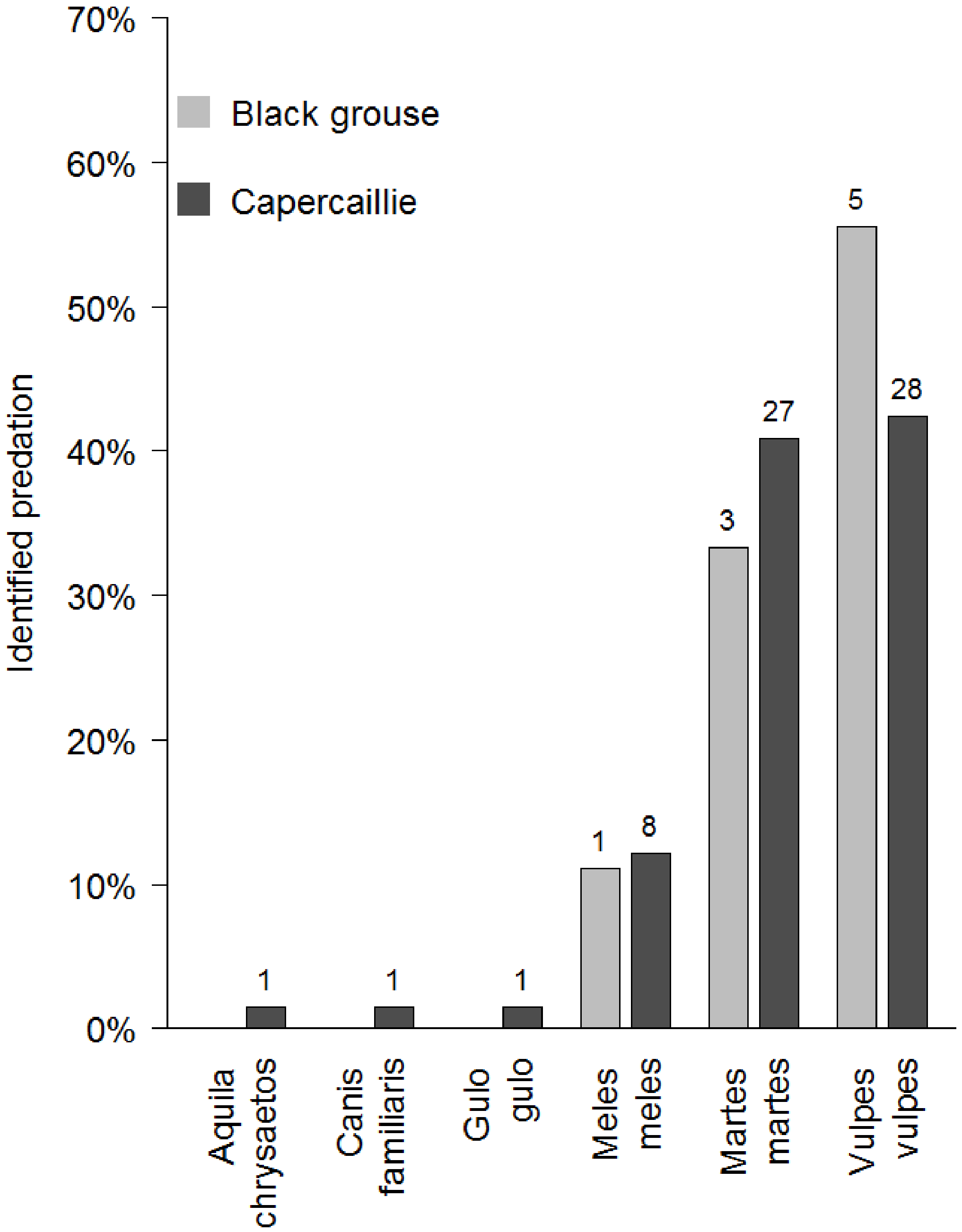

Figure 6 The distribution of camera-identified predators predating capercaillie (dark) and black grouse (light) nests.

Figure 7 Capercaillie and black grouse hens defending their nests against hooded crows and ravens

Despite lacking proof of corvid predation on capercaillie and black grouse nests, there is a general consensus that hooded crows and common ravens are important for nest survival in woodland grouse and studies frequently refer to corvid habitat as high-risk habitat for capercaillie and black grouse (e.g. Huhta *et al.* 2017). This belief originates from a set of studies conducted by the use of artificial nests (e.g. Picozzi 1975; Andren & Angelstam 1988). It is credible nonetheless, that corvid predation occur as hens may not always be successful in defending their nests but the extent of avian predation on capercaillie and black grouse nests is to a lesser extent than earlier reasoned.

Daily probabilities of pooled predation on black grouse nests were best explained by pine marten abundance, vole abundance and their interaction. The main effects of pine marten and voles were as expected. Predation increased with pine marten abundance and decreased with vole abundance. The relationship to vole abundance however, did not follow the expected trajectory when the abundance of pine marten increased. At high pine marten abundances, more voles did not relieve black grouse nests of predation (Figure 8). These patterns are not consistent with the mechanisms explained by the alternative prey hypothesis but rather those of incidental predation (Vickery, Hunter Jr. & Wells 1992; McKinnon *et al.* 2010). One possible caveat behind these results are the relatively low sample of black grouse nests when spread across each phase in the vole cycle. Nevertheless, similar uncertain relationships of nest loss in black grouse to vole abundances have been observed earlier (Wegge & Storaas 1990).

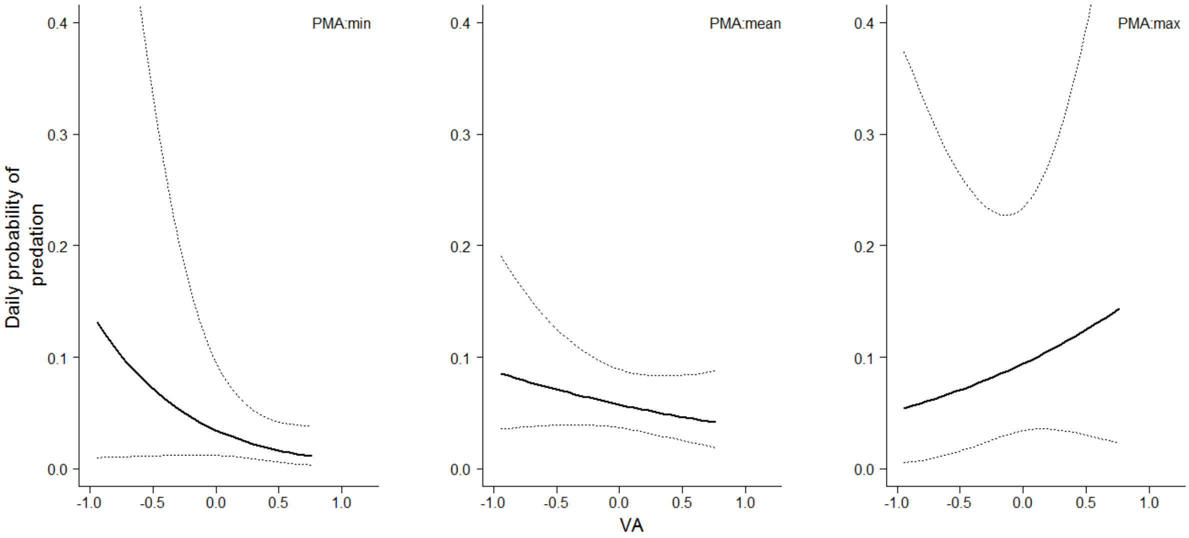

Figure 8 Estimated daily probability of pooled predation for black grouse nests as a function of standardized vole abundance (VA) under minimum, mean and maximum observed pine marten abundances (PMA).

Conversely, patterns of pooled predation on capercaillie nests followed the vole cycle as predicted by the alternative prey hypothesis. High losses to predators in the crash phase of the cycle and subsequent reduced predation as voles increased and peaked. Again, pine marten abundance affected the structure of nest predation in relation to voles. At high pine marten abundances, probabilities of predation on capercaillie nests in the peak phase succeeded those of the increase phase (Figure 9). Similar patterns were observed in a system wherein alternative prey sustained elevated densities of generalist predators which subsequently supressed cyclicity in voles. The proposed mechanism was that a numerical response in the predator population had already occurred due to alternative food and an increase (or decrease) in voles would only trigger a functional response (i.e. prey switching) (Erlinge, Göransson & Hansson 1983).

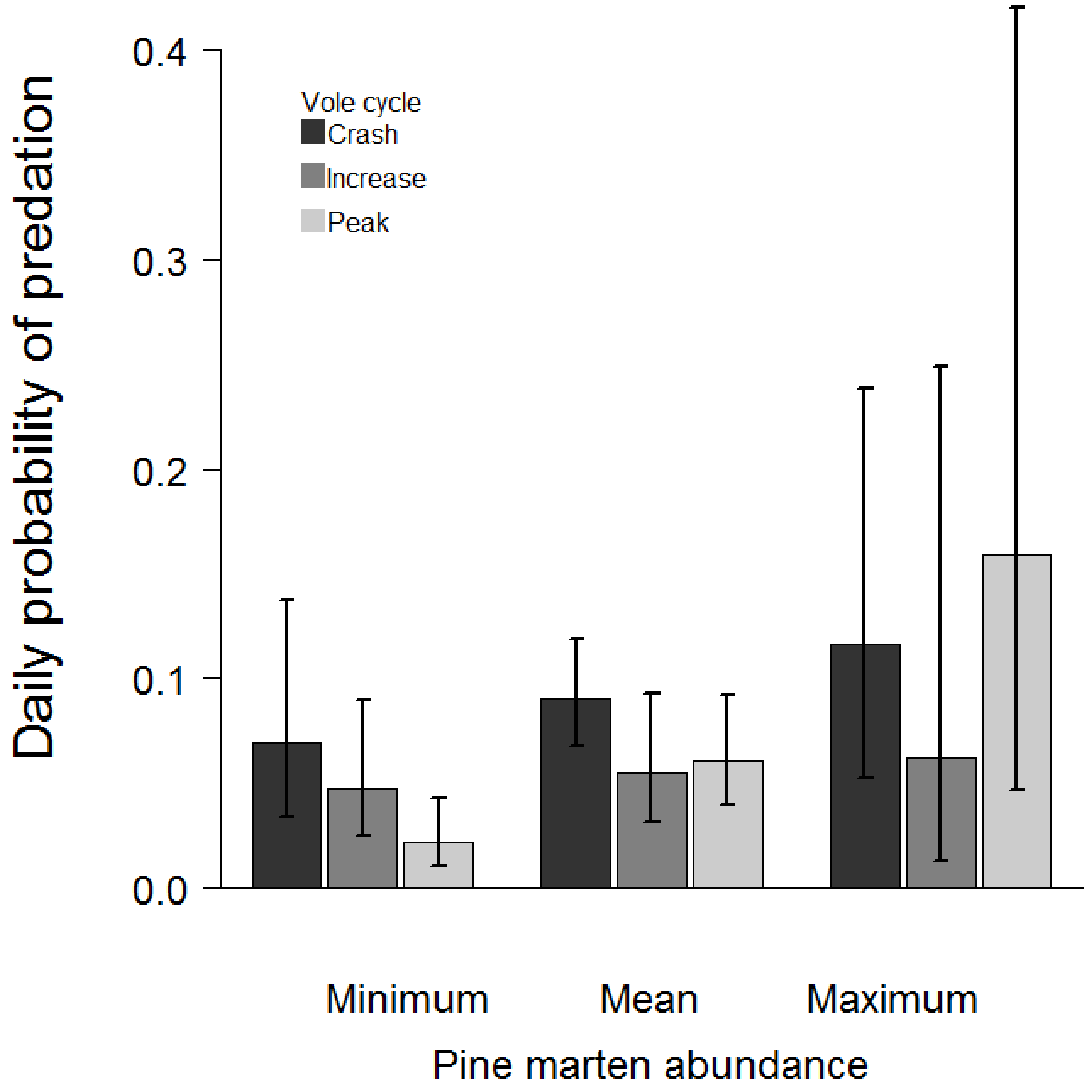

Figure 9 Estimated daily probability of pooled predation on capercaillie nests during the vole cycle with minimum, mean and maximum observed pine marten abundances.

Competing risk analysis of partitioned predation on capercaillie nests showed that pine marten predation was best explained by pine marten abundance whereas red fox predation was best explained by the vole cycle (Figure 10). Regardless of the vole situation, pine martens predated capercaillie nests. As eggs constituted half of all pine marten digs during winter (Paper III) they are important food items for long-term caching (Helldin 1999). Since caching is a form of surplus killing (i.e. higher kill-rates than immediate consumption rates) (Smith & Reichman 1984), this behaviour can affect the functional response of the predator (e.g. Fletcher *et al.* 2010) and thus mask potential effects of e.g. vole fluctuations. Pine marten predation on capercaillie eggs does therefore not coincide with the mechanics explained by the alternative prey hypothesis. The same was concluded in a study of pine marten predation on cavity nests of common goldeneye (*Bucephala clangula*) (Pöysä, Jalava & Paasivaara 2016). Interestingly, two long-term studies of small game community dynamics in the boreal forests have previously found little support for the alternative prey hypothesis in their data (Lindén 1988; Small, Marcström & Willebrand 1993). Coincidentally, these studies were based on data collected partly during the outbreak of sarcoptic mange in Finland and Sweden. During the mange, red foxes were scarce and pine martens more abundant (Lindstrom *et al.* 1994; Smedshaug *et al.* 1999). Conversely, patterns of red fox predation is predictable as described by the alternative prey hypothesis and therefore complements earlier studies on red fox predation (Hörnfeldt 1978; Danell & Hörnfeldt 1987; Angerbjörn 1989).

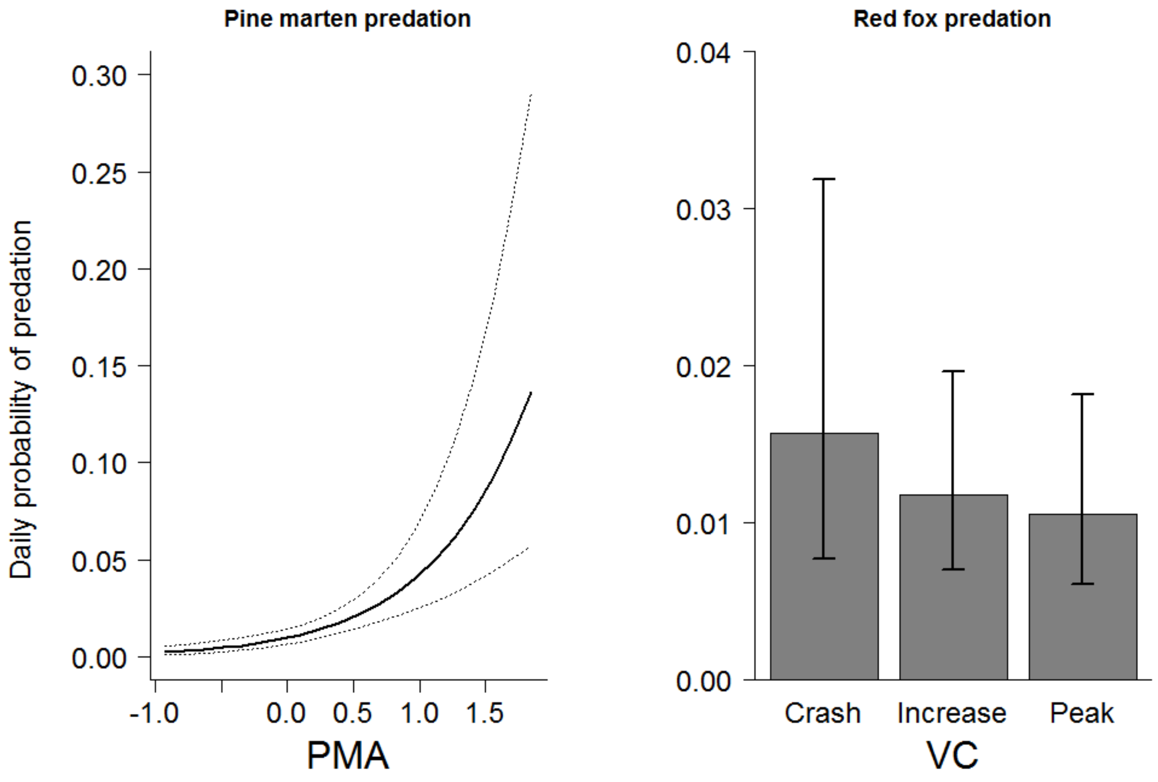

Figure 10 From left to right; pine marten and red fox predation on capercaillie nests as a function of standardized pine marten abundance (PMA) and the vole cycle (VC) respectively.

Foraging patterns of red fox and pine marten

Red fox dug for food at a higher frequency that pine marten whereas the frequency of hunting events was similar (Figure 11 a and b). Pine marten however, was more successful than red fox during both digging and hunting (Figure 11 c and d). Red fox had a wider niche breadth than pine marten in their prey selection when hunting or digging. Red fox dug mostly for voles (37 %) and ungulates (26 %) meanwhile pine marten dug for mostly for eggs (48 %) but also some small birds (22 %) and voles (21 %). Red fox hunting attempts were mostly directed towards voles (48 %) and to a smaller degree towards mountain hares (22 %) and grouse (20 %). Pine marten on the other hand, hunted mostly for small birds (59 %) and some hares (24 %). Overall, red fox had wider niche breadth than pine marten in prey selection for digs and hunting attempts. Food niche overlap was small between the two species (Table 1).

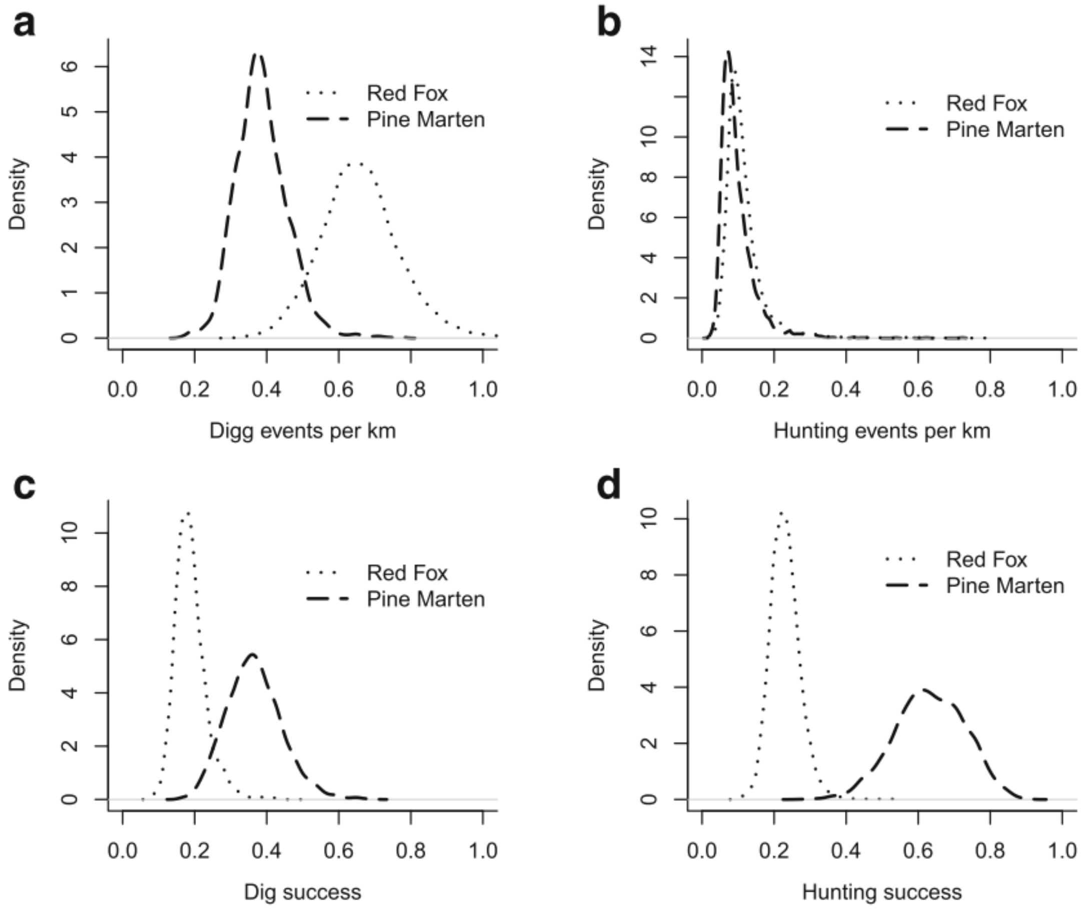

Figure 11 Predicted distributions for red fox and pine marten a) digging and b) hunting events and c) digging and d) hunting success under mean snow depth and temperatures.

Perhaps a bit surprising was the relatively small niche overlap in prey items for both dig and hunting events which suggests little competition between red fox and pine marten in these activities. Similarly, little change in pine marten habitat selection was found in response to the absence of red fox in Sweden (Storch, Lindström & de Jounge 1990). Although we did not observe intra-guild predation or attempts by red fox to kill pine marten, such a mechanism has been hypothesized to have played a part in the increase of pine marten during the sarcoptic mange (Lindstrom *et al.* 1994; Lindström & Brainerd 1995).

The consumption of cached eggs in winter by pine marten have been observed earlier (Höglund 1960; Pulliainen 1980; de Jounge 1981; Helldin 2000b) and suggest that eggs are frequently used for long-term caching since eggs are only available in spring and early summer. This is a special feature of the pine marten since only 8 % of red fox dig events were for eggs. This study also confirms the importance of both voles and ungulate remains for red foxes during winter (Needham *et al.* 2014) as well as the low utilization of ungulate remains by pine marten (Gomo *et al.* 2017).

Since Pianka's niche overlap index is symmetric (Pianka 1974), it is quite suitable for investigating the proportional use of a resource that two species depend on. Nevertheless, it also assumes that resources are equally available to the species analyzed. Although little arboreal activity by the pine marten was observed in this study, arboreal prey like birds are available to the pine marten (Brainerd *et al.* 1995) but not to the red fox.

Table 1 The proportion of different prey items identified from red fox and pine marten digs and hunting events during snow tracking.

Activity	Species	Vole	Hare	Small birds	Ungulate	Grouse	Egg	Other	Niche breadth	Niche overlap
Digging	Red fox (261)	37%	11%	8%	26%	–	8%	8%	0.54	0.14
	Pine marten (77)	21%	–	22%	1%	–	48%	8%	0.34	
Hunting	Red fox (54)	48%	22%	6%	–	20%	–	6%	0.34	0.11
	Pine marten (17)	–	24%	59%	–	12%	–	6%	0.23	

Effects of anthropogenic land use on spatiotemporal population dynamics in red fox

Red fox abundance was best explained by relative settlement density and offal density in the forest. Red fox abundance positively related to settlements whereas the relationship to offal was weak (Figure 12). We did not detect cyclicity in the red fox population and first order dynamics (i.e. direct density dependence) was the dominating pattern in population fluctuations. Among the models parameterizing first order density dependence, the relative density of agricultural land was the best performing covariate. Across the agriculture spectrum, the red fox population was more stable when the amount of agriculture was relatively high than low (i.e. population equilibrium point increased with agriculture). Moreover, the intrinsic rate of increase was asymmetrically related to abundance depending on the amount of agriculture in the landscape thus suggesting stronger density dependent processes in marginal agricultural areas (Figure 13).

Anthropogenic subsidization is a key concept explaining the relatively close relationships between red fox population dynamics and abundance to human land use. Both settlements and gut piles from big game hunting have earlier been identified as frequently used resources by red fox (Panek & Bresiński 2002; Gomo *et al.* 2017; Paper III). Offal however, is temporally important to red foxes and inversely related to the abundance of voles and lemmings (Jędrzejewski & Jędrzejewska 1992; Killengreen *et al.* 2011). Since all years were pooled in this analysis, the relationship between red fox abundance and offal encompass potential variation mediated by voles. The importance of such readily available resources to red fox population dynamics and its potential to trigger ripple effects throughout the food web is scarcely studied and mostly in winter. In general however, human-provided foods can be expected to increase consumer abundance, change the consumers dietary preferences to include subsidies and change life-history traits (e.g. sociality, survival, fecundity etc.) of the consumer (Newsome *et al.* 2015).

A criticism of direct density dependency is regression toward the mean (e.g. Kelly & Price 2005). This phenomena describes how an extreme measurement of a given parameter subsequently yield values closer to the mean of that parameter (e.g. Stigler 1997). Since annual variation was the dominating dynamic in red fox abundance, regression to the mean is a credible concept explaining this particular pattern. However, the asymmetry we show in density dependent growth for red foxes across the agricultural landscape is not consistent with regression effects as you would expect regression effects to result in uniformly distributed r_t across variations in agriculture as well as a unimodal distribution around mean N_{t-1}.

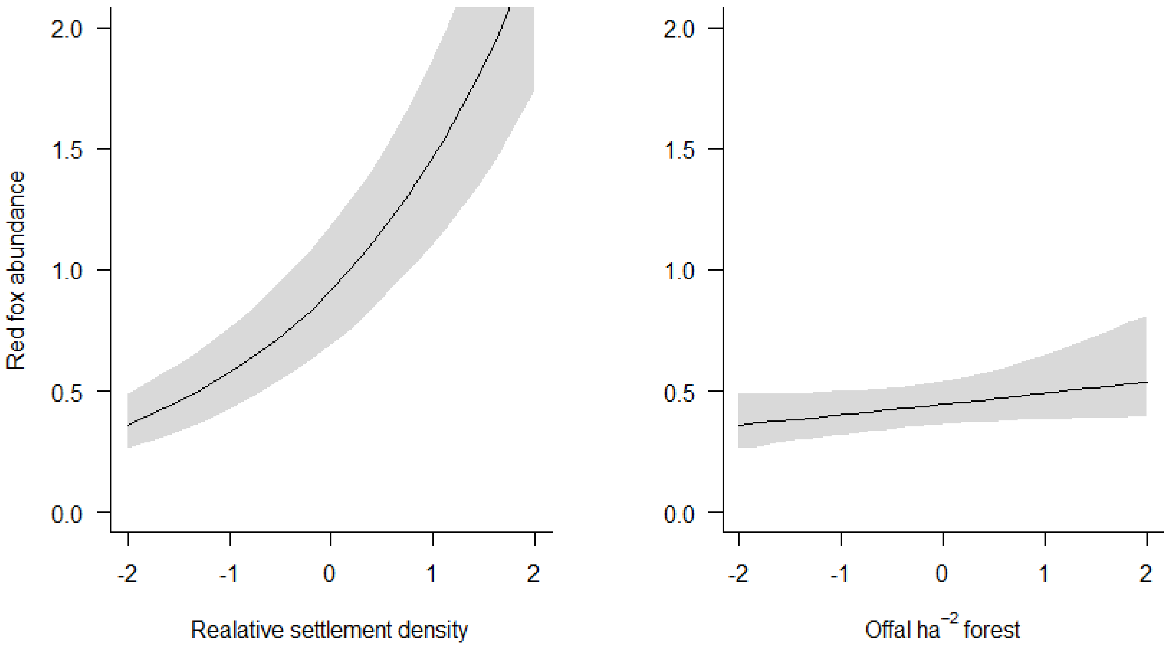

Figure 12 Model weighted predictions of red fox abundance as a function of standardized settlements (left) and standardized offal ha^{-2} productive forest (right) whilst holding the other fixed effect constant at mean value. Shaded areas are 95% highest posterior density intervals.

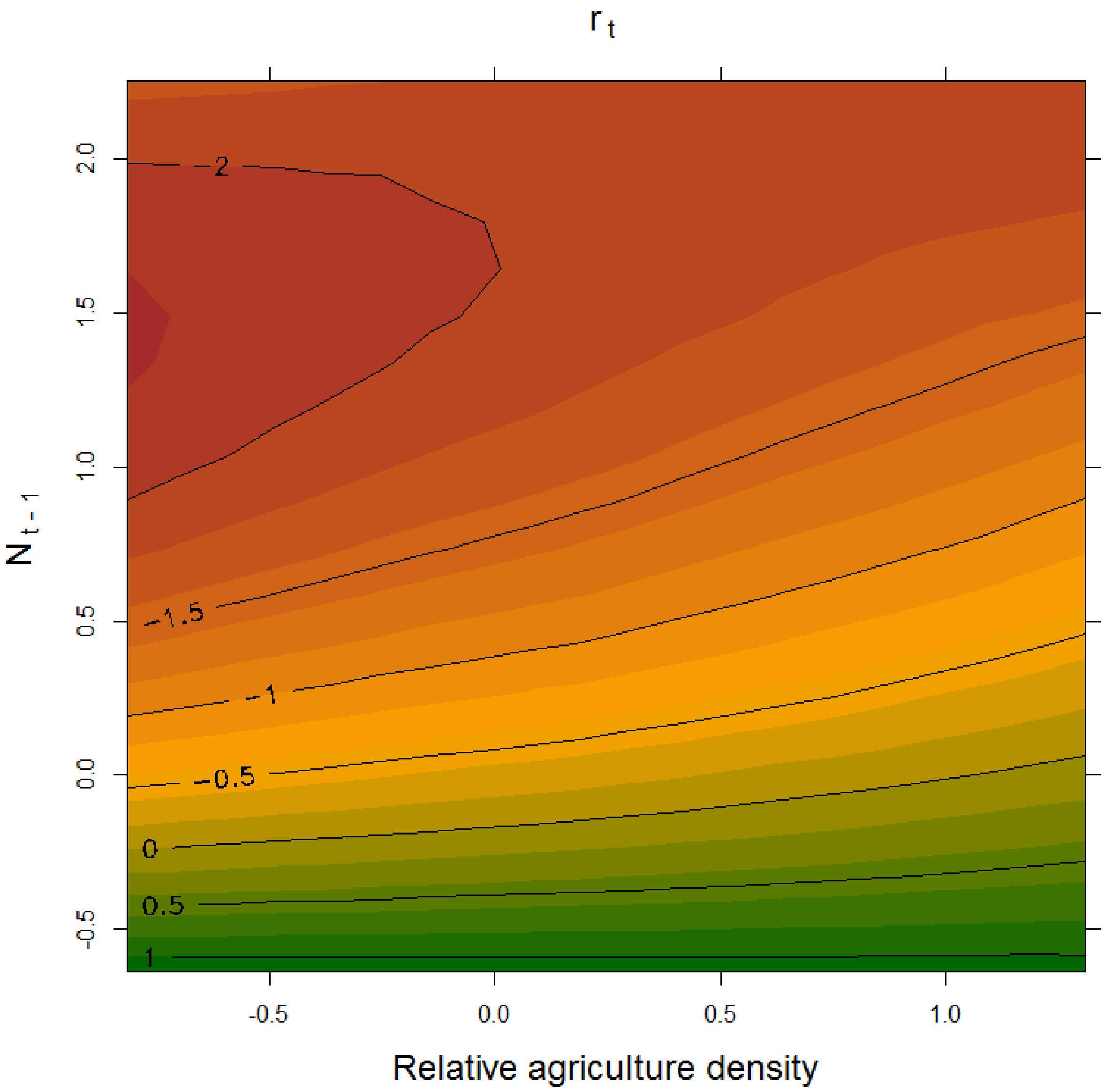

Figure 13 Model weighted predictions of the interaction between standardized agricultural land and red fox abundance (N_{t-1}) on the instantaneous rate of increase in the red fox population. Red to green gradient depict negative to positive instantaneous rate of increase.

Conclusions and future work

I have shown that Fennoscandian populations of capercaillie and black grouse have suffered from long-term declines in the number of nests that hatch and the number of chicks that survive until fall. Populations seem to be stuck around a new and lower equilibrium. Reoccurring failure in reproductive attempts is a sufficient explanation for the reported population declines and changes in the levels of predation pressure is a part of the explanation. Today, red fox and pine marten are the most common mesocarnivores in the boreal forests, and I have shown that they are main predators on capercaillie and black grouse nests. In areas outside Fennoscandia, other species e.g. wild boar (*Sus scrofa*) and stone marten (*Martes foina*) may compensate or add to red fox and pine marten predation on woodland grouse nests.

Previous studies have suggested that nest predation on ground-nesting birds in the boreal forest is a random process (Wegge & Storaas 1990) but here I show that nest predation patterns are multi-faceted depending on the predator involved. Red fox predation was modulated by the vole cycle whereas pine marten predation increased with a numerical increase in pine marten. Nest predation by red fox therefore agree with the alternative prey hypothesis whereas nest predation by pine marten does not. Density estimates (Marcström, Kenward & Engren 1988; Marcström *et al.* 1989) as well as indirect evidence (Kurki *et al.* 1998) moreover suggest that pine martens are less abundant than red foxes in the boreal forest. Pine marten appeared henceforth more specialized and efficient than red foxes in predating nests. Investigations into their foraging niche supported this interpretation. Pine martens foraged for cached eggs, whereas the foraging niche of red fox was opportunistic in comparison. The red fox is closely tied to human land use and agricultural practices may regulate red fox populations via subsidization, induce numerical stability and furthermore mask any potential relationships between naturally given landscape features and red fox population dynamics.

The massive transformation of forest structure following mechanisation of silviculture was temporally in line with population declines in Fennoscandian capercaillie and black grouse. This temporal match is probably what spurred research interests into relations of forest composition and structure to woodland grouse population performances. Still today, these relationships are considered a “black box” (Storch 2015). Besides the importance of bilberry (e.g. Storch 1993; Baines, Moss & Dugan 2004) and the extent of conifer forest cover (e.g. Sirkiä *et al.* 2011), there is no consensus on the specifics of forest habitat requirements. Previously suggested habitat requirements, e.g. capercaillie and old growth forest, have been downgraded and habitat quantity (i.e. extent) rather than quality is considered important landscape features (Angelstam 2004; Sirkiä *et* *al.* 2011; Wegge & Rolstad 2011; Lande *et al.* 2014). Perhaps the devil is not in the details as an increasing number of studies point to coarse, landscape-scale processes as important factors in shaping the mechanisms driving capercaillie and black grouse population performances rather than fine-grained and small-scale e.g. vegetation structure (e.g. Storch 2002; Graf *et al.* 2005).

Whereas capercaillie and black grouse populations in Fennoscandia are of least concern, British and central European populations are in trouble (IUCN 2016). There is good evidence that predator control will improve reproductive success and facilitate population growth. In most areas however, this approach to grouse conservation is not ethically or practically feasible. Despite a focal topic for decades (Moss, Storch & Müller 2010), there is little evidence of forest-habitat structures that directly or indirectly change demographic rates in woodland grouse, but experiments are lacking. Until such experiments are conducted, managers have to grope in the dark for alternative conservation measures to predator control.

References

Andersen, R., Fagerheim, W.I. & Solheim, J. (2009) *Hjorteviltforvaltning. Hvordan Forvalte Store Beitedyr. Tre Scenarier.* Trondheim - In Norwegian.

Andren, H. (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology*, **73**, 794–804.

Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*.

Andren, H. & Angelstam, P. (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology*, **69**, 544–547.

Angelstam, P. (1983) *Population Dynamics of Tetraonids Especially the Black Grouse* Tetrao Tetrix L. *in Boreal Forests*. Uppsala University, Uppsala, Sweden.

Angelstam, P. (1984) Sexual and seasonal differences in mortality of the black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scandinavica*, **15**, 123–134.

Angelstam, P. (2004) Habitat Thresholds and Effects of Forest Landscape Change on the Distribution and Abundance of Black Grouse and Capercaillie. *Ecological Bulletins*, 173–187.

Angelstam, P., Lindström, E. & Widén, P. (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, **62**, 199–208.

Angerbjörn, A. (1989) Mountain hare populations on islands: effects of predation by red fox. *Oecologia*, **81**, 335–340.

Arditit, R. & Ginzburg, L.R. (1989) Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology*, **139**, 311–326.

Baddeley, A., Rubak, E. & Turner, R. (2015) Spatial point patterns: methodology and applications with R.

Baines, D., Moss, R. & Dugan, D. (2004) Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology*, **41**, 59–71.

Baines, D., Richardson, M. & Warren, P. (2017) The invertebrate diet of Black Grouse Tetrao tetrix chicks: a comparison between northern England and the Scottish Highlands. *Bird Study*, **64**, 117–124.

Baines, D., Aebischer, N.J. & Macleod, A. (2016) Increased mammalian predators and climate change predict declines in breeding success and density of capercaillie *Tetrao urogallus*, an old stand specialist, in fragmented Scottish forests. *Biodiversity and Conservation*, **25**, 2171–2186.

Bartoń, K. & Zalewski, A. (2007) Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography*, **16**, 281–289.

Benson, T., Brown, J. & Bednarz, J. (2010) Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology*, **79**, 225–234.

Berryman, A. & Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos*, **92**, 265–270.

Bogdziewicz, M. & Zwolak, R. (2013) Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review. *European Journal of Forest Research*, **133**, 1–11.

Brainerd, S.M., Helldin, J.O., Lindstrom, E.R., Rolstad, E., Rolstad, J. & Storch, I. (1995) Pine marten (Martes martes) selection of resting and denning sites in Scandinavian managed forests. *Annales Zoologici Fennici*, **32**, 151–157.

Brinchmann, A. (1926) Coccidiosen hos lirype. *Bergens Museums Årbok*, p. Bergen Museum, Bergen, Norway - In Norwegian.

Brittas, R. & Willebrand, T. (1991) Nesting habitats and egg predation in Swedish black grouse. *Ornis Scandinavica*, **22**, 261–263.

Brommer, J.E., Pietiäinen, H., Ahola, K., Karell, P., Karstinen, T. & Kolunen, H. (2010) The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. *Global Change Biology*, **16**, 577–586.

Burnham, K. & Anderson, D. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer.

Cagnacci, F., Lovari, S. & Meriggi, A. (2003) Carrion dependence and food habits of the red fox in an Alpine area. *Italian Journal of Zoology*, **70**, 31–38.

Caizergues, A. & Ellison, L.N. (2000) Age-specific reproductive performance of black grouse *Tetrao tetrix* females. *Bird Study*, **47**, 344–351.

Carricondo-Sanchez, D., Samelius, G., Willebrand, O. & Willebrand, T. (2016) Spatial and temporal variation in the distribution and abundance of red foxes in the tundra and taiga of northern Sweden. *Eur J Wildl Res*.

Cavallini, P. & Lovari, S. (1991) Environmental factors influencing the use of habitat in the red fox, Vulpes vulpes. *Journal of Zoology*, **223**, 323–339.

Christiansen, E. (1979) Skog- og jordbruk, smågnagere og rev. *Tidsskrift for skogbruk*, **87**, 115–119.

Coates, P.S., Connelly, J.W. & Delehanty, D.J. (2008) Predators of greater sage-grouse nests identified by video monitoring. *Journal of Field Ornithology*, **79**, 421–428.

Coates, P.S. & Delehanty, D.J. (2010) Nest predation of greater sage-grouse in relation to microhabitat factors and predators. *Journal of Wildlife Management*, **74**, 240–248.

Conover, M. (2007) *Predator-Prey Dynamics: The Role of Olfaction*. CRC Press, Boca Raton, FL.

Cornulier, T., Yoccoz, N.G., Bretagnolle, V., Brommer, J.E., Butet, A., Ecke, F., Elston, D.A., Framstad, E., Henttonen, H., Hornfeldt, B., Huitu, O., Imholt, C., Ims, R.A., Jacob, J., Jedrzejewska, B., Millon, A., Petty, S.J., Pietiainen, H., Tkadlec, E., Zub, K. & Lambin, X. (2013) Europe-wide dampening of population cycles in eystone herbivores. *Science*, **340**, 63–66.

Dahl, K. (1924) Norges Jeger og Fiskerforbunds Tidsskrift - In Norwegian. *Norges Jeger og Fiskerforbunds Tidsskrift - In Norwegian*, pp. 169–189.

Danell, K. & Hörnfeldt, B. (1987) Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. *Oecologia*, **73**, 533–536.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, Or, the Preservation of Favoured Races in the Struggle for Life*. J. Murray, London, UK.

DeVault, T., Jr, O.R. & Shivik, J. (2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, **102**, 225–234.

Dinsmore, S.J., White, G.C. & Knopf, F.L. (2002) Advanced techniques for modeing avian nest survival. *Ecology*, **83**, 3476–3488.

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.

Elmhagen, B., Kindberg, J., Hellström, P. & Angerbjörn, A. (2015) A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio*, **44**, 39–50.

Englund, J. (1980a) Population dynamics of the red fox (Vulpes vulpes L., 1758) in Sweden. *The Red Fox*.

Englund, J. (1980b) Yearly variations of recovery and dispersal rates of fox cubs tagged in Swedish coniferous forests. *Biogeographica*.

Erikstad, K. & Spidsø, T. (1982) The influence of weather on food intake, insect prey selection and feeding behaviour in willow grouse chicks in northern Norway. *Ornis Scandinavica*.

Erlinge, S., Goransson, G., Hogstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylven, M. (1983) Can vertebrate predators regulate their prey? *The American Naturalist*, **123**, 125–133.

Erlinge, S., Goransson, G., Hogstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylven, M. (1988) More Thoughts on Vertebrate Predator Regulation of Prey. *The American Naturalist*, **132**, 148–154.

Erlinge, S., Göransson, G. & Hansson, L. (1983) Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos*, **40**, 36–52.

Erlinge, S., Agrell, J., Nelson, J. & Sandell, M. (1991) Why are some microtine populations cyclic while others are not? *Acta Theriologica*.

Errington, P. (1946) Predation and vertebrate populations. *The Quarterly Review of Biology*.

ESRI INC. (2011) ArcGIS.

Etterson, M.A., Greenberg, R. & Hollenhorst, T. (2014) Landscape and regional context differentially affect nest parasitism and nest predation for wood thrush in central Virginia, USA. *The Condor*, **116**, 205–214.

Etterson, M., Nagy, L., Robinson, T. & Johnson, D. (2007) Partitioning risk among different causes of nest failure. *The Auk*.

Fletcher, Q.E., Boutin, S., Lane, J.E., Lamontagne, J.M., Mcadam, A.G., Krebs, C.J. & Humphries, M.M. (2010) The functional response of a hoarding seed predator to mast seeding. *Ecology*, **91**, 2673–2683.

Flint, P.L. & Grand, J.B. (1997) Survival of Spectacled Eider Adult Females and Ducklings during Brood Rearing. *The Journal of Wildlife Management*, **61**, 217–221.

Foley, J.A. (2005) Global Consequences of Land Use. *Science*, **309**, 570–574.

Formosof, A.N. (1933) The Crop of Cedar Nuts, Invasions Into Europe of the Siberian Nutcracker (Nucifraga caryocatactes macrorhynchus Brehm) and Fluctuations in Numbers of the Squirrel (Sciurus vulgaris L.). *The Journal of Animal Ecology*, **2**, 70.

Frafjord, K., Becker, D. & Angerbjörn, A. (1989) Interactions between arctic and red foxes in

Scandinavia—predation and aggression. *Arctic*.

Gelman, A. & Su, Y.-S. (2016) Data Analysis Using Regression and Multilevel/Hierarchical Models - R package version 1.9-3.

Gomo, G., Mattisson, J., Hagen, B.R., Moa, P.F. & Willebrand, T. (2017) Scavenging on a pulsed resource: quality matters for corvids but density for mammals. *BMC Ecology*, **17**, 22.

González, A. de & Cox, D. (2007) Interpretation of interaction: A review. *The Annals of Applied Statistics*, **1**, 371–385.

Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M. & Nilsen, E.B. (2012) Habitat heterogeneity and mammalian predator-prey interactions: Predator-prey interactions in a spatial world. *Mammal Review*, **42**, 55–77.

Goszczyński, J. (2002) Home ranges in red fox: territoriality diminishes with increasing area. *Acta Theriologica*.

Graf, R.F., Bollmann, K., Suter, W. & Bugmann, H. (2005) The importance of spatial scale in habitat models: Capercaillie in the Swiss Alps. *Landscape Ecology*, **20**, 703–717.

Güthlin, D., Storch, I. & Küchenhoff, H. (2013) Landscape variables associated with relative abundance of generalist mesopredators. *Landscape Ecology*, **28**, 1687–1696.

Hagen, Y. (1952) *Rovfuglene Og Viltpleien*, 1st ed. Gyldendal, Oslo, Norway (in Norwegian).

Halpin, M. & Bissonette, J. (1988) Influence of snow depth on prey availability and habitat use by red fox. *Canadian Journal of Zoology*, **66**, 587–592.

Hanski, I. (1990) Density Dependence, Regulation and Variability in Animal Populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **330**, 141–150.

Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *The Journal of Animal Ecology*, **60**, 353–367.

Hansson, L. (1988) The domestic cat as a possible modifier of vole dynamics. *Mammalia*, **52**, 159–164.

Hansson, L. (1992) Landscape ecology of boreal forests. *Trends in ecology & evolution*, **7**, 299–302.

Hansson, L. & Henttonen, H. (1988) Rodent dynamics as community processes. *Trends in ecology & evolution*, **3**, 195–200.

Hedwall, P. & Brunet, J. (2013) Changes in the abundance of keystone forest floor species in response to changes of forest structure. *Journal of vegetation Science*, **24**, 296–306.

Heiberg, G. (1995) *Essays Og Artikler*. Grøndahl og Dreyer, Oslo, Norway.

Helldin, J.-O. (1999) Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography*, **22**, 324–336.

Helldin, J.O. (2000a) Population trends and harvest management of pine marten *Martes martes* in Scandinavia. *Wildlife Biology*, **6**, 111–120.

Helldin, J.O. (2000b) Seasonal diet of pine marten Martes martes in southern boreal Sweden. *Acta Theriologica*, **45**, 409–420.

Helle, P. & Ikonen, K. (2015) Wildlife monitoring in Finland - on-line information to game administration, hunters and wider public, http://www.metla.fi/life/lifedata/pdf/Helle_IBFRA_2015.pdf

Henden, J., Ims, R. & Yoccoz, N. (2009) Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. *Journal of Animal Ecology*.

Henden, J., Ims, R., Yoccoz, N. & Hellström, P. (2010) Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. *Oikos*.

Henden, J., Stien, A. & Bårdsen, B. (2014) Community-wide mesocarnivore response to partial ungulate migration. *Journal of Applied Ecology*, **51**.

Henttonen, H. (1989) Does an increase in the rodent and predator densities, resulting from modern forestry, contribute to the long-term decline in Finnish tetraonids? *Suomen Riista*, **35**, 83–90.

Herman-Brunson, K.M., Jensen, K.C., Kaczor, N.W., Swanson, C.C., Rumble, M.A. & Klaver, R.W. (2009) Nesting ecology of greater sage-grouse Centrocercus urophasianus at the eastern edge of their historic distribution. *Wildlife Biology*, **15**, 395–404.

Hersteinsson, P. & MacDonald, D.W. (1992) Interspecific Competition and the Geographical Distribution of Red and Arctic Foxes Vulpes Vulpes and Alopex lagopus. *Oikos*, **64**, 505–515.

Hijmans, R.J. (2016) raster: Geographic Data Analysis and Modeling.

Hjeljord, O. (2015) *INA Fagrapport 30: Ryper Før Og Nå*. Fakultet for miljøvitenskap og teknologi Institutt for naturforvaltning, Ås, Norway - In Norwegian.

Holling, C. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385–398.

Hone, J. (1999) On rate of increase(r): patterns of variation in Australian mammals and the implications for wildlife management. *Journal of Applied Ecology*.

Hornfeldt, B. & Carlsson, B. (1990) Effects of cyclic food supply on breeding performance in Tengmalm's owl (Aegolius funereus). *Canadian Journal of Zoology*, **68**, 522–530.

Hudson, P.J. (1992) *Grouse in Space and Time : The Population Biology of a Managed Gamebird*. Game Conservancy Ltd.

Huhta, E., Helle, P., Nivala, V. & Nikula, A. (2017) The effect of human-modified landscape structure on forest grouse broods in two landscape types. *Ecosphere*, **8**, e01950.

Höglund, N. (1953) Vem tar tjäderns egg? *Svensk Jakt - In Swedish*, **91**, 416–420.

Höglund, N. (1960) Studies of the winter diet of pine marten *(Martes m. martes)* in County Jämtland. *Viltrevy (Swedish Wildlife)*, **1**, 319–337.

Hörnfeldt, B. (1978) Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia*, **32**, 141–152.

Hörnfeldt, B., Hipkiss, T. & Eklund, U. (2005) Fading out of vole and predator cycles? *Proceedings of the Royal Society*, **272**, 2045–2049.

Ims, R., Henden, J. & Killengreen, S. (2008) Collapsing population cycles. *Trends in Ecology & Evolution*, **23**, 79–86.

IUCN. (2016) IUCN, http://www.iucnredlist.org

Jahren, T., Storaas, T., Willebrand, T., Fossland Moa, P. & Hagen, B.-R. (2016) Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years. *Animal Biology*, **66**, 363–

400.

Johnson, D.H. (2007) Methods for estimating nest success: An historical tour. *Studies in Avian Biology*, **34**, 1–12.

Josefsson, T., Gunnarson, B., Liedgren, L., Bergman, I. & Östlund, L. (2010) Historical human influence on forest composition and structure in boreal Fennoscandia. *Canadian Journal of Forest Research*, **40**, 872–884.

de Jounge, J. (1981) *Predation of the Pine Marten* (Martes Martes) *in Relation to Habitat Selection and Food Abundance during Winter in Central Sweden*.

Jędrzejewski, W. & Jędrzejewska, B. (1992) Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Biatowieza National Park, Poland. *Ecography*, **15**, 212–220.

Kauhala, K., Helle, P. & Helle, E. (2000) Predator Control and the Density and Reproductive Success of Grouse Populations in Finland. *Ecography*, **23**, 161–168.

Kelly, C. & Price, T.D. (2005) Correcting for Regression to the Mean in Behavior and Ecology. *The American Naturalist*, **166**, 700–707.

Kidd, N.A.C. & Lewis, G.B. (1987) Can Vertebrate Predators Regulate Their Prey? A Reply. *The American Naturalist*, **130**, 448.

Killengreen, S.T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N.G. & Ims, R.A. (2011) The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. *Journal of Animal Ecology*, **80**, 1049–1060.

Kjellén, N. & Roos, G. (2000) Population trends in Swedish raptors demonstrated by migration counts at Falsterbo, Sweden 1942–97. *Bird Study*, **47**, 195–211.

Klaus, S. (1985) Predation among capercaillie in a reserve in Thuringia. *Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. World Pheasant Association, Reading, UK.

Kolstad, M., Wegge, P. & Bø, T. (1985) *The Habitat Ecology of Black Grouse (*Tetrao Tetrix L.*) during Spring and Summer in East Norway*. Direktoratet for Vilt og Ferskvannsfisk, Trondheim, Norway (in Norwegian).

Korpela, K. (2014) *Biological Interactions in the Boreal Ecosystem Under Climate Change - Are the Vole and Predator Cycles Disappearing?* University of Jyväskylä.

Krebs, C.J., Bryant, J., Kielland, K., O'Donoghue, M., Doyle, F., Carriere, S., DiFolco, D., Berg, N., Boonstra, R., Boutin, S., Kenney, A.J., Reid, D.G., Bodony, K., Putera, J., Timm, H.K., Burke, T., Maier, J.A.K. & Golden, H. (2014) What factors determine cyclic amplitude in the snowshoe hare (*Lepus americanus*) cycle? *Canadian Journal of Zoology*, **92**, 1039–1048.

Krott, P. & Lampio, T. (1983) Naadan esiintymisesta Suomessa 1900-luvulla. (In Finnish with English summary: occurrence of the pine marten *(Martes martes)* in Finland in the 1900s). *Suomen riista*, **30**, 60–63.

Kurki, S., Nikula, a, Helle, P. & Linden, H. (1998) Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology*, **67**, 874–886.

Kämmerle, J.-L., Coppes, J., Ciuti, S., Suchant, R. & Storch, I. (2017) Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. *Ecosphere*, **8**, e01934.

Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford, Uk.

Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen press, London, UK.

Lakka, J. & Kouki, J. (2009) Patterns of field layer invertebrates in successional stages of managed boreal forest: Implications for the declining Capercaillie Tetrao urogallus L. population. *Forest Ecology and Management*, **257**, 600–607.

Lande, U., Herfindal, I., Willebrand, T., Fossland Moa, P. & Storaas, T. (2014) Landscape characteristics explain large-scale variation in demographic traits in forest grouse. *Landscape Ecology*, **29**, 127–139.

Lehikoinen, A., Ranta, E. & Pietiäinen, H. (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia*, **165**, 349–355.

Leopold, A. (1933) *Game Management*. Charles Scribner's Sons, New York.

Leopold, A. (1937) Pheasant Nesting Study. *The Wilson Bulletin*, **49**, 91–95.

Leopold, A. (1949) *A Sand County Almanac - and Sketches Here and There*. Oxford University Press.

Lesley, A.. & Shipley, A.E. (1912) *Grouse in Health and in Disease*. Smith, Elder & Company, London, UK.

Lindén, H. (1981) Estimation of juvenile mortality in capercaillie, Tetrao urogallus and the black grouse, Tetrao tetrix from indirect evidence. *Finnish Game Research*, **39**, 35–51.

Lindén, H. (1988) Latitudinal gradients in predator-prey interactions, cyclicity and synchronism in voles and small game populations in Finland. *Oikos*, **52**, 341–349.

Lindén, H. & Helle, P. (2003) The rise and fall of Black Grouse populations in Finland since 1860s. *Proceedings of the European Conference Black Grouse – Endangered Species of Europe* (eds P. Málková & P. Procházka), pp. 113–114. Journal of Ornithology, Prague, Czech Republic.

Lindstrom, E.R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., Lemnell, P.A., Martinsson, B., Skold, K. & Swenson, J.E. (1994) Disease reveals the predators: Sarcoptic mange, red fox predation, and prey populations. *Ecology*, **75**, 1042–1049.

Lindström, E. (1982) *Population Ecology of the Red Fox (Vulpes Vulpes L.) in Relation to Food Supply*. University of Stockholm.

Lindström, E. & Brainerd, S. (1995) Pine marten—red fox interactions: a case of intraguild predation? *Annales Zoologici Fennici*, **32**, 123–130.

Lindström, J., Ranta, E., Lindén, M. & Lindén, H. (1997) Reproductive Output, Population Structure and Cyclic Dynamics in Capercaillie, Black Grouse and Hazel Grouse. *Journal of Avian Biology*, **28**, 1–8.

Lindström, E., Angelstam, P., Widén, P. & Andrén, H. (1987) Do predators synchronize vole and grouse fluctuations? An experiment. *Oikos*, **48**, 121–124.

Linnell, J.D.C., Broseth, H., Odden, J. & Nilsen, E.B. (2010) Sustainably harvesting a large carnivore? Development of eurasian lynx populations in Norway during 160 years of shifting policy. *Environmental Management*, **45**, 1142–1154.

Linnell, J.D.C., Fiske, P., Odden, J., Brøseth, H., Herfindal, I. & Andersen, R. (2007) An evaluation of structured snow-track surveys to monitor Eurasian lynx Lynx lynx populations. *Wildlife Biology*, **13**, 456–466.

Linnell, J.D.C., Odden, J., Pedersen, V. & Andersen, R. (1998) Records of intra-guild predation by

Eurasian lynx, *Lynx lynx*. *Canadian Field Naturalist*, **112**, 707–708.

Linnell, J.D.C., Swenson, J.E. & Anderson, R. (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, **4**, 345–349.

Livezey, B.C. (1980) Effects of selected observer-related factors on fates of duck nests. *Wildlife Society Bulletin*, **8**, 123–128.

Loison, A. & Langvatn, R. (1998) Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia*, **116**, 489–500.

Lovel, T. (ed). (1979) Woodland Grouse Symposium., p. 180pp. WPA, Inverness, Scotland.

Ludwig, G. (2007) *Mechanisms of Population Declines in Boreal Forest Grouse*. University of Jyväskylä.

Ludwig, G., Alatalo, R. V, Helle, P. & Siitari, H. (2010) Individual and environmental determinants of daily black grouse nest survival rates at variable predator densities. *Annales Zoologici Fennici*, **47**, 387–397.

Magnússon, K., Brynjarsdóttir, J. & Nielsen, O. (2004) *Population Cycles in Rock Ptarmigan* Lagopus Muta*: Modelling and Parameter Estimation*. University of Iceland, Division of Applied Mathematics and Computer Science / Icelandic Institute of Natural History, Reykjavik, Iceland.

Major, R. & Kendal, C. (1996) The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*, **138**, 298–307.

Marcström, V. (1960) Studies on the Physiological and Ecological Background to the Reproduction of the Capercaillie, Tetrao Urogallus Lin.(Reprinted from Viltrevy.)[A Thesis. With.

Marcström, V., Keith, L.B., Engren, E. & Cary, J.R. (1989) Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Canadian Journal of Zoology*, **67**, 658–668.

Marcström, V., Kenward, R. & Engren, E. (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *The Journal of Animal Ecology*, **57**, 859–872.

Marjakangas, A. & Törmälä, L. (1997) Female age and breeding performance in a cyclic population of black grouse *Tetrao tetrix*. *Wildlife Biology*, **3**, 195–203.

Martin, T. (1993) Nest predation and nest sites. *BioScience*, **43**, 523–532.

Mayfield, H.F. (1975) Suggestions for calculating nest success. *The Wilson Bulletin*, **87**, 456–466.

McElreath, R. (2016) *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. CRC-Press.

McKinney, M. (2002) Urbanization, biodiversity, and conservation the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population. *BioScience*, **52**, 883–890.

McKinnon, L., Berteaux, D., Gauthier, G. & Bêty, J. (2013) Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos*, **122**, 1042–1048.

McKinnon, L., Smith, P. a, Nol, E., Martin, J.L., Doyle, F.I., Abraham, K.F., Gilchrist, H.G., Morrison, R.I.G. & Bêty, J. (2010) Lower predation risk for migratory birds at high latitudes. *Science*, **327**, 326–327.

Messmer, T.A., Brunson, M.W., Reiter, D. & Hewitt, D.G. (1999) United States Public Attitudes regarding Predators and Their Management to Enhance Avian Recruitment. *Wildlife Society Bulletin*, **27**, 75–85.

Miljødirektoratet & Naturdata. (2016) Hjorteviltregisteret, www.hjorteviltregisteret.no

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Csanyi, S. & Stenseth, N.C. (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology*, **43**, 721–734.

Moen, A. (1999) *Vegetation* (ed A. Lillethun). National Mapping Authority, Hønefoss, Norway.

Montgomerie, R.D. & Weatherhead, P.J. (1988) Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology*, **63**, 167.

Moore, R.P. & Robinson, W.D. (2014) Artificial bird nests ,external validity, and bias in ecological field studies. *Ecology*, **85**, 1562–1567.

Moran, P.A.P. (1950) Notes on Continuous Stochastic Phenomena. *Biometrika*, **37**, 17–23.

Moreno-Opo, R., Afonso, I., Jiménez, J., Fernández-Olalla, M., Canut, J., García-Ferré, D., Piqué, J., García, F., Roig, J., Muñoz-Igualada, J., González, L.M. & López-Bao, J.V. (2015) Is it necessary managing carnivores to reverse the decline of endangered prey species? Insights from a removal experiment of mesocarnivores to benefit demographic parameters of the pyrenean capercaillie. *PLoS ONE*, **10**, 1–17.

Moss, R. (1986) Rain, breeding success and distribution of capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* in Scotland. *Ibis*, **128**, 65–72.

Moss, R., Storch, I. & Müller, M. (2010) Trends in grouse research. *Wildlife Biology*, **16**, 1–11.

Myrberget, S. (ed). (1977) Foredrag fra Nordisk Skogsfuglsymposium 1976. *Nordisk Skogsfuglsymposium 1976*, p. 94. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway - In Norwegian.

Myrberget, S. & Hagen, Y. (1974) Reproduksjon hos lirype og skogsfugl i Setesdalen 1919-1934. *Sterna - In Norwegian*, **13**, 23–33.

Mörner, T. (1992) Sarcoptic mange in Swedish wildlife. *Revue Scientifique et Technique (International Office of Epizootics)*, **11**, 1115–1121.

Naturresursinstitutet. (2017) Luke, http://stat.luke.fi/sv/tilasto/4481

Needham, R., Odden, M., Lundstadsveen, S. & Wegge, P. (2014) Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. *Acta theriologica*.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. & Dickman, C.R. (2015) The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, **24**, 1–11.

Newton, I. (1998) *Population Limitation in Birds*. Academic Press, New York.

Novoa, C., Desmet, J.-F., Brenot, J.-F., Muffat-Joly, B., Arvin-Bérod, M., Resseguier, J. & Tran, B. (2011) Demographic traits of two alpine populations of Rock Ptarmigan. *Ecology conservation and management of grouse* (eds B. Sandercock, K. Martin, & G. Segelbacher), pp. 267–280. University of California Press, Los Angeles, United States.

Nur, N. (1984) The Consequences of Brood Size for Breeding Blue Tits I. Adult Survival, Weight Change and the Cost of Reproduction. *The Journal of Animal Ecology*, **53**, 479–496.

O'Donoghue, M., Boutin, S., Krebs, C. & Zuleta, G. (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208.

Odden, J., Linnell, J.D.C. & Andersen, R. (2006) Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research*, **52**, 237–244.

Ordiz, A., Milleret, C., Kindberg, J., Månsson, J., Wabakken, P., Swenson, J.E. & Sand, H. (2015) Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere*, **6**, art284.

Panek, M. & Bresiński, W. (2002) Red foxVulpes vulpes density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. *Acta Theriologica*.

Panzacchi, M., Linnell, J.D.C., Melis, C., Odden, M., Odden, J., Gorini, L. & Andersen, R. (2010) Effect of land-use on small mammal abundance and diversity in a forest-farmland mosaic landscape in south-eastern Norway. *Forest Ecology and Management*, **259**, 1536–1545.

Panzacchi, M., Linnell, J.D.C., Odden, J., Odden, M. & Andersen, R. (2008a) When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. *Canadian Journal of Zoology*, **86**, 116–126.

Panzacchi, M., Linnell, J.D.C., Odden, M., Odden, J. & Andersen, R. (2009) Habitat and roe deer fawn vulnerability to red fox predation. *Journal of Animal Ecology*, **78**, 1124–1133.

Panzacchi, M., Linnell, J.D.C., Serrao, G., Eie, S., Odden, M., Odden, J. & Andersen, R. (2008b) Evaluation of the importance of roe deer fawns in the spring-summer diet of red foxes in southeastern Norway. *Ecological Research*, **23**, 889–896.

Pasanen-Mortensen, M., Pyykönen, M. & Elmhagen, B. (2013) Where lynx prevail, foxes will fail – limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography*, **22**, 868–877.

Pebesma, E. (2004) Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, **30**, 683–691.

Pianka, E.R. (1974) Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*, **71**, 2141–5.

Picozzi, N. (1975) Crow predation on marked nests. *The Journal of Wildlife Management*, **39**, 151–155.

Picozzi, N., Moss, R. & Kortland, K. (1999) Diet and survival of capercaillie Tetrao urogallus chicks in Scotland. *Wildlife Biology*.

Prugh, L.R., Stoner, C.J., Clinton, W.E., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The Rise of the Mesopredator. *BioScience*, **59**, 779–791.

Pulliainen, E. (1980) Food and feeding habits of the pine marten in Finnish Forest Lapland forest in winter. *Proceedings of the Worldwide Furbearer Conference*, p. Frostburg, Md.

Pulliainen, E. (1981) A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish Forest Lapland over 13 winters. *Annales Zoologici Fennici*.

Pöysä, H., Jalava, K. & Paasivaara, A. (2016) Generalist predator, cyclic voles and cavity nests: testing the alternative prey hypothesis. *Oecologia*, **182**, 1083–1093.

R Core Team. (2016) R: A Language and Environment for Statistical Computing.

Rajala, P. (1974) The Structure and Reproduction of Finnish Populations of Capercaillie, Tetrao Urogallus, and Black Grouse, Lyrurus Tetrix, on the Basis of Late Summer Census Data from 1963-66. *Finnish Game Research*, 1–51.

Ranta, E., Helle, P. & Lindén, H. (2004) Forty years of grouse monitoring in Finland. *Suomen Riista*.

Ranta, E., Lindstrom, J. & Linden, H. (1995) Synchrony in tetraonid population dynamics. *Journal of Animal Ecology*.

Redpath, S. & Thirgood, S. (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology*, **68**, 879–892.

Richardsen, K. (2012) *Den Store Rovviltkrigen - En Undersøkelse Av Lov Om Udrydding Af Rovdyr Og Om Freding Af Andet Vildt (1845)*. University of Tromsø (In Norwegian).

Richardson, T.W., Gardali, T. & Jenkins, S.H. (2009) Review and meta-analysis of camera effects on avian nest success. *Journal of Wildlife Management*, **73**, 287–293.

Rosalino, L., Sousa, M., Pedroso, N. & Basto, M. (2010) The influence of food resources on red fox local distribution in a mountain area of the western Mediterranean. *Vie et milieu*.

Sandercock, B.K., Martin, K. & Hannon, S.J. (2005) Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. *Oecologia*, **146**, 13–24.

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

Seiskari, P. (1962) On the winter ecology of the capercaillie, *Tetrao urogallus*, and the black grouse, *Lyrurus tetrix*, in Finland. *Papers on Game Research*, **22**, 1–119.

Selås, V., Johnsen, B. & Eide, N. (2010) Arctic fox Vulpes lagopus den use in relation to altitude and human infrastructure. *Wildlife Biology*.

Selås, V., Sonerud, G.A., Framstad, E., Kalas, J.A., Kobro, S., Pedersen, H.B., Spidso, T.K. & Wiig, O. (2011) Climate change in Norway: warm summers limit grouse reproduction. *Population Ecology*, **53**, 361–371.

Selås, V. & Vik, J.O. (2006) Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897-1976. *Journal of Zoology*, **269**, 299–308.

Semenow Tjan Shanskiy, O.I. (1979) *Ecology of Tetraonids* (ed T. from R. by A.A.C. for S. Translations). U.S. Department of Agriculture and National Science Foundation, Whashington D.C., USA.

Sibly, R. & Hone, J. (2002) Population growth rate and its determinants: an overview. *of the Royal Society B: Biological …*.

Sidorovich, V., Sidorovich, A. & Izotova, I. (2006) Variations in the diet and population density of the red fox Vulpes vulpes in the mixed woodlands of northern Belarus. *Mammalian Biology-Zeitschrift*, **71**, 74–89.

Siivonen, L. (1953) On the destruction of gallinaceous birds. *Suomen Riista*, **8**, 46–48.

Siivonen, L. (1957) The problem of the short-term fluctuations in numbers of tetraonids in Europe.

Papers on Game Research, **19**, 1–44.

Silverman, B.W. (1986) *Density Estimation for Statistics and Data Analysis*. Chapman and Hall.

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

Sirkiä, S., Nikula, A., Helle, P., Lindén, H., Norrdahl, K., Suorsa, P. & Valkeajärvi, P. (2011) Contemporary mature forest cover does not explain the persistence of Capercaillie (Tetrao urogallus) lekking areas in Finland. *Ornis Fennica*, **88**, 208–216.

Skara, A.B. & Steinset, T.A. (2016) Statistics Norway, https://www.ssb.no/jord-skog-jakt-og-fiskeri/statistikker/elgjakt

Small, R., Marcström, V. & Willebrand, T. (1993) Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography*, **16**, 360–364.

Smedshaug, C., Selås, V., Lund, S. & Sonerud, G. (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biology*, **5**, 157–166.

Smith, C.C. & Reichman, O.J. (1984) The Evolution of Food Caching by Birds and Mammals. *Annual Review of Ecology and Systematics*, **15**, 329–351.

Solomon, M.E. (1949) The Natural Control of Animal Populations. *The Journal of Animal Ecology*, **18**, 1.

Solvang, H., Pedersen, H.C., Storaas, T. & Hagen, B.R. (2009) *Rapport for Skogsfugltaksering 2005-2008*. Høgskolen i Hedmark, Elverum, Norway (in Norwegian).

Spence, J. (2001) The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology & Evolution*, **16**, 591–593.

Spidsø, T., Wegge, P. & Storaas, T. (1984) Renesting in capercaillie in southern Norway. *The Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. York, UK.

Statistics Norway. (1934) *Pelsdyrtellingen I Norge*. H Aschehoug & Co. - In Norwegian, Oslo, Norway - In Norwegian.

Statistics Norway. (2016) Statistics Norway, https://www.ssb.no/statistikkbanken/selectvarval/Define.asp?subjectcode=&ProductId=&MainTable=Smaavilt2&nvl=&PLanguage=0&nyTmpVar=true&CMSSubjectArea=jord-skog-jakt-og-fiskeri&KortNavnWeb=srjakt&StatVariant=&checked=true

Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, Uk.

Stigler, S.M. (1997) Regression towards the mean, historically considered. *Statistical methods in medical research*, **6**, 103–14.

Storch, I. (1993) Habitat selection by capercaillie in summer and autumn: Is bilberry important? *Oecologia*, **95**, 257–265.

Storch, I. (1994) Habitat and survival of capercaillie Tetrao urogallus nests and broods in the Bavarian Alps. *Biological Conservation*, **70**, 237–243.

Storch, I. (2002) On spatial resolution in habitat models: Can small-scale forest structure explain capercaillie numbers? *Conservation Ecology*.

Storch, I. (2007) *Grouse: Status Survey and Conservation Action Plan 2006-2010* (ed I. Storch). WPA, IUCN and Fordingbridge, UK, Gland, Switzerland.

Storch, I. (2015) Conservation status and threats to grouse worldwide: an update. *Oral presentation - International Grouse Symposium*, p. Reykjavik, Iceland.

Storch, I., Lindström, E. & de Jounge, J. (1990) Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriologica*, **35**, 311–320.

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

Storaas, T., Kastdalen, L. & Wegge, P. (1999) Detection of forest grouse by mammalian predators: A possible explanation for high brood losses in fragmented landscapes. *Wildlife Biology*, **5**, 187–192.

Storaas, T. & Wegge, P. (1984) High nest losses in capercaillie and black grouse in Norway. *The Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. York, UK.

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

Storaas, T., Wegge, P. & Kastdalen, L. (2000) Weight-related renesting in capercaillie *Tetrao urogallus*. *Wildlife Biology*, **6**, 299–303.

Stubsjøen, T., Sæther, B.-E., Solberg, E.J., Heim, M. & Rolandsen, C.M. (2000) Moose (*Alces alces*) survival in three populations in northern Norway. *Canadian Journal of Zoology*, **78**, 1822–1830.

Summers, R.W., Green, R.E., Proctor, R., Dugan, D., Lambie, D., Moncrieff, R., Moss, R. & Baines, D. (2004) An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *Journal of Applied Ecology*, **41**, 513–525.

Summers, R.W., Willi, J. & Selvidge, J. (2009) Capercaillie *Tetrao urogallus* nest loss and attendance at Abernethy Forest, Scotland. *Wildlife Biology*, **15**, 319–327.

Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology*, **73**, 167–178.

Sundell, J., O'hara, R., Helle, P., Hellstedt, P. & Henttonen, H. (2013) Numerical response of small mustelids to vole abundance: delayed or not? *Oikos*.

Swenson, J. & Angelstam, P. (1993) Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Canadian Journal of Zoology*, **71**, 1303–1310.

Søilen, E. (1995) *Sportsmenn I Veideland - Norges Jeger- Og Fiskerforbund*. StikkaTrykk, Billingstad, Norway (In Norwegian).

The Norwegian Mapping Authority. (2017) The Norwegian Mapping Authority, http://kartverket.no/en/

Thompson, I.D., Davidson, I.J., O'Donnell, S. & Brazeau, F. (1989) Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Canadian Journal of Zoology*, **67**, 1816–1823.

Thorson, J., Skaug, H., Kristensen, K. & Shelton, A. (2015) The importance of spatial models for estimating the strength of density dependence. *Ecology*.

Tjernberg, M. (1981) Diet of the golden eagle *Aquila chrysaetos* during the breeding season in Sweden. *Ecography*, **4**, 12–19.

Tonteri, T., Salemaa, M., Rautio, P., Hallikainen, V., Korpela, L. & Merilä, P. (2016) Forest management regulates temporal change in the cover of boreal plant species. *Forest Ecology and Management*, **381**, 115–124.

Tornberg, R. (2001) Pattern of goshawk *Accipiter gentilis* predation on four forest grouse species in northern Finland. *Wildlife Biology*, **7**, 245–256.

Tovmo, M., Mattisson, J., Kleven, O. & Brøseth, H. (2016) *Overvaking Av Kongeørn I Noreg 2015. Resultat Frå 12 Intensivt Overvaka Område*, NINA Rappo. Trondheim - In Norwegian.

Trewhella, W., Harris, S. & McAllister, F. (1988) Dispersal distance, home-range size and population density in the red fox (Vulpes vulpes): a quantitative analysis. *Journal of Applied Ecology*.

Tryjanowski, P., Hartel, T., Báldi, A. & Szymański, P. (2011) Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. *Acta Ornithologica*.

Turchin, P. (2003) *Complex Population Dynamics : A Theoretical/empirical Synthesis*. Princeton University Press.

Vanha-Majamaa, I. & Jalonen, J. (2001) Green Tree Retention in Fennoscandian Forestry. *Scandinavian Journal of Forest Research*, **16**, 79–90.

Vickery, P., Hunter Jr., M. & Wells, J. (1992) Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos*, **63**, 281–288.

Viltdata. (2017) Viltdata, https://rapport.viltdata.se/statistik/

Vos, A. (1995) Population dynamics of the red fox (Vulpes vulpes) after the disappearance of rabies in county Garmisch-Partenkirchen, Germany, 1987—1992. *Annales Zoologici Fennici*, **32**, 93–97.

Vuorisalo, T., Talvitie, K., Kauhala, K., Bläuer, A. & Lahtinen, R. (2014) Urban red foxes (Vulpes vulpes L.) in Finland: A historical perspective. *Landscape and Urban Planning*, **124**, 109–117.

Walther, G., Post, E., Convey, P., Menzel, A. & Parmesan, C. (2002) Ecological responses to recent climate change. *Nature*.

Walton, Z., Samelius, G., Odden, M. & Willebrand, T. (2017) Variation in home range size of red foxes Vulpes vulpes along a gradient of productivity and human landscape alteration. *PLoS ONE*, **12**.

Watanabe, S. (2010) Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, **11**, 3571–3594.

Wegge, P. (1985) *The Sociobiology, Reproduction, and Habitat of Capercaillie Tetrao Urogallus L. in Southern Norway*. University of Montana.

Wegge, P. & Grasaas, T. (1977) Bestandsstudier av storfugl på Sørlandet. *Viltrapport 5* (ed S. Myrberget), pp. 22–39. Direktoratet for vilt og ferskvannsfisk - In Norwegian, Trondheim, Norway - In Norwegian.

Wegge, P. & Kastdalen, L. (2007) Pattern and causes of natural mortality of capercaille, *Tetrao urogallus*, chicks in a fragmented boreal forest. *Annales Zoologici Fennici*, **44**, 141–151.

Wegge, P. & Kastdalen, L. (2008) Habitat and diet of young grouse broods: resource partitioning between Capercaillie *(Tetrao urogallus)* and Black Grouse *(Tetrao tetrix)* in boreal forests.

Journal of Ornithology, **149**, 237–244.

Wegge, P. & Rolstad, J. (2011) Clearcutting forestry and Eurasian boreal forest grouse: Long-term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix* reveals unexpected effects on their population performances. *Forest Ecology and Management*, **261**, 1520–1529.

Wegge, P. & Storaas, T. (1990) Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway. *Oecologia*, **82**, 527–530.

Willebrand, T. (1992) Breeding and age in female black grouse Tetrao tetrix. *Ornis Scandinavica*, **23**, 29–32.

Willebrand, T. & Marcström, V. (1988) On the danger of using dummy nests to study predation. *Auk*, **105**, 378–379.

Willebrand, T., Willebrand, S., Jahren, T. & Marcström, V. (2017) Snow tracking reveals different foraging patterns of red foxes and pine martens. *Mammal Research*, **In print**, 1–10.

Wood, S.N. (2006) *Generalized Additive Models : An Introduction with R*. Chapman & Hall/CRC.

Zwickel, F.C. & Bendell, J.F. (1967) Early mortality and the regulation of numbers in blue grouse. *Canadian Journal of Zoology*, **45**.

Östlund, L., Zackrisson, O. & Axelsson, A. (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, **27**, 1198–1206.

Åhlen, P.-A., Willebrand, T., Sjöberg, K. & Hörnell-Willebrand, M. (2013) Survival of female capercaillie Tetrao urogallus in northern Sweden. *Wildlife Biology*, **19**, 368–373.

Paper I

BRILL
Animal Biology 66 (2016) 363–400
Animal Biology
brill.com/ab

Review

Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years

Torfinn Jahren[1,*], **Torstein Storaas**[1], **Tomas Willebrand**[1], **Pål Fossland Moa**[2] and **Bjørn-Roar Hagen**[2]

[1] Faculty of Applied Ecology and Agricultural Sciences, Hedmark University of Applied Sciences, Koppang, Norway
[2] Nord University, Steinkjer, Norway

Submitted: June 10, 2016. Final revision received: November 2, 2016. Accepted: November 3, 2016

Abstract
Declines in populations of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) have been reported from both Central Europe and the continuous boreal forests of Fennoscandia. While intensified land-use is assumed to be the underlying cause of these declines, the mechanisms are not yet understood. Predation is the proximate cause of mortality of eggs, chicks and adults throughout capercaillie and black grouse ranges, but the link between predation and habitat and/or climate change remains unclear. To investigate temporal trends in reproductive output of woodland grouse, we collated previously published and unpublished data of reproduction in capercaillie and black grouse throughout their ranges from 1930 to 2012. We show that, overall, reproductive success has decreased and stabilized at low levels in most regions whilst capercaillie reproductive output in Scotland is still declining. With today's net reproduction, capercaillie and black grouse adult survival is too low to compensate for reproduction declines. Consequently, populations are expected to further decline unless reproductive performances improve. We put our findings in the context of changes in land use, climate and generalist predator numbers. By critically reviewing how these factors limit reproductive success in capercaillie and black grouse, we hope to shed light on the underlying mechanisms causing the decline. Our results imply that measures should be undertaken to reduce mortality of capercaillie and black grouse chicks and eggs. We suggest that future studies should aim to better understand which predators limit capercaillie and black grouse populations and how predation rates are mediated by continuously changing habitat and climate.

Keywords
Capercaillie; climate; decline; grouse; land use; predation; reproduction success; survival

---

*) Corresponding author; e-mail: torfinn.jahren@hihm.no

DOI:10.1163/15707563-00002514

Introduction

Long-term declines in population densities of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) have been documented from continental Europe, the British Isles and throughout the continuous boreal forests of Fennoscandia (Wegge, 1979; Lindén & Rajala, 1981; Helle & Helle, 1991; Baines & Hudson, 1995; Moss et al., 2000; Lindén & Helle, 2003; Storch, 2007; Ludwig et al., 2008; Sirkiä et al., 2010). These declines began earlier in the southern than in the northern range (Lovel, 1979, and references therein). In addition, previously characteristic fluctuations in population size have diminished over the past 50 years (Ludwig et al., 2006).

Intensified land-use is considered to be the underlying cause of the declines in tetraonid populations but the mechanisms are not clearly understood. In the Fennoscandian context, intensified land-use refers primarily to the expansion of modern forestry which has been the focus of several studies (i.e. Lindén & Helle, 2003; Storch, 2007; Sirkiä et al., 2010). In continental Europe and Britain, land-use change also refers to the intensification of agriculture and changes in grazing pressure by livestock, as well as increased browsing by ungulates. Nonetheless, within the suite of processes accompanying the population decline and reduction in cyclic amplitude, climate change (Moss et al., 2001; Ludwig et al., 2006; Selås et al., 2011) and an increase in generalist predators (Baines, 1991; Vos, 1995; Kurki et al., 1998) are factors that may also contribute to the negative trends in European woodland grouse. To date, these factors have received comparatively little attention.

Since the 1930s, no studies in Fennoscandia have identified malnutrition or disease as major mortality factors in capercaillie or black grouse. However, chicks of both species may be vulnerable to low insect abundance because invertebrates are an important source of protein during the first couple of weeks after hatching (Rajala, 1959; Atlegrim & Sjöberg, 2008; Wegge & Kastdalen, 2008) and food limitation may predispose chicks to predation. Predation is the dominant proximate cause of losses of woodland grouse eggs, chicks and adults (Hagen, 1952; Hörnfeldt, 1978; Angelstam, 1984; Storaas & Wegge, 1987; Kurki et al., 1997; Borchtchevski et al., 2003; Wegge & Kastdalen, 2007; Ludwig et al., 2010; Wegge & Rolstad, 2011; Åhlen et al., 2013). Mammalian predation has also been shown, in both experimental and correlative studies, to play an important role in short-term grouse population dynamics in the sense that predators predominantly limit reproduction and thus population growth rates (Marcström et al., 1988; Lindström et al., 1994; Kurki et al., 1997; Kauhala et al., 2000; Summers et al., 2004).

Capercaillie and black grouse are sympatric forest dwelling species, but traditionally, they are perceived to have contrasting habitat preferences along the forest succession continuum. Capercaillie prefer older and climax conifer forest whilst black grouse prefer open forest of younger successional stages that also include peat-bogs, heaths, sub-alpine pastures, marshes and grasslands (Seiskari, 1962; Swenson & Angelstam, 1993; Ludwig et al., 2009). Given the wide distribution of capercaillie and black grouse, they can also be considered habitat generalists within their respective niches, at least in the boreal forest of Fennoscandia (Lande & Herfindal, 2010; Sirkiä et al., 2011a, b; Lande et al., 2014). In that sense, habitat alteration induced by forestry does not necessarily result in a shared response between capercaillie and black grouse. In the central European lowlands and Britain however, capercaillie and black grouse habitat-ranges are comparably disjointed and less overlapping. This results in a more segregated pattern of local distributions of the two species.

Forestry has dramatically altered the coniferous forest throughout the past 80 years by clear-cutting practices, increased fragmentation and a shortening of the rotation of forest stands (Storch, 2007). Whilst the proximate cause of grouse mortality is predation, the underlying (i.e. ultimate) mechanisms that relate habitat quality to survival are less obvious. Habitat fragmentation and distortion of forest stand structure affect capercaillie and black grouse reproduction negatively (Kurki & Lindén, 1995; Kurki et al., 2000). In Scotland, forest maturation is suggested to accelerate black grouse declines by reducing brood-rearing and nesting habitat following canopy closure (Pearce-Higgins et al., 2007). These man-made habitat changes may also affect mortality indirectly by altering the distribution and composition of predators in the landscape (Borchtchevski et al., 2003). Likewise, changes in habitat can affect predator-prey relationships by making predators more efficient in locating and killing grouse through edge-related effects (Andren & Angelstam, 1988).

Capercaillie and black grouse broods select for certain habitat types (Wegge & Kastdalen, 2008), and a reduction in availability of these habitats may create ecological traps by increasing the search efficiency of predators (Storaas et al., 1999). In continental Europe and Britain, more than in the Fennoscandian countries, habitat fragmentation has isolated and separated populations from one another by non-habitat and woodland grouse habitats have continuously contracted over the past century. Consequently, the phenomenon of ecological traps may be present in these areas, not only in terms of brood-rearing but also during other phases of the grouse life cycle. Conversely, in Fennoscandia, fragmentation has divided and separated optimal forest habitat with less optimal forest habitat of a different successional stage but the overall extent of the Fennoscandian boreal forest has not changed in this time period (Östlund, 1997).

In Scandinavia, and probably the rest of Fennoscandia, there has been a 0.75 to 1.5°C increase in temperature since 1900, which has primarily arisen during two periods between 1900 and 1940 and since 1980. This is in line with the pattern of temperature increase in continental Europe and Britain (IPCC, 2013). Climate change can affect grouse reproduction indirectly because increasing variability in weather conditions may predispose chicks to increased predation, particularly during wet and cold weather (Wegge & Kastdalen, 2007). Climate change may also create a mismatch between the onset of seasons and important biological events like egg production or hatching of chicks (Moss et al., 2001; Ludwig et al., 2006). Furthermore, it is suggested that increasingly warm summers can negatively affect reproduction in capercaillie indirectly by increasing herbivory deterrents in bilberry foliage (*Vaccinium myrtillus*) (Selås et al., 2011).

Corvids, certain raptors, especially goshawk (*Accipiter gentilis*) and common buzzard (*Buteo buteo*), and generalist mammalian predators are common throughout the distribution range of capercaillie and black grouse. The raccoon dog (*Nyctereutes procyonoides*) has fairly recently become common throughout central Europe and in Finland but is absent from parts of the woodland grouse range and has not yet established noteworthy populations in Sweden or Norway (Kauhala & Kowalczyk, 2011). In Sweden, a dramatic increase in the goshawk population was shown between the early 1940s and late 1990s whilst the common buzzard decreased in the same period (Kjellén & Roos, 2000). Grouse, and especially black grouse, are important prey for goshawks, but grouse chicks might be an alternative to small mammal prey for buzzards (Valkama et al., 2005).

Both red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) are regarded as important mammalian predators of forest dwelling grouse and their populations have increased since the early 1900s (Grakov, 1978; Krott & Lampio, 1983; Vos, 1995; Helldin, 2000; Selås & Vik, 2006) due to land-use changes, legal protection, an increase in prey-base and declines in fur prices. Predation caused by high densities of generalist predators can limit reproductive output of prey, reduce amplitude in prey population peaks, and reduce prey populations to a low and stable level (Erlinge et al., 1983; Hanski et al., 1991). This was evident in tetraonids during an outbreak of sarcoptic mange (*Sarcoptes scabei*) in the Scandinavian red fox population during the late 1970s and 1980s, when capercaillie and black grouse densities increased and declined in synchrony with the appearance and disappearance of the mange (Lindström et al., 1994; Smedshaug et al., 1999).

In this study, we attempt to describe the long-term changes in reproductive output of capercaillie and black grouse throughout large parts of their range using data with varying temporality from the past 80 years. We also infer the consequences of today's net reproduction for the future status of their populations. We place our findings in the context of changes in land-use, climate and generalist predators and critically review how these factors limit reproductive success in capercaillie and black grouse in the hope of shedding light on the underlying mechanisms causing their decline. With the ever-present population declines in mind and the fact that grouse population dynamics are largely dependent on reproduction, we expect to find negative trends in nest success, proportion of hens with a brood and number of chicks per hen.

Material and methods

Data

We collated various time series of capercaillie and black grouse populations from within the period 1907-2014 from Fennoscandia and compared them with published trends from Britain and continental Europe. Population indices of capercaillie and

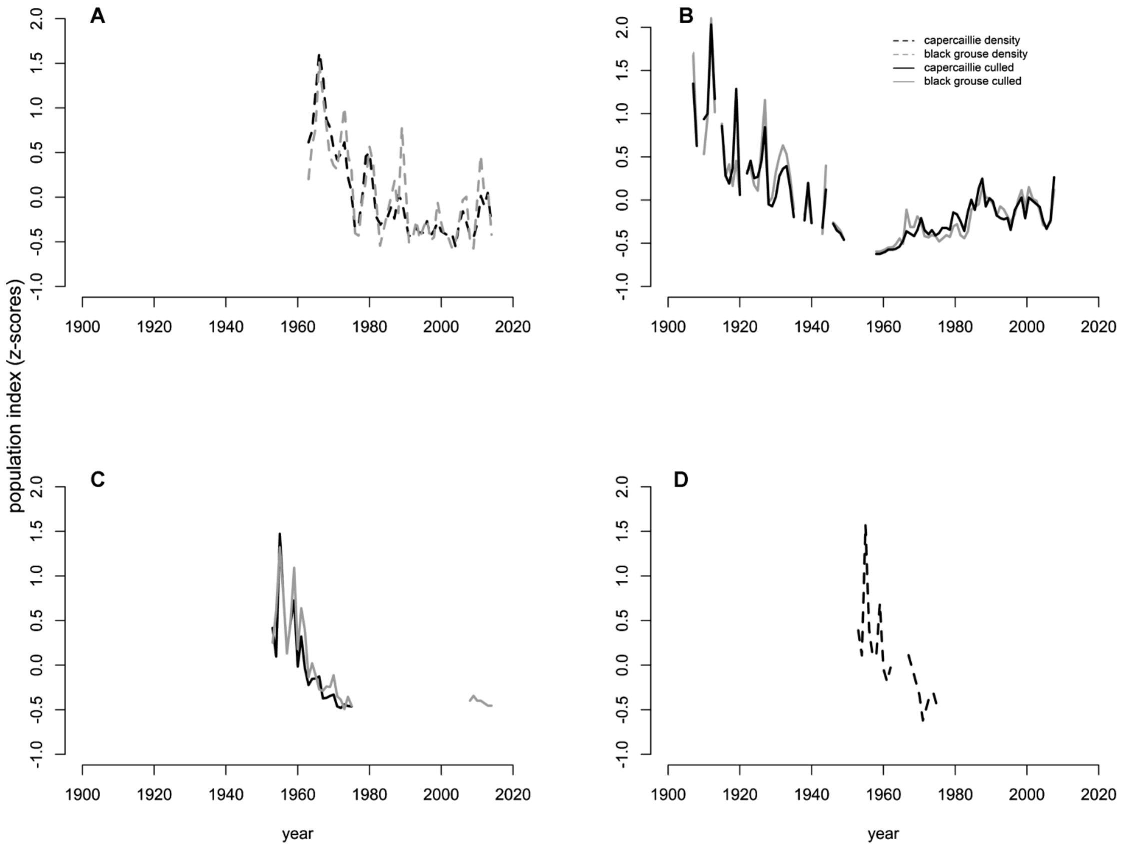

Figure 1. (A) Nationwide capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) density estimates from Finland 1964-2014. (B) Capercaillie and black grouse bagged in county of Dalarna, Sweden between 1907 and 2007. (C) Bagged capercaillie and black grouse in Hurdal municipality, Norway, in the years 1953-1975 and 2008-2014. (D) Capercaillie density in Vegårshei, Norway between 1953-1962 and 1967-1976. All values are z-scores (standardized).

black grouse from Finland were from nationwide density estimates between 1964 and 2014 (Helle & Ikonen, 2015). From Norway we had snippets of density estimates of capercaillie in Vegårshei municipality between 1953-62 and 1967-76, together with harvest data from Hurdal municipality for both species in the periods 1953-75 and 2008-14 (only black grouse was culled in the latter period) (Sørensen, 1977a, b; Wegge & Grasaas, 1977; Statistics Norway, 2016). From Sweden we collated harvest data for both species in Dalarna county between 1907 and 2007 (Mattson & Zakariasson, 2009; Danell et al., 2011) (fig. 1). Trends for black grouse in lowland Europe and Britain are presented in Ludwig et al. (2008) and Baines & Hudson (1995). Capercaillie trends in Scotland are described in Catt et al. (1998), Wilkinson & Langston (2002), Eaton et al. (2007). In fig. 2 we present a timeline of important processes occurring in Fennoscandia related to climate, forestry and predators during the investigation period.

In addition, we collated published and unpublished data from studies of nest success, proportion of hens with a brood and the number of chicks per hen (not to be confused with brood size) conducted in Fennoscandia, the British Isles and

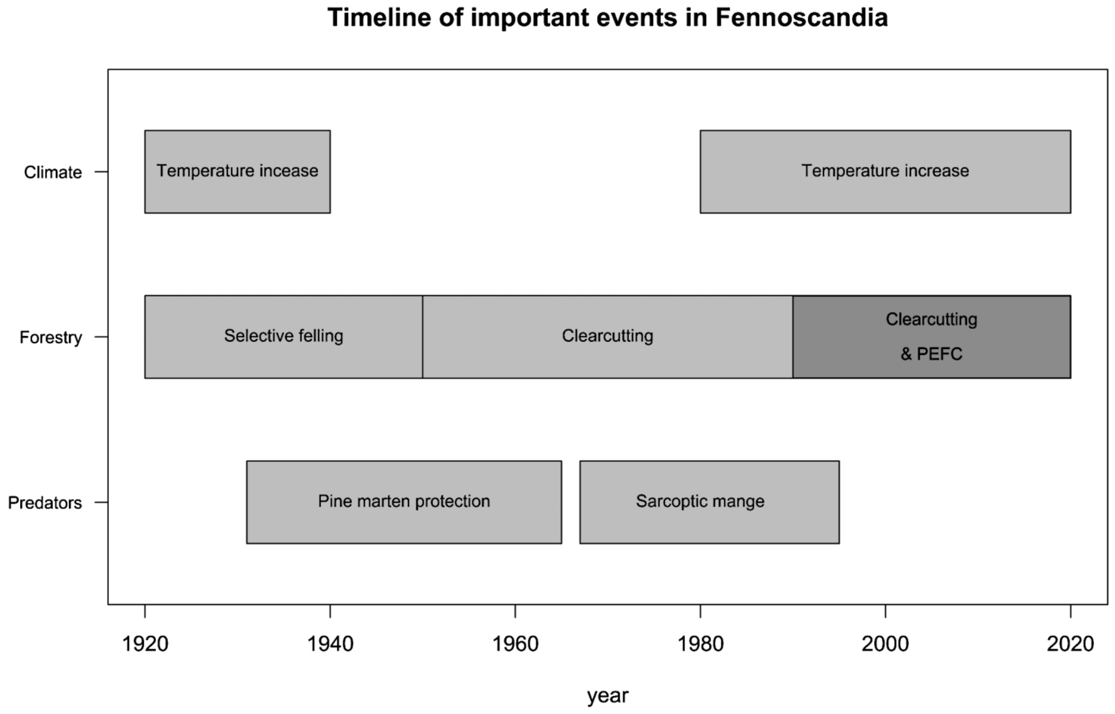

Figure 2. Overview of important processes in the boreal forests of Fennoscandia.

continental Europe between 1930 and 2012. Data were included from Finland, Karelia, Sweden, Norway, Scotland, England, Wales, Germany, Switzerland, Austria, France, Andorra, Estonia, Italy, Poland and Slovakia (tables A1-A3). Where data were presented graphically, we extracted them with GetData Graph Digitizer (2016). In total, capercaillie crude nest-success data (i.e. proportion successful to total nests found) spanned the period from 1930 to 2012 and included 17 studies from seven countries with 33 unique values of nest-success data. Black grouse nest-success data were available for 58 unique values from 18 studies in seven countries, conducted between 1932 and 2012. The proportion of hens with a brood were from 1934 for black grouse and 1946 for capercaillie to 2012 and included 16 studies with 143 unique values for capercaillie and 24 studies with 230 unique values for black grouse from seven and 10 countries, respectively. Numbers of chicks per hen were collated from 29 capercaillie and 33 black grouse studies in nine and 11 countries conducted between 1930 or 1934 and 2012 with 366 and 357 unique years, respectively. An overview of the data is shown in table 1.

Nests were primarily located in two ways across studies (see Appendix and references therein for more details of each study). Either birds were captured and fitted with radio transmitters, or nests were found by chance or actively searched for with pointing dogs. Systematic nest-searches also occurred in one study (Summers et al., 2009). Typically, nests located by radio-tracking females will give less biased estimates of nest success than nests found by chance or otherwise since nests found by chance rarely includes nests that are already predated (discussed further elsewhere). Radio transmitters, where fitted, were also used to assess the proportion of

Table 1.
Demographic variables used in the analysis, together with time span and number of unique years (N) per species and region. Apparent nest success (proportion of successful nests to total number of nests found), proportion of hens with brood (proportion of females with ⩾1 chick in July/August) and chicks per hen ratio in July/August are shown. (See tables A1-A3 for details.)

Region	Variable	Capercaillie			Black grouse		
		Time span	Studies	N	Time span	Studies	N
Fennoscandia	Nest success	1930-2012	11	27	1932-2012	12	39
	Hens with brood	1946-2012	8	55	1946-2012	9	68
	Chicks per hen	1930-2012	17	197	1946-2012	15	166
British Isles	Nest success	1950-2007	3	3	1935-2004	3	12
	Hens with brood	1976-2012	3	34	1934-2002	6	42
	Chicks per hen	1975-2012	6	89	1934-2009	8	66
Continental Europe	Nest success	1971-2001	3	3	1977-1998	3	7
	Hens with brood	1976-2010	5	54	1970-2007	9	120
	Chicks per hen	1976-2010	6	80	1970-2007	10	125

hens with a brood in late summer (July/August) or this was assessed by line transects, wildlife triangle censuses and in some studies, broods detected by chance in relation to other field work. Wildlife triangle censuses are the main census method in Finland, whilst line transect counts occurred throughout most of the other studies. The number of chicks per hen was either from radio-marked birds, censuses or age determination of wing samples from harvested birds. The use of wings to assess this particular measure has been reported by several authors (Siivonen, 1954; Helminen, 1963; Semenow Tjan Shanskiy, 1979; Hörnfeldt et al., 2001). Asmyhr et al. (2012) found increased harvest risk for successful willow ptarmigan adults, meaning that adults experienced higher mortality than chicks in hunter-grouse encounters. Whether and how this differs from capercaillie and black grouse, we do not know. However, if the effect is directionally similar, it follows that our estimates of chicks per female (from harvest data) are biased low (also discussed elsewhere).

Statistical analysis

We evaluated regional changes in nest success, broods per hen and chicks per hen over time for Fennoscandia, continental Europe and The British Isles, fitting year as the only co-variate. Due to violations of linear model assumptions, we fitted generalized additive mixed models (GAMM) via the mgcv library (Wood, 2006) in R (R Development Core Team, 2012) with "study" and "method" as random effects, thereby accounting for non-independence within studies. We used the median year for studies where results were presented as an average across more than one year.

Nest success and proportion of hens with brood models were fitted with quasi-binomial error structures and chicks per hen models were fitted with quasi-Poisson error structures to allow for overdispersion. Number of knots were automatically selected via the implemented generalized cross-validation which balances simplicity with explanatory power (Wood, 2006). Each model was fitted with a cubic regression spline. The number of nests per study-year was used to weight nest success models whilst chick and brood models were weighted by study duration since sample sizes were often missing from these studies.

To make interpretation of the temporal trends easier, we identified periods along the trend line where the slope was different from zero. For this, we extracted first order derivatives and their respective confidence intervals according to Curtis & Simpson (2014), but see also Simpson (2014). Periods of significant change were considered to occur when zero was outside the 95% confidence interval. These are highlighted in red (decrease phase) or green (increase phase) (figs. 3-5).

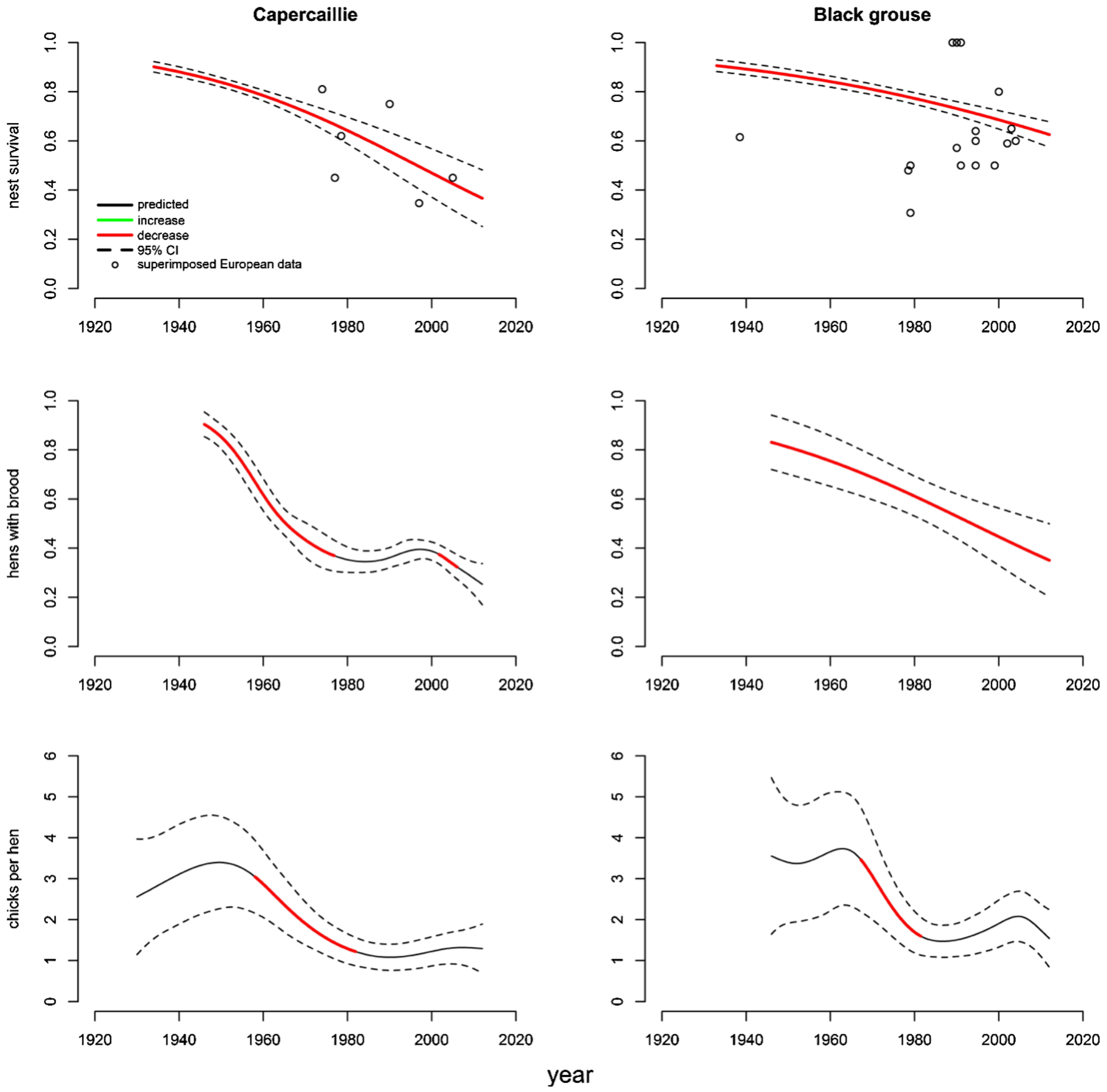

Figure 3. Predicted values from additive mixed models of reproduction in Fennoscandian capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Periods of significant change are highlighted red (decrease) and green (increase). From top to bottom; nest success, proportion of hens with brood and chicks per hen. British and continental European nest data are superimposed.

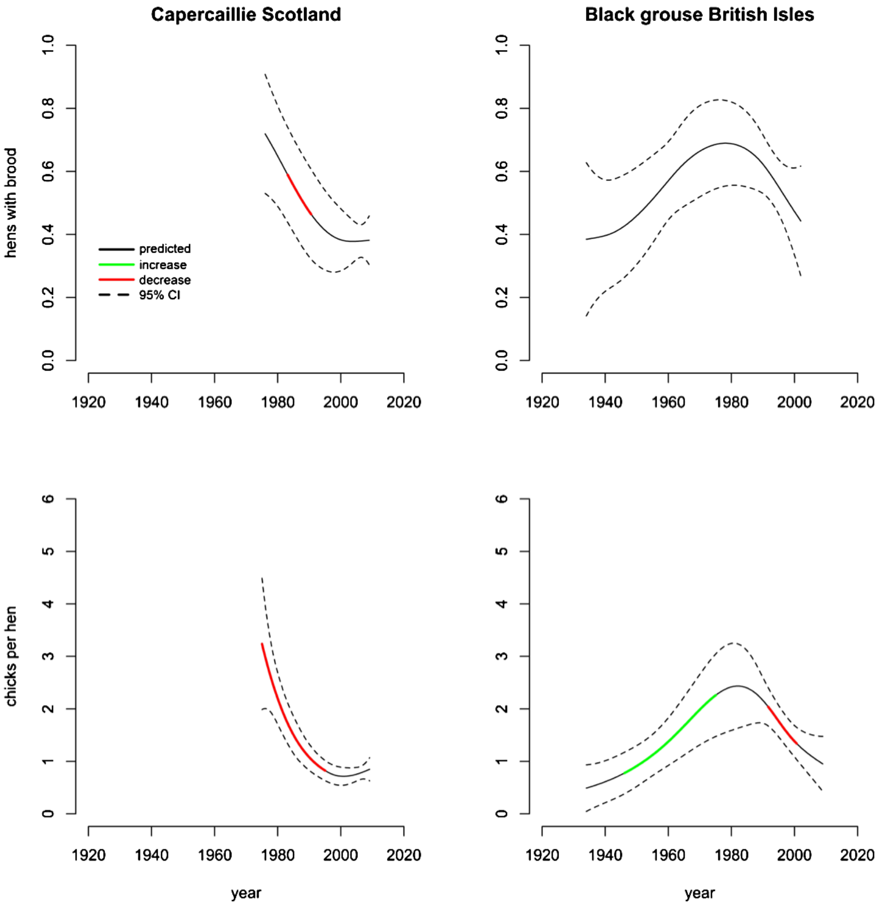

Figure 4. Predicted values from additive mixed models of reproduction in British capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Periods of significant change are highlighted red (decrease) and green (increase). From top to bottom; proportion of hens with brood and chicks per hen.

Numerical fluctuations are the hallmark of woodland grouse population dynamics. To assess trends in variation of net reproductive output we extracted residuals (absolute values) from the fitted chicks per hen models and fitted a locally weighted regression to the residuals (LOESS). Limited data on nest success and proportion of hens with brood prevented us from repeating this for these models.

Finally, based on the fitted trends from the chicks per hen models, we estimated the adult survival needed to offset modelled reproduction (i.e. to bring about zero population change). We used per capita chick production in July/August as an estimate of recruitment. Then we estimated the survival needed to keep the numbers of adults constant from one year to another, assuming equal survival of adults and juveniles. This assumption is not fulfilled as chicks have lower survival than adults and henceforth our estimates of required adult survival are conservative. We used female survival rates where available, otherwise we used survival rates for both sexes combined. We then compared estimates of required adult survival to the fitted trends from additive models (same procedure as reproduction models but no random effects) of actual adult survival reported from several Fennoscandian studies. From

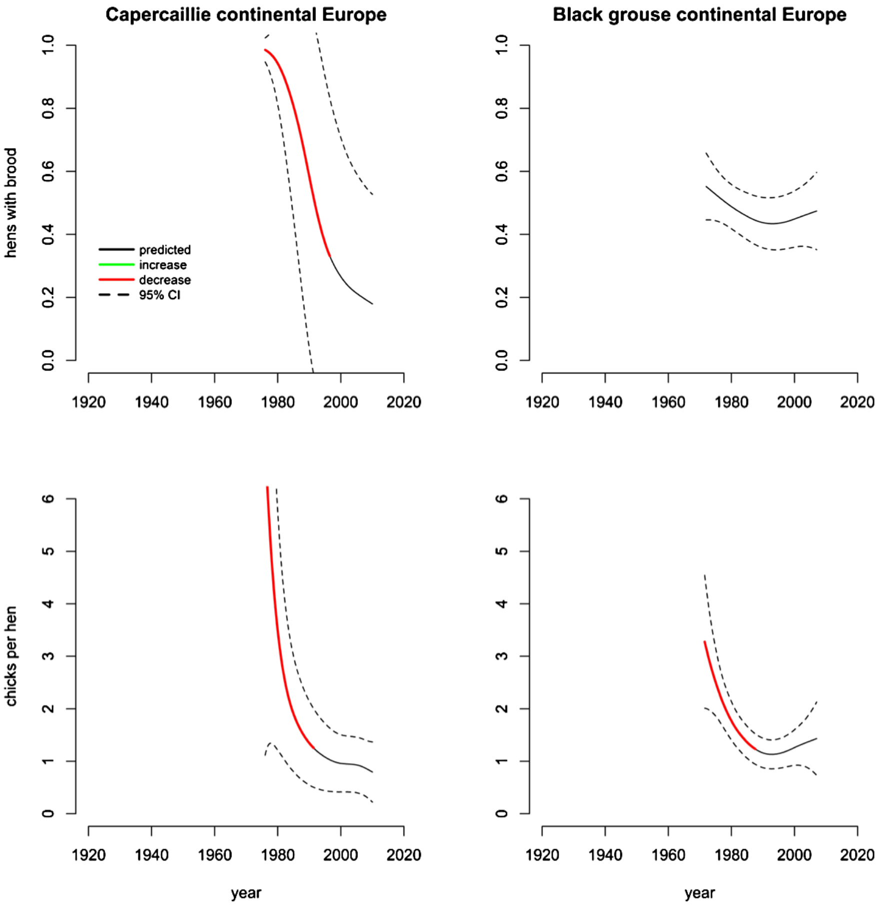

Figure 5. Predicted values from additive mixed models of reproduction in continental European capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Periods of significant change are highlighted red (decrease) and green (increase). From top to bottom; proportion of hens with brood and chicks per hen.

continental Europe and Britain, the number of estimates of adult survival was not sufficient for additive modelling. In these cases, the reported values are visualized in the figures (see table A4).

Results

Fennoscandia

Population indices for capercaillie and black grouse in Finland decreased from the early 1960s until they stabilized around 1980. A similar decrease was observed in the Norwegian data, although since 1975 bag data only existed between 2008 and 2014 at this resolution and no capercaillie were culled in this time-period. The Swedish data showed steep negative trends from 1907, reaching a minimum 20 years earlier than in Finland and Norway (around 1960), before increasing slightly towards the 1990s and then leveling off (fig. 1).

First order derivatives from cross-population model predictions in Fennoscandia suggested significant declines in crude nest success from 0.89 to 0.35 for capercaillie, and from 0.90 to 0.55 for black grouse, between 1934 and today. Similarly, broods per capercaillie hen decreased from 0.9 to 0.37 between 1946 and 1977 and then stabilized before decreasing again from 0.37 to 0.32 between 2001 and 2006. The proportion of black grouse hens with a brood decreased continually from 0.83 to 0.35 throughout the whole period between 1946 and 2012. The number of chicks per capercaillie hen decreased from 3.1 to 1.2 chicks per hen between 1958 and 1982. The chicks per black grouse hen showed a similar trend between 1967 and 1987 from 3.5 to 1.6 chicks per hen (fig. 3, highlighted red).

Residuals from chicks per hen models complemented the observed declines with decreasing year-to-year variation in net reproductive success for both species. They fluctuated considerably early in the period and the variation diminished throughout the time series, however with some slightly increasing trends the past 20 years. The variation decreased four-fold for capercaillie and two and a half-fold for black grouse from the beginning until today (fig. 6A, B).

The estimated adult survival required to counterbalance the observed decline in chicks per hen and so stabilize population growth has increased in line with decreasing reproductive output for both capercaillie and black grouse. Although reported adult survival has been increasing in Fennoscandian capercaillie and black grouse, rates have not been sufficient to offset the diminishing reproductive output and allow populations to grow since before the 1970s (fig. 7A, B).

British Isles

Broods per capercaillie hen in Scotland decreased from 0.59 to 0.46 between 1983 and 1991. For the British Isles as a whole, we did not detect any significant changes in black grouse brood frequencies between 1934 and 2002. The capercaillie chicks per hen in Scotland declined from 3.2 to 0.8 chicks over the 20 years between 1975 and 1995. Chicks per black grouse hen on the British Isles increased from 0.8 to 2.3 between 1946 and 1975 before decreasing from 2.0 to 1.3 chicks between 1992 and 2001 (fig. 4).

Variation in net reproductive success for capercaillie in Scotland increased from 1975 to a peak in the mid-1980s and has steadily decreased since then. Variation in black grouse reproductive output had a similar curve as capercaillie, but variation increased from 1934 until it peaked in the early 1990s. Since then, variation in reproductive output for black grouse on the British Isles has decreased (fig. 6C, D).

There are few reports of adult survival of capercaillie and black grouse in Scotland or the rest of the British Isles, so the assessment of population growth should be treated cautiously. In capercaillie, the survival required to maintain population size overshot reported values in the 1990s. Reported values for adult black grouse survival vary (range 0.39 to 0.72). The higher survival rate reported is more in line with those reported for capercaillie, which typically have higher adult survival than

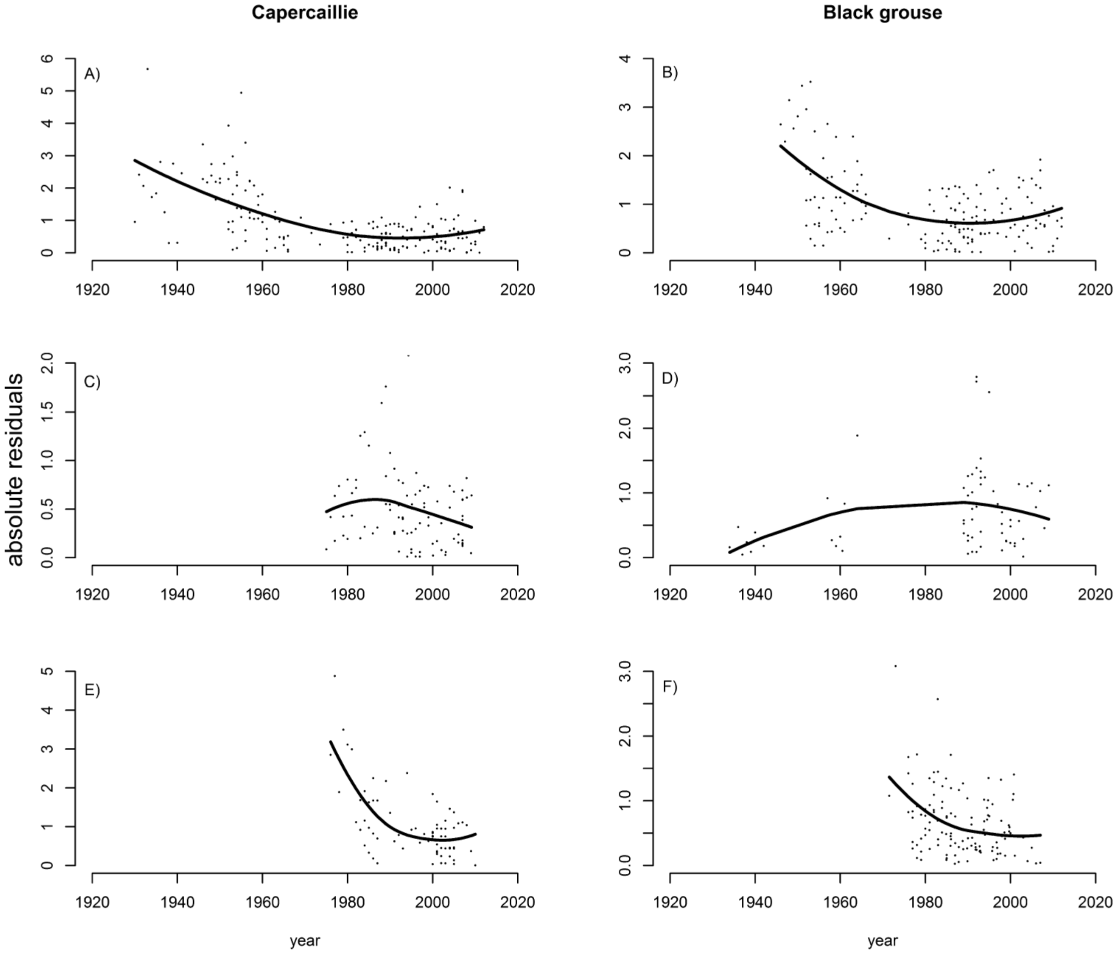

Figure 6. (A) Absolute residuals (dots) from Fennoscandian chicks per capercaillie (*Tetrao urogallus*). (B) Black grouse (*Lyrurus tetrix*) hen models with fitted locally-weighted regression function (lines). (C, D) depict variation in capercaillie reproduction in Scotland and black grouse reproduction on the British Isles. (E, F) show variation in reproduction for capercaillie and black grouse in continental Europe.

black grouse. Disregarding the lower value, last reports indicate that adult British black grouse counterbalance reproduction (fig. 7C, D).

Continental Europe

No temporal changes were detected in the proportion of black grouse hens with a brood. A decrease in the proportion of capercaillie hens with a brood from 0.98 to 0.33 was estimated between 1976 and 1997. Chicks per hen declined for both species. In 1976, capercaillie hens averaged an estimated 7.1 chicks which decreased to 1.3 chicks by 1991. Black grouse hens had 3.3 chicks in 1971 decreasing to 1.2 chicks in 1988 (fig. 5).

Residuals from capercaillie chick models exhibit a similar pattern to that of Fennoscandia. The overall trend is decreasing variation with a slight increase to-

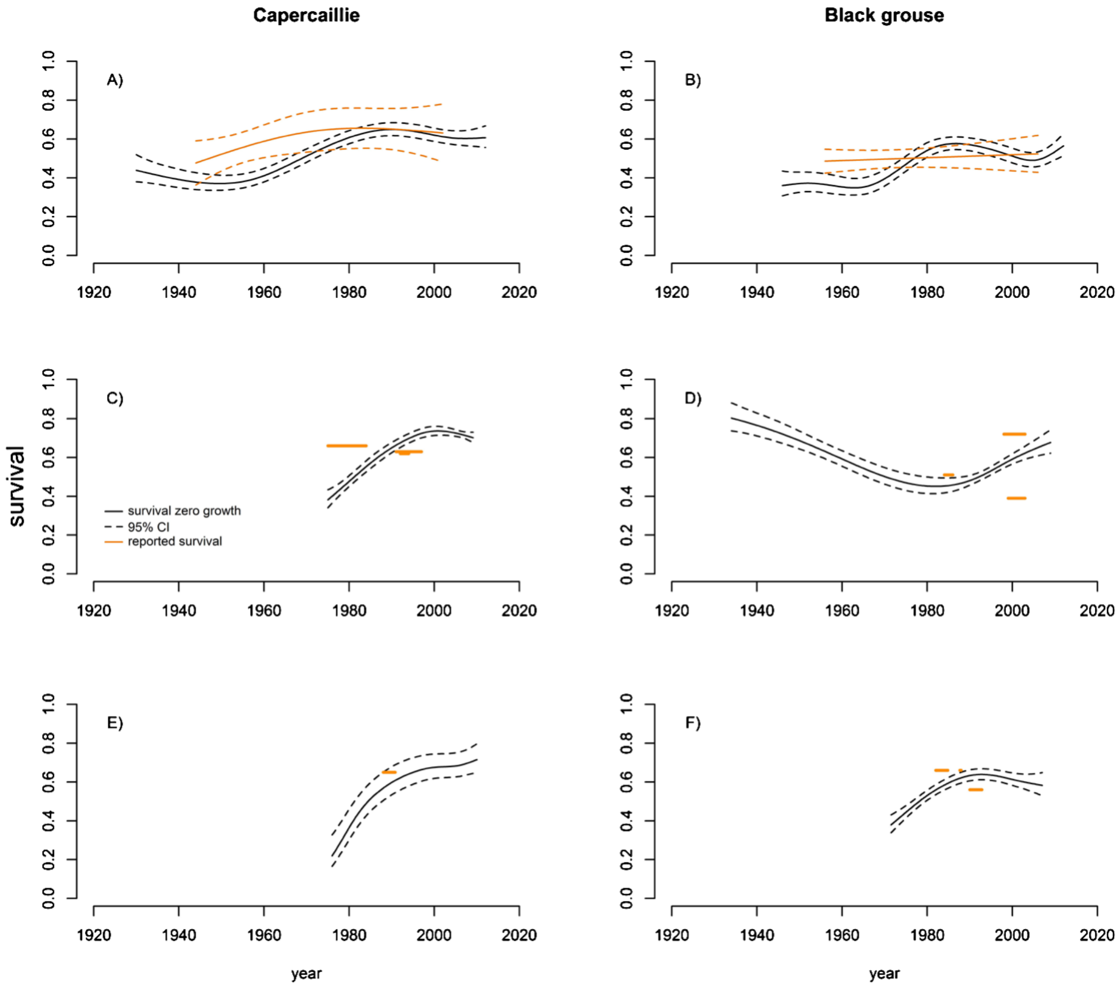

Figure 7. (A, B) Estimated adult survival required in Fennoscandia to counterbalance number of chicks per hen in a zero population-growth scenario with 95% CI for capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Orange lines are most parsimonious models of observed adult survival estimates reported from different Fennoscandian studies (see table A4). (C, D) depict estimated adult survival required to counterbalance reproduction for Scottish capercaillie and British black grouse. Reported adult survival is superimposed orange line segments. (E, F) show estimated adult survival required to counterbalance reproduction for continental European capercaillie and black grouse. Reported adult survival rates are highlighted in orange.

wards the end of the time series. This trend was similar for black grouse, but the decrease alleviates in the last 10 years (fig. 6E, F).

As for the British Isles, there were few reports of adult survival rates for continental European capercaillie and black grouse. For both species however, reported adult survival has been within the range of what is needed to counterbalance current reproductive output (fig. 7E, F).

Discussion

Reproductive success of Fennoscandian capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) has declined throughout the past 80 years and year-to-year variation in net reproductive output has decreased by a factor of four for capercaillie and two and a half for black grouse. The decrease in reproductive success has brought about large-scale population declines. Although adult survival trends are positive for both species, the decline in net reproductive output has not been compensated for. Assuming that adult survival has not increased since the last reports, then there has been no large-scale population growth in Fennoscandian capercaillie or black grouse since the 1970s. When investigating the discrepancy between required and actual adult survival, the consequences of declining reproduction appear more severe for black grouse. The parallel decline in reproduction of both species supports the view that they are affected by the same extrinsic forces in the boreal forests (Wegge & Rolstad, 2011).

Our results suggest that black grouse populations were performing better in Britain for a period than contemporary populations elsewhere. Although a decrease in the net reproduction occurred during the 1990s, British black grouse produced an increasing number of chicks until then. Furthermore, we did not detect any change in number of broods per hen in Britain or in continental Europe. For grouse in general, in which the vast majority of females attempt to reproduce each year (Bergerud et al., 1988), the proportion of hens with brood maxima is a direct consequence of nest success. Any variation in proportion of hens with brood beyond what may be ascribed to nesting success is due to variation in chick survival. Hence, the observed pattern in chicks per hen in British and continental European black grouse may well be caused by varying chick survival rather than overall changes in black grouse nest success. This is somewhat supported by the apparent lack of trends (albeit few data points) in the combined nest success data for the British Isles and continental Europe (fig. 3, top). In which case, black grouse chick survival to late summer has decreased by 77% in Britain and 83% in the continental European countries since 1992 and 1971 respectively. Reported values of annual black grouse adult survival were quite high in northern England (Warren & Baines, 2002) whereas in Wales, Bowker et al. (2006) reported an estimated annual adult survival of 0.39 which is very low. It is therefore unclear to what extent population declines of black grouse in Britain are related to adult survival failing sufficiently offset poor reproduction. Less variation was reported in adult survival of continental European black grouse. When data of adult survival and offset-rates were overlapping, reproduction levelled off. Today however, black grouse females in continental Europe must have annual survival rates in the range of 0.7-0.8 to allow populations to grow, which is high, but similar to 0.72 reported by Warren & Baines (2002).

Our analysis of capercaillie reproduction in both Scotland and countries of continental Europe showed steep declines over a relatively short time period (ca. 40 years). However, the situation pre-1970s remains speculative for both areas. For continental Europe, the negative slope has probably been less steep than what we present here as it seems unlikely that almost all hens had a brood and that there were seven chicks per hen in late summer in the mid-1970s, considering the long term declines described in several studies.

Within Fennoscandia, nest success was probably over-estimated because some nests were predated before detection and most studies detected nests by chance (Mayfield, 1975). Similarly the loss of chicks could be under-estimated because it is easier to detect a brood than a single individual female (Buckland et al., 2005) or because in harvest data, number of chicks might be biased low (Asmyhr et al., 2012). At any rate, studies that collected data from harvest occurred before or in the early part of the decline phase (Siivonen, 1954; Helminen, 1963; Semenow Tjan Shanskiy, 1979). We suspect that continental European capercaillie data suffer partly from detection differences between single birds and broods, especially due to low sample sizes early in the series. Below we discuss our findings in the context of historical changes of three major environmental factors and their possible interactions that could contribute to the observed declines; 1) Intensified land-use, 2) Climate change, and 3) Increased generalist predator densities.

Intensified land-use

In the Fennoscandian context, intensified land use refers mainly to the expansion of modern forestry. Forestry practices have changed from manual single-tree cutting via mechanical stand-level clear-cutting to ecological sustainable forestry. Ecological sustainable forestry, whereby key biotopes are preserved and deciduous species are not targeted as before, is today implemented at various extents across Fennoscandia (see also Wegge & Rolstad, 2011). These changes have probably not affected nest predation directly (Wegge, 1985) as predation of cryptic eggs laid by cryptic birds can be regarded as incidental (Vickery et al., 1992). In general, it occurs when predators searching for their main prey come close enough to detect or flush the incubating female, thus exposing the nest. Capercaillie and black grouse nest in all the habitat types that they commonly use (Storaas & Wegge, 1987) and considering the high population turnover rates, a stronger preference for certain nesting habitat types could be expected if there was selection brought about by predation. Forestry practices might however, make nest predators more efficient by limiting or confining optimal nesting or brooding habitats, or by making these habitats more accessible to predators. In artificial nest experiments, proximity to forest edges, roads or agricultural land have all been found to increase egg predation (Andren, 1992; Paton, 1994). Nonetheless, this probably relates to the distribution of predators in the landscape (Kurki et al., 1998) rather than the innate ability of edges, roads or agricultural fields to improve predator searching efficiency and nest predation.

Nest survival of species that nest in open landscapes where nest predators are identified (e.g. greater sage grouse (*Centrocercus urophasianus*) in the presence of raven (*Corvus corax*)) has been found to depend strongly on vegetation structure and the availability of nest cover (Coates & Delehanty, 2010). However, corvids have not been identified as important nest predators of capercaillie and black grouse eggs, effects of habitat are ambiguous and no single effect of habitat on nest predation has been identified and agreed upon in forest dwelling woodland grouse

(Storaas & Wegge, 1987; Brittas & Willebrand, 1991; Storch, 1994; Ludwig et al., 2010). This could partly be because visually hunting predators (e.g. corvids) are less important in the boreal forests of Fennoscandia than in the sagebrush grassland of North America. In a recent study, Jahren et al. (2015) showed that red fox and pine marten together accounted for nearly all identified predation incidents of capercaillie and black grouse nests in Norway while corvids, even though present, were not important. In Abernethy, Scotland, where foxes are controlled and pine martens are protected, pine martens were the only predators recorded predating capercaillie nests (Summers et al., 2009).

Sirkiä et al. (2010) proposed that capercaillie persistence at a landscape scale relates to conifer forest cover in general, and is independent of configuration of stand age-classes. A similar hypothesis has also been put forward for black grouse in relation to abundance of birch (*Betula pubescens*) (Lindén & Helle, 2003). In this context, population declines related to habitat deterioration or loss may be true for the Fennoscandian black grouse, but the extent of conifer forest cover (i.e. capercaillie habitat) has not changed in the time period at hand (Östlund, 1997). Moreover, reduced carrying capacity induced by habitat loss will not necessarily reduce per capita reproductive output directly, so much that it forces adults to vacate poorer areas in favor of more suitable habitat. Something similar has been observed in willow ptarmigan (*Lagopus lagopus*), in which reproduction seems to be spatially independent (Hörnell-Willebrand et al., 2006; Kvasnes et al., 2014).

Hens with broods are more constrained in their habitat selection than brood-less hens (Wegge & Kastdalen, 2008). Storaas et al. (1999) hypothesized that during the development of clear-cut stands into thickets, good quality brood habitat becomes scarce and its limited availability could be regarded as an ecological trap. However, this probably has a finite temporal effect in the boreal forests as broods have recently been reported to forage in re-developing stands as they transition into older forest (Wegge & Kastdalen, 2008; Wegge & Rolstad, 2011). A similar mechanism was reported from Finland and Scotland, where broods survived better with increasing bilberry (*Vaccinium myrtillus*) cover (Baines et al., 2004; Lakka & Kouki, 2009). After clear-cutting, bilberry is usually replaced by forbs and graminoids but, after a short-term reduction in bilberry cover coinciding with increasing forest density and younger-aged forest, it later reappears in post sapling-stands (Lakka & Kouki, 2009; Hedwall & Brunet, 2013).

Forest management in Fennoscandia is undergoing rapid development and previous habitat conditions suspected of having negative effects on grouse vital rates may no longer be present. Over the past few decades, the forestry industry has been attempting to accommodate both timber management and biodiversity considerations (Spence, 2001; Vanha-Majamaa & Jalonen, 2001; Indufor Oy, 2005) and the importance of habitat diversity for chick production in both capercaillie and black grouse is now recognized (Lande et al., 2014). As such, there should be ongoing improvements in habitat for both capercaillie and black grouse in Fennoscandia that should in turn be reflected by a recovery in reproductive rates. However, today's habitat structure in Fennoscandia has not been shown to limit chick production under contemporary densities (i.e. Sirkiä et al., 2010) and the suggested habitat requirements for both capercaillie and black grouse are not as rigid as previously suspected (e.g. Sirkiä et al., 2011a, b; Lande et al., 2014).

In continental Europe and Britain, intensified land-use refers to a number of processes. These are primarily intensified agriculture, changes in grazing pressure, afforestation, forest maturation and increased disturbance from leisure activities such as ski-resorts (Storch, 2007). In Swiss alpine populations of black grouse, there are concerns that reduced grazing pressure by domestic livestock along the timberline brought about by the abandonment of traditional farming techniques will lead to shrub encroachment of alpine pastures (Patthey et al., 2012). This may also affect the capercaillie in Switzerland, which selects for open and grazed forests during winter (Sachot et al., 2003). Lower biodiversity might be a consequence of reduced grazing pressure as well as negative impacts on the trade-offs between cover and food-searching that brood-rearing hens exhibit (Signorell et al., 2010). By contrast, in Britain, over-grazing by both red deer (*Cervus elaphus*) and domestic sheep (*Ovis aries*) is associated with lower densities of black grouse, lower insect abundance and reduce black grouse reproduction (Baines, 1996; Calladine et al., 2002).

Climate change

Production of eggs and incubation are costly activities (Storaas et al., 2000). A change in onset of spring due to climate change could be leading to a mismatch between production of eggs and nutritional development of forage plants which may have adverse effects on female body condition and subsequent endurance during incubation and the production of good quality offspring (Moss et al., 2001). Additionally, it might lead to lower re-nesting rates as this is weight-related (Storaas et al., 2000). Effects of climate change on female vitality have, however, scarcely been studied and we found no data of body weights or declining egg numbers consistent with lowered female spring body condition. Furthermore, we could not separate between first nests and re-nests in our analysis so any potential decline in re-nesting rates could not be evaluated. We have no data indicating that a large proportion of the increasingly unsuccessful nests were due to female desertion or adverse weather events.

Climate is probably a more important driver of chick survival than nest success as chicks are reliant on insectivorous foods for the first couple of weeks post-hatching (Rajala, 1959; Atlegrim & Sjöberg, 2008; Wegge & Kastdalen, 2008). Furthermore, chick survival is positively related to temperature during the first two weeks post hatching and chick mortality directly related to adverse weather is rare, but cold and wet weather can predispose chicks to higher predation (Wegge & Kastdalen, 2007).

In vast areas of Fennoscandia, the start of the growing season is not only increasingly early but also increasingly irregular (Karlsen et al., 2009). The south to north distribution of capercaillie and black grouse covers a wide range of mean temperatures and season start dates. Black grouse have exhibited plasticity as they adapt to earlier spring by advancing egg laying, but a mismatch can occur when the chicks hatch in unseasonably warm summer temperatures or in advance of insect phenology (Ludwig et al., 2006). Although some aspects of climate change obviously have adverse effects on reproduction, the irregular nature of today's climate is not manifested in a variable reproductive output that is detectible in our data. Moreover, the discrepancy in results from the bulk of studies investigating relationships between weather and different reproduction parameters indicate that climatic factors might be overridden or masked by other forces (i.e. Tornberg et al., 2012), at least in short-term capercaillie and black grouse population dynamics.

Our results suggest that there are considerable differences in reproductive success between capercaillie and black grouse in Britain. For capercaillie, links between climate change and reproduction have been established (Moss et al., 2001), but not so for black grouse (Moss, 1986). In Britain and central Europe, the two species are not sympatric to the same extent as in the boreal forests. Where they coexist in Scotland, capercaillie inhabit mature forest plantations which are considered unsuitable for black grouse (Pearce-Higgins et al., 2007). The range of black grouse habitat is also larger and possibly provides more variation in, e.g., precipitation and thus climate refuges. Similarly, climate trends also failed to explain variation in black grouse reproduction in the French Alps (Barnagaud et al., 2010). Consequences of climate change are predicted to increase in severity with increasing latitude (Houghton et al., 2001) and species may not simply have latitudinal or altitudinal range-shifts to compensate for e.g. warmer climate. The lack of negative effects of climate on black grouse reproduction in the Alps and Britain but not Finland might be related to seasonality. Boreal forest grouse might have comparatively restricted seasonal ranges to match timing of hatching of chicks, for example.

Increased predator densities

Both red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) are potentially important predators of forest grouse chicks and eggs. Whilst reliable long-term population indices of these carnivores are lacking in general, a few studies suggest long-term increases in both pine marten and red fox populations (Krott & Lampio, 1983; Helldin, 2000; Selås & Vik, 2006). The evidence of an increase in pine marten populations is stronger than that of the red fox. Pine marten populations were decimated by over-harvesting and so were totally protected in Scandinavia from the early 1930s. The period of legal protection varied in length between countries but by the 1960s and 1970s, the harvest re-opened across all Scandinavia (Helldin, 2000). By contrast, the red fox has never been protected from harvest, but the economic incentives for hunting them have declined since the era when furs could be worth more than a month's wage (Statistics Norway, 1934, 1936, 1946). Furthermore, there are indications that foxes remained regionally scarce in Finland because of persecution until the early 1960s (Vuorisalo et al., 2014).

In large parts of Britain, black grouse share habitat with red grouse (*Lagopus lagopus scoticus*) which is managed for shooting. It follows that British black grouse may benefit from management actions undertaken on grouse moors (e.g. killing of predators and habitat improvement). It is therefore unexpected that the presence of gamekeepers has been found to have little or no effect on black grouse reproduction (Baines, 1996). Whilst gamekeepers can legally kill red foxes and crows, pine martens and raptors are protected and both goshawk and pine marten populations in Britain have increased since legal protection (Strachan et al., 1996; Lensink, 1997) and numbers of gamekeepers have declined (Summers et al., 2009). Hooded crows have been shown to be important predators of willow ptarmigan nests on an island where mammals were absent (Erikstad et al., 1982) but knowledge of their importance to nest survival in capercaillie and black grouse nests is derived from artificial nest experiments. If they have little impact on reproduction in capercaillie and black grouse, their removal may not have any effect. Moreover, our results might indicate that a recent change in chick survival is more likely to have occurred than changes in nest success for British and continental European black grouse, particularly because we do not see changes in broods per hen which is closely related to nest success. The relative importance of corvids to chick survival remains unclear, while the importance of raptors (Park et al., 2008; Tornberg et al., 2012) and mammalian predators (Marcström et al., 1988) is more certain.

We argue that the decrease in Fennoscandian capercaillie (61%) and black grouse (39%) nest success that we report here cannot be explained by increased predator efficiency alone. Irrespective of predation, grouse eggs occur at low densities and are difficult to find. Hence, they are not a reliable source of food for either red foxes or pine martens (Angelstam, 1983; Storaas & Wegge, 1984). It is therefore likely that nest predation occurs opportunistically when generalist predators find them while searching for other prey. Under such a scenario, predation could be expected to increase in relation to predator abundance. During the time span of our study, the proximate causes of nest failure have changed. In early studies, nest failure was often not related to predation and, in some cases, direct and indirect anthropogenic causes were more prominent (Siivonen, 1953) whereas in later studies, the proximate causes have been nest- and chick predation (Storaas & Wegge, 1987; Brittas & Willebrand, 1991; Wegge & Kastdalen, 2007). In a recent Finish study, nest loss among 210 black grouse nests was solely due to predation (Ludwig et al., 2010).

Chicks per hen in autumn is the product of nest success and chick survival. The varying pattern we present for chicks per hen in the first half of our Fennoscandian time series coincides well with that of the alternative prey hypothesis (Angelstam et al., 1984) or other density dependent regulators like parasites, as shown in willow ptarmigan and red grouse (*Lagopus lagopus scoticus*) (Hudson et al., 1998; Holmstad et al., 2005). In fact, preceding the start of the time series presented here, frequent observations of dead forest grouse initiated extensive work on grouse parasites and disease in Fennoscandia (Brinkmann, 1926). Since then, parasites have not been suspected to play an important role in capercaillie and black grouse population dynamics.

The subsequent dampening of variation in Fennoscandian chicks per hen coincides with the simultaneous dampening in vole cycles and increases in pine marten and red fox populations. Vole cycles, the main driver of small game fluctuations in Fennoscandia, shifted from regular 4 to 6 year amplitude intervals, to diminished or irregular patterns (Ims et al., 2008; Kausrud et al., 2008; Cornulier et al., 2013). The collapse of vole cycles is a phenomenon to be considered together with the increase in generalist predators. Until the early 1970s, voles were highly cyclic and constituted an unpredictable food source for vole-eating predators (Hörnfeldt et al., 2005). Since then, the large-scale dampening of the vole cycles (Ims et al., 2008; Cornulier et al., 2013) may have resulted in voles constituting a new type of stable and predictable food source allowing vole-eaters to reproduce regularly as opposed to only in years with vole peaks.

Furthermore, across the whole region, large herbivore populations have undergone an exponential increase throughout the same period (Milner et al., 2006; Elmhagen et al., 2015), and today there is an unprecedented availability of offal and carcasses for small and medium-sized carnivores. As such, seasonal bottlenecks like winter, are not necessarily regulating small and medium-sized carnivores as they might have done earlier (Selås & Vik, 2006). In combination with the ready availability of food resources before and during the winter period, a reduction in seasonality and winter severity brought about by climate change may have facilitated mesopredators such as the red fox (Hersteinsson & MacDonald, 1992; Bartoń & Zalewski, 2007; Elmhagen et al., 2015). Reduced snow cover may also remove protection from predators for black grouse (Spidsø, Hjeljord & Dokk, 1997).

Population change and conclusion

In such long-term and spatially comprehensive trends, it is hard to separate between causal and correlative relationships. Throughout the time-period, capercaillie and black grouse habitats have undergone substantial biotic and abiotic changes. It is likely that there is not one single factor causing declines in woodland grouse reproduction but several acting in unison. Interregional comparisons of population status in continental Europe and the British Isles with Fennoscandia illuminates key differences in which limiting factors are important. Limiting factors expected to interact with habitat deterioration, habitat retraction and small population size, are important in continental Europe and Britain and should not be underestimated. By contrast, Fennoscandia comprises about 1.2 million km^2 of land of which large parts are continuous capercaillie and black grouse habitat (74, 37 and $>50\%$ of Finland, Norway and Sweden respectively). Currently, there are few cues to any single effect of habitat, direct or indirect, that could change the demographic rates of capercaillie and black grouse in the northern boreal forests.

It has been shown that predation can override effects of, for example, intensified land-use on small herbivores (Schmidt et al., 2004) and potential effects of habitat change might be obscured further when grouse densities are low. Most habitat-related studies on capercaillie and black grouse in the Fennoscandian boreal forests have been conducted during low grouse densities. Despite the different challenges facing Fennoscandian compared with British and continental European populations, a common limiting factor is predation. It is unlikely that declines in reproduction of this spatiotemporal magnitude can be explained without an increase in small and medium-sized mammalian carnivores.

Despite their sympatry, capercaillie and black grouse diverge in their habits and life histories. Their winter diet is essentially different and whilst capercaillie lek in closed canopy forest, black grouse lek in open habitat types. Forces mediated through habitat change that suppress one of the two species will not necessarily suppress the other. Their joint decline is therefore somewhat contrary to the idea of one common habitat-linked causal mechanism. In addition, a strikingly similar development in the dynamics of the Norwegian willow ptarmigan (*Lagopus lagopus*) population has been reported (Hjeljord, 2015), despite not being directly related to forestry.

In the Fennoscandian countries, bag limits are common and hunting is seasonally and regionally restricted. Censuses are also carried out (apart from Sweden) before the onset of harvest. Hence, in large parts of Fennoscandia, stakeholders are attempting to reduce the impact of harvest on capercaillie and black grouse populations but with unknown effects. In Finland, harvest was found to strongly affect black grouse populations in the subsequent year (i.e. additive mortality), but to a lesser extent in capercaillie, although harvest did not induce negative population trends (Lampila et al., 2011). In Finland at the time, harvest recommendations for the upcoming season were not based on August censuses. This may partly explain the need for a lag-term when describing harvest mortality as a function of population size in this particular study, which caused over-harvest in the decline phase of the population cycle. From studies conducted on willow ptarmigan, bag size is more closely related to hunter effort than population density and harvest rate is relatively higher at low than high densities (Willebrand et al., 2011). More needs to be understood of harvest and its effect on grouse populations and studies on this should be welcomed. Therefore, caution should be valued in grouse management and managers need to be proactive in their restrictions. According to the last Fennoscandian reports on adult female survival, our results imply that populations of capercaillie need 1.6 and black grouse need 1.9 chicks per hen annually to remain stable. This is higher than our model predictions of contemporary values of 1.2 and 1.6 chicks per hen respectively. Reproduction-based threshold harvesting is a management strategy that may be suitable in this case.

Grouse reproduce at an early age. They invest in many offspring and have high growth rates. It follows that losses in net production can be high, but when reproductive outputs are continuously declining and fluctuating patterns diminishing, it is a sign of mortality rates to which the populations are not adapted. The consistent absence of periods with sequential years of positive growth rates are preventing populations of capercaillie and black grouse from breaking out of the current negative trends. Attributing this to a functional and/or numerical response remains speculative but there is little doubt that reducing predator numbers would improve grouse reproduction and densities (Marcström et al., 1988; Lindström et al., 1994; Kauhala et al., 2000). It is also clear that changes in forestry practices over the last 20 years (e.g. Green Tree Retention and The Programme for the Endorsement of Forest Certification, PEFC standards) have yet to have any detectible positive effects on capercaillie and black grouse reproduction.

Our results imply that capercaillie and black grouse populations should be intensively monitored and measures should be undertaken to reduce mortality of eggs and chicks. Most of recently reported adult survival rates are in line with or higher than the earliest reports obtainable. More needs to be understood of the complex spatial and temporal mechanisms involved in generalist predator dynamics and their prey. There is a need to investigate not only the suite of predators acting on grouse but also how they limit grouse in different phases of their life history. We suggest that future studies should aim to better understand the predators limiting grouse reproduction throughout their ranges and how predation rates are mediated by continuously changing habitat and climate.

References

Åhlen, P.-A., Willebrand, T., Sjöberg, K. & Hörnell-Willebrand, M. (2013) Survival of female capercaillie *Tetrao urogallus* in northern Sweden. *Wildlife Biol.*, 19, 368-373.

Andren, H. (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology*, 73, 794-804.

Andren, H. & Angelstam, P. (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology*, 69, 544-547.

Angelstam, P. (1983) *Population dynamics of tetraonids especially the black grouse Tetrao tetrix L. in boreal forests*. Ph.D. Thesis. Uppsala University, Uppsala, Sweden.

Angelstam, P. (1984) Sexual and seasonal differences in mortality of the black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scand.*, 15, 123-134.

Angelstam, P., Lindström, E. & Widén, P. (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, 62, 199-208.

Asmyhr, L., Willebrand, T. & Hörnell-Willebrand, M. (2012) Successful adult willow grouse are exposed to increased harvest risk. *J. Wildlife Manage.*, 76, 940-943.

Atlegrim, O. & Sjöberg, K. (2008) Lepidoptera larvae as food for capercaillie chick (*Tetrao urogallus*): a field experiment. *Scand. J. Forest Res.*, 10, 278-283.

Baines, D. (1991) Factors contributing to local and regional variation in black grouse breeding success in northern Britain. *Ornis Scand.*, 22, 264-269.

Baines, D. (1996) The implications of grazing and predator management on the habitats and breeding success of black grouse *Tetrao tetrix*. *J. Appl. Ecol.*, 33, 54-62.

Baines, D. & Hudson, P. (1995) The decline of black grouse in Scotland and northern England. *Bird Study*, 42, 122-131.

Baines, D., Moss, R. & Dugan, D. (2004) Capercaillie breeding success in relation to forest habitat and predator abundance. *J. Appl. Ecol.*, 41, 59-71.

Baines, D., Warren, P. & Richardson, M. (2007) Variations in the vital rates of black grouse *Tetrao tetrix* in the United Kingdom. *Wildlife Biol.*, 13, 109-116.

Baines, D., Aebischer, N., Brown, M. & Macleod, A. (2011) *Analysis of capercaillie brood count data: long term analysis*. Scottish Natural Heritage Commissioned Report No. 435, 35.

Barikmo, J., Spidsø, T. & Wegge, P. (1984) *Skogsfuglprosjektet 1980-1984* (ed S. Myrberget). Direktoratet for vilt og ferskvannsfisk Viltforskningen, Trondheim. (In Norwegian).

Barnagaud, J.-Y., Crochet, P.A., Magnani, Y., Bernard Laurent, A., Ménoni, E., Novoa, C. & Gimenez, O. (2010) Short-term response to the North Atlantic Oscillation but no long-term effects of climate change on the reproductive success of an alpine bird. *J. Ornithol.*, 152, 631-641.

Bartoń, K. & Zalewski, A. (2007) Winter severity limits red fox populations in Eurasia. *Global Ecol. Biogeogr.*, 16, 281-289.

Bergerud, A.T., Davies, R.G., Gardarsson, A., Gratson, M.W., Hartzler, J.E., Huempfner, R.A., Jenni, D.A., Mossop, D.H., Myrberget, S., Page, R.E., Schmidt, R.K., Svedarsky, W.D. & Tester, J.R. (1988) *Adaptive Strategies and Popululation Ecology of Northern Grouse*, A. Bergerud & M. Gratson (Eds). University of Minnesota Press, Minneapolis, USA.

Borchtchevski, V.G., Hjeljord, O., Wegge, P. & Sivkov, A.V. (2003) Does fragmentation by logging reduce grouse reproductive success in boreal forests? *Wildlife Biol.*, 9, 275-282.

Bowker, G., Bowker, C. & Baines, D. (2006) Survival rates and causes of mortality in black grouse *Tetrao tetrix* at Lake Vyrnwy, North Wales, UK. *Wildlife Biol.*, 13, 231-237.

Brinkmann, A. (1926) *Coccidiosen hos lirype*. Bergens Museums Årbok. Bergen Museum, Bergen, Norway. (In Norwegian).

Brittas, R. & Willebrand, T. (1991) Nesting habitats and egg predation in Swedish black grouse. *Ornis Scand.*, 22, 261-263.

Buckland, S., Anderson, D., Burnham, K. & Laake, J. (2005) *Distance Sampling*. John Wiley & Sons, Ltd.

Caizergues, A. & Ellison, L. (1997) Survival of black grouse *Tetrao tetrix* in the French Alps. *Wildlife Biol.*, 3, 177-186.

Caizergues, A. & Ellison, L.N. (2000) Age-specific reproductive performance of black grouse *Tetrao tetrix* females. *Bird Study*, 47, 344-351.

Calladine, J., Baines, D. & Warren, P. (2002) Effects of reduced grazing on population density and breeding success of black grouse in northern England. *J. Appl. Ecol.*, 39, 772-780.

Catt, D., Baines, D. & Picozzi, N. (1998) Abundance and distribution of capercaillie *Tetrao urogallus* in Scotland 1992-1994. *Biol. Conserv.*, 85, 257-267.

Catt, D., Dugan, D. & Green, R. (1994) Collisions against fences by woodland grouse in Scotland. *Forestry*, 67, 105-118.

Coates, P.S. & Delehanty, D.J. (2010) Nest predation of greater sage-grouse in relation to microhabitat factors and predators. *J. Wildlife Manage.*, 74, 240-248.

Colloque galliformes de montagne (1987) Actes Du Colloque Galliformes de Montagne. Office Nationale de la Chasse, Saint-Just-La-Pendue. (In French).

Cornulier, T., Yoccoz, N.G., Bretagnolle, V., Brommer, J.E., Butet, A., Ecke, F., Elston, D.A., Framstad, E., Henttonen, H., Hörnfeldt, B., Huitu, O., Imholt, C., Ims, R.A., Jacob, J., Jędrzejewska, B., Millon, A., Petty, S.J., Pietiäinen, H., Tkadlec, E., Zub, K. & Lambin, X. (2013) Europe-wide dampening of population cycles in keystone herbivores. *Science*, 340, 63-66.

Curtis, C.J. & Simpson, G.L. (2014) Trends in bulk deposition of acidity in the UK, 1988-2007, assessed using additive models. *Ecol. Indic.*, 37, 274-286.

Danell, K., Bergström, R. & Wallgren, M. (2011) *Vilthistoriska data – en bortglömd resurs*. Svenska Jägareforbundet/Swedish Sportsmen Association. Available at http://www.slu.se/globalassets/.gamla_strukturen/externwebben/overgripande-slu-dokument/miljoanalys-dok/rapporter/vilthistoriskadatafoma101115.pdf. (In Swedish).

De Franceschi, P., Mattedi, S. & Perco, F. (1991) *Status and research in progress on the black grouse population in province of Udine (eastern Alps, Friuli-Venezia Giulia, Italy)*. Grouse News, 2, D. Lovel (Ed.), pp. 7-9.

Eaton, M., Marshall, K. & Gregory, R. (2007) Status of capercaillie *Tetrao urogallus* in Scotland during winter 2003/04. *Bird Study*, 54, 145-153.

Ellison, L.N. (1978) Black grouse population characteristics on a hunted and three unhunted areas in the French Alps. In: T.W.I. Lovel (Ed.) *Woodland Grouse*, pp. 64-73. WPA.

Ellison, L.N., Magnani, Y. & Corti, R. (1982) Comparison of a hunted and three protected black grouse populations in the French Alps. In: T.W.I. Lovel (Ed.) *Conference Proceedings*.

Ellison, L.N., Bernard-Laurent, A., Magnani, Y., Gindre, R. & Corti, R. (1984) *Le Tetras Lyre – Dynamique Des Populations, Chasse et Biotope de Reproduction Dans Les Alpes Francaises*. Report, Office Nationale de la Chasse. (In French).

Elmhagen, B., Kindberg, J., Hellström, P. & Angerbjörn, A. (2015) A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio*, 44, 39-50.

Erikstad, K., Blom, R. & Myrberget, S. (1982) Territorial hooded crows as predators on willow ptarmigan nests. *J. Wildlife Manage.*, 46, 109-114.

Erlinge, S., Göransson, G. & Hansson, L. (1983) Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos*, 40, 36-52.

GetData Graph Digitizer (2016).

Grakov, N.N. (1978) Long-term changes in the abundance of the pine marten (*Martes martes*) and some patterns of this process. Бюллетень Московского общества испытателей природы. Отдел биологический, 83, 46-56. (In Russian with English summary).

Grubbström, E. (1979) Kläckningstidpunkten kan variera med en månad. *Jaktjournalen*, 44-45. (In Swedish).

Hagen, Y. (1952) *Rovfuglene Og Viltpleien*. 1st Edition. Gyldendal, Oslo, Norway. (In Norwegian).

Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.*, 60, 353-367.

Hedwall, P. & Brunet, J. (2013) Changes in the abundance of keystone forest floor species in response to changes of forest structure. *J. Veg. Sci.*, 24, 296-306.

Helldin, J.O. (2000) Population trends and harvest management of pine marten *Martes martes* in Scandinavia. *Wildlife Biol.*, 6, 111-120.

Helle, P. & Helle, T. (1991) How do changes in forest structure explain recent changes in Finnish grouse populations? *Suomen Riista*, 37, 56-66.

Helle, P. & Ikonen, K. (2015) *Wildlife monitoring in Finland – on-line information to game administration, hunters and wider public*. Oral presentation, IBFRA – The Natural Resource Institute, Finland, Rovaniemi, Finland. Available at http://www.metla.fi/life/lifedata/pdf/Helle_IBFRA_2015.pdf.

Helminen, M. (1963) *Composition of the Finnish Populations of Capercaillie, Tetrao urogallus, and Black Grause, Lyrurus tetrix, in the Autumns of 1952-1961, as Revealed by a Study of Wings*. Finnish Game and Fisheries Research Institute, Game Division.

Hersteinsson, P. & MacDonald, D.W. (1992) Interspecific competition and the geographical distribution of red and Arctic foxes *Vulpes Vulpes* and *Alopex lagopus*. *Oikos*, 64, 505-515.

Hjeljord, O. (2015) INA Fagrapport 30: *Ryper Før Og Nå*. Fakultet for miljøvitenskap og teknologi Institutt for naturforvaltning, Ås, Norway. (In Norwegian).

Höglund, N. (1953) Vem tar tjäderns egg? *Svensk Jakt*, 91, 416-420. (In Swedish).

Holmstad, P., Hudson, P. & Skorping, A. (2005) The influence of a parasite community on the dynamics of a host population: a longitudinal study on willow ptarmigan and their parasites. *Oikos*, 11, 377-391.

Hörnell-Willebrand, M., Marcström, V., Brittas, R. & Willebrand, T. (2006) Temporal and spatial correlation in chick production of willow grouse *Lagopus lagopus* in Sweden and Norway. *Wildlife Biol.*, 12, 347-355.

Hörnfeldt, B. (1978) Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia*, 32, 141-152.

Hörnfeldt, B., Hipkiss, T. & Eklund, U. (2001) Juvenile sex ratio in relation to breeding success in capercaillie *Tetrao urogallus* and black grouse *T. tetrix*. *Ibis*, 143, 627-631.

Hörnfeldt, B., Hipkiss, T. & Eklund, U. (2005) Fading out of vole and predator cycles? *Proceedings. Biological sciences/The Royal Society*, 272, 2045-2049.

Houghton, J., Ding, Y. & Griggs, D. (2001) Climate Change 2001: the scientific basis.

Hudson, P., Dobson, A. & Newborn, D. (1998) Prevention of population cycles by parasite removal. *Science*, 282, 2256-2258.

Ims, R., Henden, J. & Killengreen, S. (2008) Collapsing population cycles. *Trends Ecol. Evol.*, 23, 79-86.

Indufor Oy, S. (2005) *Effectiveness and Efficiency of FSC and PEFC Forest Certification on Pilot Areas in Nordic Countries*. Helsinki, Finland.

IPCC (2013) *Climate Change 2013: the Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. Stocker, D. Qin, G. Plattner, M. Tignor & S. Allen (Eds). Cambridge University Press, Cambridge, England.

Jahren, T., Storaas, T., Fossland Moa, P. & Hagen, B.R. (2015) *Multi-fate nest predation in black grouse and capercaillie and effects of habitat – preliminary results*. International Grouse Symposium, Oral presentation, 13th International Grouse Symposium, Reykjavik, Iceland.

Jones, A.M. (1982) *Aspects of the ecology and behaviour of capercaillie Tetrao urogallus L. in two Scottish plantations*. Dissertation. Univeristy of Aberdeen, Aberdeen, UK.

Karlsen, S., Høgda, K., Wielgolaski, F., Tolvanen, A., Tømmervik, H., Poikolainen, J. & Kubin, E. (2009) Growing-season trends in Fennoscandia 1982-2006, determined from satellite and phenology data. *Clim. Res.*, 39, 275-286.

Kastdalen, L. (1992) *Skogshøns Og Jakt*. Norges bondelag. Oslo, Norway. (In Norwegian).

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. *Curr. Zool.*, 57, 584-598.

Kauhala, K., Helle, P. & Helle, E. (2000) Predator control and the density and reproductive success of grouse populations in Finland. *Ecography*, 23, 161-168.

Kausrud, K., Mysterud, A., Steen, H. & Vik, J. (2008) Linking climate change to lemming cycles. *Nature*, 456, 93-98.

Kjellén, N. & Roos, G. (2000) Population trends in Swedish raptors demonstrated by migration counts at Falsterbo, Sweden 1942-97. *Bird Study*, 47, 195-211.

Klaus, S. (1985) Predation among capercaillie in a reserve in Thuringia. In: T.W.I. Lovel & P.J. Hudson (Eds) *Third International Grouse Symposium*. Conference Proceedings, pp. 334-346. World Pheasant Association, Reading, UK.

Kortland, K. & Peace, A. (2013) *Capercaillie monitoring in the national forest estate in Scotland: 2002 to 2012*. Grouse News, 45, T.K. Spidsø (Ed.), pp. 9-16.

Krott, P. & Lampio, T. (1983) Naadan esiintymisesta Suomessa 1900-luvulla. *Suomen riista*, 30, 60-63. (In Finnish with English summary: occurrence of the pine marten (*Martes martes*) in Finland in the 1900s).

Kurki, S. & Lindén, H. (1995) Forest fragmentation due to agriculture affects the reproductive success of the ground-nesting black grouse *Tetrao tetrix*. *Ecography*, 18, 109-113.

Kurki, S., Helle, P., Lindén, H. & Nikula, A. (1997) Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. *Oikos*, 79, 301-310.

Kurki, S., Nikula, A., Helle, P. & Lindén, H. (1998) Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *J. Anim. Ecol.*, 67, 874-886.

Kurki, S., Nikula, A., Helle, P. & Lindén, H. (2000) Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology*, 81, 1985-1997.

Kvasnes, M.A.J., Pedersen, H.C., Solvang, H., Storaas, T. & Nilsen, E.B. (2014) Spatial distribution and settlement strategies in willow ptarmigan. *Popul. Ecol.*, 57, 151-161.

Lakka, J. & Kouki, J. (2009) Patterns of field layer invertebrates in successional stages of managed boreal forest: implications for the declining capercaillie *Tetrao urogallus L.* population. *Forest Ecol. Manag.*, 257, 600-607.

Lampila, P., Ranta, E., Mönkkönen, M., Lindén, H. & Helle, P. (2011) Grouse dynamics and harvesting in Kainuu, northeastern Finland. *Oikos*, 120, 1057-1064.

Lande, U. & Herfindal, I. (2010) Use of hunters in wildlife surveys: does hunter and forest grouse habitat selection coincide? *Eur. J. Wildlife Res.*, 56, 107-115.

Lande, U., Herfindal, I., Willebrand, T., Fossland Moa, P. & Storaas, T. (2014) Landscape characteristics explain large-scale variation in demographic traits in forest grouse. *Landscape Ecology*, 29, 127-139.

Lensink, R. (1997) Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual-based diffusion model. *J. Anim. Ecol.*, 66, 811-826.

Lindén, H. (1981) Estimation of juvenile mortality in capercaillie *Tetrao urogallus* and the black grouse, *Tetrao tetrix* from indirect evidence. *Finnish Game Research*, 39, 35-51.

Lindén, H. & Rajala, P. (1981) Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland, 1964-77. *Riistatieteellisiä julkaisuja*, 39, 13-34. (In Finnish).

Lindén, H. & Helle, P. (2003) The rise and fall of black grouse populations in Finland since 1860s. In: P. Málková & P. Procházka (Eds) *Proceedings of the European Conference Black Grouse – Endangered Species of Europe*, pp. 113-114. *J. Ornithol.*, Prague, Czech Republic.

Lindström, E.R., Andren, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jaderberg, L., Lemnell, P.A., Martinsson, B., Skold, K. & Swenson, J.E. (1994) Disease reveals the predator – sarcoptic mange, red fox predation, and prey populations. *Ecology*, 75, 1042-1049.

Lovel, T. (Ed.) (1979) *Woodland Grouse Symposium*. WPA, Inverness, Scotland.

Ludwig, G., Alatalo, R.V., Helle, P. & Siitari, H. (2010) Individual and environmental determinants of daily black grouse nest survival rates at variable predator densities. *Ann. Zool. Fenn.*, 47, 387-397.

Ludwig, G., Alatalo, R.V., Helle, P., Lindén, H., Linström, J. & Siitari, H. (2006) Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. *P. R. Soc. B.*, 273, 2009-2016.

Ludwig, T., Storch, I. & Gärtner, S. (2009) Large-scale land use change may explain bird species declines in semi-natural areas: the case of black grouse population collapse in Lower Saxony, Germany. *J. Ornithol.*, 150, 871-882.

Ludwig, T., Storch, I. & Wuebbenhorst, J. (2008) How the black grouse was lost: historic reconstruction of its status and distribution in Lower Saxony (Germany). *J. Ornithol.*, 149, 587-596.

Marcström, V., Kenward, R. & Engren, E. (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *J. Anim. Ecol.*, 57, 859-872.

Marjakangas, A. & Törmälä, L. (1997) Female age and breeding performance in a cyclic population of black grouse *Tetrao tetrix*. *Wildlife Biol.*, 3, 195-203.

Marti, C. & Pauli, H.-R. (1983) Bestand und Altersstruktur der Birkhuhnpopulation im Reservat Aletschwald (Aletschgebiet, VS). *Bull. Murithienne*, 101, 23-28. (In German).

Mattson, E. & Zakariasson, P. (2009) *Viltövervakning Dalarnas och Gävleborgs län 2007/2008*. Svenska Jägareforbundet/Swedish Sportsmen Association. Available at http://old.viltdata.se/media/v_vrapport0708.pdf. (In Swedish).

Ménoni, E. & Novoa, C. (1988) *Contribution of shooting bag analyses of the knowledge of capercaillie (Tetrao urogallus L.) populations*. Gibier Faune Sauvage (France).

Ménoni, E., Novoa, C., Berducou, C., Canut, J., Mossol-Torres, M., Monta, M., Marin, S., Piqué, J., Campion, D. & Gil Gallus, J.A. (2002) Status of the capercaillie metapopulation in the Pyrenees (France, Spain and Andorra). *9th International Grouse Symposium*, Beijing, China.

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Csanyi, S. & Stenseth, N.C. (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J. Appl. Ecol.*, 43, 721-734.

Miquet, A. (1988) *Effects of winter disturbance on the black grouse (Tetrao tetrix)*. Gibier Faune Sauvage (France).

Moss, R. (1986) Rain, breeding success and distribution of capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* in Scotland. *Ibis*, 128, 65-72.

Moss, R. (1987) Demography of capercaillie *Tetrao urogallus* in North-East Scotland. II. Age and sex distribution. *Ornis Scand.*, 18, 135-140.

Moss, R. & Oswald, J. (1985) Population dynamics of capercaillie in a north-east Scottish glen. *Ornis Scand.*, 16, 229-238.

Moss, R. & Weir, D.N. (1987) Demography of capercaillie *Tetrao urogallus* in north-east Scotland. III. Production and recruitment of young. *Ornis Scand.*, 18, 141-145.

Moss, R., Oswald, J. & Baines, D. (2001) Climate change and breeding success: decline of the capercaillie in Scotland. *J. Anim. Ecol.*, 70, 47-61.

Moss, R., Picozzi, N., Summers, R.W. & Baines, D. (2000) Capercaillie *Tetrao urogallus* in Scotland – demography of a declining population. *Ibis*, 142, 259-267.

Mossol-Torres, M. & Ménoni, E. (2006) *The capercaillie in Andorra: a population in good health*. Grouse News, 32, T.K. Spidsø (Ed.), pp. 18-23.

Myrberget, S. & Hagen, Y. (1974) Reproduksjon hos lirype og skogsfugl i Setesdalen 1919-1934. *Sterna*, 13, 23-33. (In Norwegian).

Niewold, F. (1981) *Proceedings of the Second International Symposium on Grouse*, T.W.I. Lovel (Ed.). WPA, Edingburgh, Scotland.

Östlund, L. (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Can. J. Forest Res.*, 27, 1198-1206.

Park, K., Graham, K., Calladine, J. & Wernham, C. (2008) Impacts of birds of prey on gamebirds in the UK: a review. *Ibis*, 150, 9-26.

Paton, P.W.C. (1994) The effect of edge on avian nest success – how strong is the evidence. *Conserv. Biol.*, 8, 17-26.

Patthey, P., Signorell, N., Rotelli, L. & Arlettaz, R. (2012) Vegetation structural and compositional heterogeneity as a key feature in alpine black grouse microhabitat selection: conservation management implications. *Eur. J. Wildlife Res.*, 58, 59-70.

Pearce-Higgins, J.W., Grant, M.C., Robinson, M.C. & Haysom, S.L. (2007) The role of forest maturation in causing the decline of black grouse *Tetrao tetrix*. *Ibis*, 149, 143-155.

Pekkola, M., Alatalo, R., Pöysä, H. & Siitari, H. (2014) Seasonal survival of young and adult black grouse females in boreal forests. *Eur. J. Wildlife Res.*, 60, 477-488.

Picozzi, N. & Hepburn, L. (1986) A study of black grouse in north-east Scotland. In: *Proceedings of the 3rd International Grouse Symposium*, pp. 462-480.

Proctor, R. & Summers, R.W. (2002) Nesting habitat, clutch size and nest failure of capercaillie *Tetrao urogallus* in Scotland. *Bird Study*, 49, 190-192.

R Development Core Team (2012) *R: A language and environment for statistical computing*.

Rajala, P. (1959) On the food habits of capercaillie juveniles. *Suomen Riista*, 13, 143-155. (In Finnish).

Rajala, P. (1974) The structure and reproduction of Finnish populations of capercaillie, *Tetrao urogallus*, and black grouse, *Lyrurus tetrix*, on the basis of late summer census data from 1963-66. *Finnish Game Research*, 1-51.

Ringaby, E. (2014) *Tjäder: Bland Skogsbruk, Rävar Och Andra Jägare*. Malou K Media. (In Swedish).

Sachot, S., Perrin, N. & Neet, C. (2003) Winter habitat selection by two sympatric forest grouse in western Switzerland: implications for conservation. *Biol. Conserv.*, 112, 373-382.

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

Saniga, M. (2011) *Why the capercallie population Tetrao urogallus (L.) in the West Carpathians decline?* Grouse News, 41, T.K. Spidsø (Ed.), pp. 6-13.

Schmidt, N.M., Asferg, T. & Forchhammer, M.C. (2004) Long-term patterns in European brown hare population dynamics in Denmark: effects of agriculture, predation and climate. *BMC Ecology*, 4.

Seiskari, P. (1962) *On the Winter Ecology of the Capercaillie, Tetrao urogallus, and the Black Grouse, Lyrurus tetrix, in Finland. Papers on Game Research Helsinki, vol. 22*, pp. 1-119.

Selås, V. & Vik, J.O. (2006) Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897-1976. *Journal of Zoology*, 269, 299-308.

Selås, V., Sonerud, G.A., Framstad, E., Kalas, J.A., Kobro, S., Pedersen, H.B., Spidso, T.K. & Wiig, O. (2011) Climate change in Norway: warm summers limit grouse reproduction. *Popul. Ecol.*, 53, 361-371.

Semenow Tjan Shanskiy, O.I. (1979) *Ecology of Tetraonids* (ed T from R by AAC for S translations). U.S. Department of Agriculture and National Science Foundation, Washington D.C., USA.

Signorell, N., Wirthner, S., Patthey, P., Schranz, R., Rotelli, L. & Arlettaz, R. (2010) Concealment from predators drives foraging habitat selection in brood-rearing alpine black grouse *Tetrao tetrix* hens: habitat management implications. *Wildlife Biol.*, 16, 249-257.

Siivonen, L. (1953) On the destruction of gallinaceous birds. *Suomen Riista*, 8, 46-48.

Siivonen, L. (1954) Some essential features of short-term population fluctuation. *J. Wildlife Manage.*, 18, 38-45.

Siivonen, L. (1955) *On the Reflection of the Short-Term Fluctuations in Numbers in the Reproduction of Tetraonids*. Suomen Riistanshoito-säätiö.

Simpson, G. (2014) Identifying periods of change in time series with GAMs. Available at http://www.fromthebottomoftheheap.net/2014/05/15/identifying-periods-of-change-with-gams/.

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

Sirkiä, S., Helle, P., Lindén, H., Nikula, A., Norrdahl, K., Suorsa, P. & Valkeajärvi, P. (2011a) Persistence of capercaillie (*Tetrao urogallus*) lekking areas depends on forest cover and fine-grain fragmentation of boreal forest landscapes. *Ornis Fennica*, 88, 14-29.

Sirkiä, S., Nikula, A., Helle, P., Lindén, H., Norrdahl, K., Suorsa, P. & Valkeajärvi, P. (2011b) Contemporary mature forest cover does not explain the persistence of capercaillie (*Tetrao urogallus*) lekking areas in Finland. *Ornis Fennica*, 88, 208-216.

Smedshaug, C., Selås, V., Lund, S. & Sonerud, G. (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biol.*, 5, 157-166.

Solvang, H., Pedersen, H.C., Storaas, T. & Hagen, B.R. (2009) *Rapport for Skogsfugltaksering 2005-2008*. Høgskolen i Hedmark, Elverum, Norway. (In Norwegian).

Sørensen, O.J. (1977a) En fellingstatistikk, Hurdal. Foredrag fra Nordisk skogsfuglsymposium 1976 – *Vilrtapport* 5, pp. 39-46. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway. (In Norwegian).

Sørensen, O.J. (1977b) *Augusttakseringer av hønsefugl i Hurdal og Aurskog/Høland, 1976*. Nordisk Skogsfuglsymposium (ed S. Myrberget), pp. 6-10. Direktoratet for Naturforvaltning, Røros, Norway. (In Norwegian).

Spence, J. (2001) The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends Ecol. Evol.*, 16, 591-593.

Spidsø, T.K. & Stuen, O.H. (1983) *Skogsfuglstudier På Sørlandet*. Trondheim. (In Norwegian).

Spidsø, T.K., Hjeljord, O. & Dokk, J.G. (1997) Seasonal mortality of black grouse *Tetrao tetrix* during a year with little snow. *Wildlife Biol.*, 3, 205-209.

Starling, A.E. (1992) *The Ecology of Black Grouse Tetrao tetrix in north-east England*. University of Newcastle-upon-Tyne.

Statistics Norway (1934) *Pelsdyrtellingen i Norge*. H Aschehoug & Co., Oslo, Norway. (In Norwegian).

Statistics Norway (1936) *Pelsdyrtellingen i Norge*. H Aschehoug & Co., Oslo, Norway. (In Norwegian).

Statistics Norway (1946) *Pelsdyrtellingen i Norge*. H Aschehoug & Co., Oslo, Norway. (In Norwegian).

Statistics Norway (2016) *Statistics Norway*. Available at https://www.ssb.no/statistikkbanken/selectvarval/Define.asp?subjectcode=&ProductId=&MainTable=Smaavilt2&nvl=&PLanguage=0&nyTmpVar=true&CMSSubjectArea=jord-skog-jakt-og-fiskeri&KortNavnWeb=srjakt&StatVariant=&checked=true [accessed 28 March 2016].

Steiner, H., Schmalzer, A. & Pühringer, N. (2007) *Limitierende Faktoren Für Alpine Raufußhuhn-Populationen: Management-Grundlagen Nach Untersuchungen Im Nationalpark Kalkalpen*. Biologiezentrum, Linz, Austria. (In German).

Storaas, T. & Wegge, P. (1984) High nest losses in capercaillie and black grouse in Norway. In: T.W.I. Lovel & P.J. Hudson (Eds) *The 3rd International Grouse Symposium*. Conference Proceedings, York, UK.

Storaas, T. & Wegge, P. (1987) Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. *J. Wildlife Manage.*, 51, 167-172.

Storaas, T., Kastdalen, L. & Wegge, P. (1999) Detection of forest grouse by mammalian predators: a possible explanation for high brood losses in fragmented landscapes. *Wildlife Biol.*, 5, 187-192.

Storaas, T., Wegge, P. & Kastdalen, L. (2000) Weight-related renesting in capercaillie *Tetrao urogallus*. *Wildlife Biol.*, 6, 299-303.

Storch, I. (1993) *Habitat Use and Spacing of Capercaillie in Relation to Forest Fragmentation Patterns*. Ludwig-Maximilian, University of Munich, Munich, Germany.

Storch, I. (1994) Habitat and survival of capercaillie *Tetrao urogallus* nests and broods in the Bavarian Alps. *Biol. Conserv.*, 70, 237-243.

Storch, I. (2007) *Grouse: Status Survey and Conservation Action Plan 2006-2010*, I. Storch (Ed.). WPA, Fordingbridge, UK and IUCN, Gland, Switzerland.

Strachan, R., Jefferies, D. & Paul, R. (1996) *Pine Marten Survey of England and Wales, 1987-1988*. JNCC, Peterbourough, UK.

Summers, R.W., Willi, J. & Selvidge, J. (2009) Capercaillie *Tetrao urogallus* nest loss and attendance at Abernethy Forest, Scotland. *Wildlife Biol.*, 15, 319-327.

Summers, R.W., Dugan, D. & Proctor, R. (2010) Numbers and breeding success of capercaillies *Tetrao urogallus* and black grouse *T. tetrix* at Abernethy Forest, Scotland. *Bird Study*, 57, 437-446.

Summers, R.W., Green, R.E., Proctor, R., Dugan, D., Lambie, D., Moncrieff, R., Moss, R. & Baines, D. (2004) An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *J. Appl. Ecol.*, 41, 513-525.

Swenson, J. & Angelstam, P. (1993) Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Can. J. Zool.*, 71, 1303-1310.

Tornberg, R., Reif, V. & Korpimäki, E. (2012) What explains forest grouse mortality: predation impacts of raptors, vole abundance, or weather conditions? *Int. J. Ecol.*, 2012, 1-10.

Valkama, J., Korpimäki, E. & Arroyo, B. (2005) Birds of prey as limiting factors of gamebird populations in Europe: a review. *Biol. Rev.*, 80, 171-203.

Valkeajärvi, P. & Ijäs, L. (1994) Comparison of breeding success between fed and unfed black grouse in central Finland. *Suomen Riista*, 40, 98-109.

Vanha-Majamaa, I. & Jalonen, J. (2001) Green tree retention in Fennoscandian forestry. *Scand. J. Forest Res.*, 16, 79-90.

Vickery, P., Hunter Jr., M. & Wells, J. (1992) Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos*, 63, 281-288.

Vos, A. (1995) Population dynamics of the red fox (*Vulpes vulpes*) after the disappearance of rabies in county Garmisch-Partenkirchen, Germany, 1987-1992. *Ann. Zool. Fenn.*, 32, 93-97.

Vuorisalo, T., Talvitie, K., Kauhala, K., Bläuer, A. & Lahtinen, R. (2014) Urban red foxes (*Vulpes vulpes* L.) in Finland: a historical perspective. *Landscape Urban Plan.*, 124, 109-117.

Warren, P. & Baines, D. (2002) Dispersal, survival and causes of mortality in black grouse *Tetrao tetrix* in northern England. *Wildlife Biol.*, 8, 91-97.

Watson, A. (2010) *Popul. ecol. of black grouse on north-east Scottish moorland in 1959-82*. Grouse News, 40, T.K. Spidsø (Ed.), pp. 6-13.

Watson, A. & Nethersole-Thompson, D. (2006) Black grouse and western capercaillie on Upper Speyside in 1934-42. *Scottish Birds – The Journal of the SOC*, 26, 55-59.

Wegge, P. (1979) Status of capercaillie and black grouse in Norway. In: *Proceedings of the International Grouse Symposium, vol. 1*, pp. 17-26.

Wegge, P. (1985) *The Sociobiology, Reproduction, and Habitat of Capercaillie Tetrao urogallus L. in southern Norway*. University of Montana.

Wegge, P. & Grasaas, T. (1977) Bestandsstudier av storfugl på Sørlandet. *Viltrapport* 5 (ed S. Myrberget), pp. 22-39. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway. (In Norwegian).

Wegge, P. & Kastdalen, L. (2007) Pattern and causes of natural mortality of capercaille, *Tetrao urogallus*, chicks in a fragmented boreal forest. *Ann. Zool. Fenn.*, 44, 141-151.

Wegge, P. & Kastdalen, L. (2008) Habitat and diet of young grouse broods: resource partitioning between capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) in boreal forests. *J. Ornithol.*, 149, 237-244.

Wegge, P. & Rolstad, J. (2011) Clearcutting forestry and Eurasian boreal forest grouse: long-term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix* reveals unexpected effects on their population performances. *Forest Ecol. Manag.*, 261, 1520-1529.

Wilkinson, N. & Langston, R. (2002) Capercaillie *Tetrao urogallus* abundance and habitat use in Scotland, in winter 1998-99. *Bird Study*, 49, 177-185.

Willebrand, T. (1988) *Demography and Ecology of a Black Grouse (Tetrao tetrix L.) Population*. Uppsala University, Uppsala, Sweden.

Willebrand, T. (1992) Breeding and age in female black grouse *Tetrao tetrix*. *Ornis Scand.*, 23, 29-32.

Willebrand, T., Hornell-Willebrand, M. & Asmyhr, L. (2011) Willow grouse bag size is more sensitive to variation in hunter effort than to variation in willow grouse density. *Oikos*, 120, 1667-1673.

Wood, S. (2006) *Generalized Additive Models: an Introduction with R*. CRC Press.

Zawadzki, J. & Zawadzka, D. (2012) Population decline of capercaillies *Tetrao urogallus* in the Augustów Forest (NE Poland). *Acta Ornithol.*, 47, 199-204.

Zbinden, N. & Salvioni, M. (2003) Verbreitung, Siedlungsdichte und Fortpflanzungserfolg des Birkhuhns *Tetrao tetrix* im Tessin 1981-2002. *Ornithol. Beob*, 100, 211-226. (In German).

Appendix

Table A1.
Summary of nest success data used in analysis, for capercaillie and black grouse.

Region	Source	Year(s) of study	Resoluton	Method	Country
Capercaillie					
Fennoscandia	Barikmo et al., 1984	1980-1984	mean	telemetry	Norway
	Höglund, 1953	1953	yearly	conventional	Sweden
	Lindén, 1981	1966-1977	mean	conventional	Finland
	Myrberget & Hagen, 1974	1934	yearly	conventional	Norway
	Semenow Tjan Shanskiy, 1979	1930-1957	mean	conventional	Russia
	Siivonen, 1953	1946-1952	mean	conventional	Finland
	Storaas & Wegge, 1984	1979-1983	yearly	both	Norway
	Wegge & Grasaas, 1977	1953-1976	mean	conventional	Norway
	Grubbström, 1979	1977-1978	yearly	conventional	Sweden
	This study, Hedmark	2009-2012	yearly	conventional	Norway
	This study, Nord-Trøndelag	2010-2012	yearly	conventional	Norway
British Isles	Jones, 1982	1978-1979	mean	conventional	Scotland
	Proctor & Summers, 2002	1950-1998	mean	conventional	Scotland
	Summers et al., 2009	2003-2007	mean	conventional	Scotland
Continental Europe	Klaus, 1985	1971-1983	mean	conventional	Germany
	Saniga, 2002	1993-2001	mean	conventional	Slovakia
	Storch, 1994	1988-1992	mean	telemetry	Germany
Black grouse					
Fennoscandia	Angelstam, 1983	1977-1982	mean	telemetry	Sweden
	Lindén, 1981	1966-1977	mean	conventional	Finland
	Ludwig et al., 2010	2003-2006	mean	telemetry	Finland
	Marjakangas & Törmälä, 1997	1989-1993	yearly	telemetry	Finland
	Myrberget & Hagen, 1974	1932-1934	yearly	conventional	Norway
	Siivonen, 1953	1946-1952	mean	conventional	Finland
	Storaas & Wegge, 1984	1980-1983	yearly	both	Norway
	Valkeajärvi & Ijäs, 1994	1988-1992	mean	telemetry	Finland
	This study, Hedmark	2010-2012	yearly	conventional	Norway

Table A1.
(Continued.)

Region	Source	Year(s) of study	Resoluton	Method	Country
	This study, Nord-Trøndelag	2010-2012	yearly	conventional	Norway
	Willebrand, T. unpubl.	1990-1992	mean	telemetry	Sweden
	Willebrand, 1988	1984-1987	yearly	telemetry	Sweden
British Isles	Baines et al., 2007	1999-2004	mean	telemetry	Wales, England & Scotland
	Starling, 1992	1989-1991	yearly	telemetry	England
	Watson & Nethersole-Thompson, 2006	1935-1942	mean	conventional	Scotland
Continental Europe	Caizergues & Ellison, 2000	1991-1998	mean	telemetry	France
	Ellison et al., 1982	1977-1980	mean	conventional	France
	Niewold, 1981	1978-1980	mean	conventional	The Netherlands

Table A2.
Summary of data on broods per hen used in analysis, for capercaillie and black grouse.

Region	Source	Year(s) of study	Resoluton	Method	Country
Capercaillie					
Fennoscandia	Kurki et al., 2000	1989-1994	yearly	census	Finland
	Rajala, 1974	1963-1966	yearly	census	Finland
	Sørensen, 1977a, b	1976	yearly	census	Norway
	Wegge & Rolstad, 2011	1979-2008	yearly	census	Norway
	Siivonen, 1955	1946-1952	yearly	calculaton	Finland
	Census Norway	2001-2012	yearly	census	Norway
British Isles	Baines et al., 2011	1991-2009	yearly	census	Scotland
	Kortland & Peace, 2013	2002-2012	yearly	census	Scotland
	Moss & Oswald, 1985	1976-1983	yearly	census	Scotland
Continental Europe	Colloque galliformes de montagne, 1987	1976-1986	yearly	census	France
	Ménoni & Novoa, 1988	1984-1987	yearly	census	France
	Mossol-Torres & Ménoni, 2006	2000-2005	yearly	census	Andorra
	Saniga, 2011	1983-2010	yearly	census	Slovakia
	Steiner et al., 2007	2000-2002	yearly	census	Austria
Black grouse					
Fennoscandia	Kurki et al., 2000	1989-1994	yearly	census	Finland
	Marjakangas & Törmälä, 1997	1989-1993	yearly	telemetry	Finland
	Rajala, 1974	1963-1966	yearly	census	Finland
	Sørensen, 1977a, b	1976	yearly	census	Norway
	Siivonen, 1955	1946-1952	yearly	calculaton	Finland
	Census Norway	2002-2012	yearly	census	Norway
	Willebrand, T. unpubl.	1990-1992	yearly	telemetry	Sweden
	Willebrand, 1988	1984-1987	yearly	telemetry	Sweden
British Isles	Baines, 1996	1991-1993	yearly	census	Scotland
	Bowker et al., 2006	2000-2002	yearly	telemetry	Wales
	Calladine et al., 2002	1996-2000	yearly	census	England
	Baines, 1991	1989-1990	yearly	census	England
	Watson, 2010	1957-1964	yearly	census	Scotland
	Watson & Nethersole-Thompson, 2006	1934-1942	yearly	census	Scotland
Continental Europe	Barnagaud et al., 2010	1990-2007	yearly	census	France
	Colloque galliformes de montagne, 1987	1985-1987	yearly	census	France & Italy
	De Franceschi et al., 1991	1987-1991	yearly	census	Italy
	Ellison, 1978	1977-1978	yearly	census	France
	Ellison et al., 1982	1976-1980	yearly	census	France
	Ellison et al., 1984	1977-1981	yearly	census	France
	Miquet, 1988	1985-1987	yearly	census	France

Table A2.
(Continued.)

Region	Source	Year(s) of study	Resoluton	Method	Country
	Zbinden & Salvioni, 2003	1981-2002	yearly	census	Switzerland
	Vith, 1974	1970-1973	mean	census	Estonia

Table A3.
Summary of chicks per hen data used in analysis, for capercaillie and black grouse.

Region	Source	Year(s) of study	Resoluton	Method	Country
Capercaillie					
Fennoscandia	Helminen, 1963	1952-1961	yearly	harvest	Finland
	Kurki et al., 2000	1989-1994	yearly	census	Finland
	Lindén, 1981	1967-1976	mean	census	Finland
	Rajala, 1974	1963-1966	yearly	census	Finland
	Semenow Tjan Shanskiy, 1979	1930-1957	yearly	harvest	Russia
	Siivonen, 1954	1946-1954	yearly	harvest	Finland
	Solvang et al., 2009	2007-2012	yearly	census	Norway
	Spidsø & Stuen, 1983	1979-1982	yearly	telemetry	Norway
	Sørensen, 1977a, b	1976	yearly	census	Norway
	Wegge & Grasaas, 1977	1968-1976	mean	census	Norway
	Wegge & Rolstad, 2011	1979-2008	yearly	census	Norway
	Kastdalen, 1992	1987-1989	yearly	census	Norway
	Ringaby, 2014	2000-2005	yearly	telemetry	Sweden
	Census Boda, Sweden	1980-2010	yearly	census	Sweden
	Census Norway	2001-2012	yearly	census	Norway
British Isles	Baines et al., 2011	1991-2009	yearly	census	Scotland
	Kortland & Peace, 2013	2002-2012	mean	census	Scotland
	Moss & Weir, 1987	1977-1984	yearly	census	Scotland
	Moss et al., 2001	1975-1998	yearly	census	Scotland
	Summers et al., 2004	1989-1999	yearly	census	Scotland
	Summers et al., 2010	1989-2009	yearly	census	Scotland
Continental Europe	Colloque galliformes de montagne, 1987	1976-1986	yearly	census	France
	Ménoni & Novoa, 1988	1984-1987	yearly	census	France
	Ménoni et al., 2002	2000-2005	yearly	census	France
	Mossol-Torres & Ménoni, 2006	2000-2005	yearly	census	Andorra
	Saniga, 2011	1983-2010	yearly	census	Slovakia
	Zawadzki & Zawadzka, 2012	1996-2010	mean	census	Poland
Black grouse					
Fennoscandia	Helminen, 1963	1952-1961	yearly	harvest	Finland
	Kurki et al., 2000	1989-1994	yearly	census	Finland
	Lindén, 1981	1967-1976	mean	census	Finland
	Rajala, 1974	1963-1966	yearly	census	Finland
	Siivonen, 1954	1946-1954	yearly	harvest	Finland
	Solvang et al., 2009	2007-2012	yearly	census	Norway
	Sørensen, 1977a, b	1976	yearly	census	Norway
	Wegge & Rolstad, 2011	1979-2008	yearly	census	Norway
	Willebrand, 1992	1984-1987	mean	telemetry	Sweden
	Kastdalen, 1992	1987-1989	yearly	census	Norway
	Census Boda, Sweden	1980-2010	yearly	census	Sweden
	Census Norway	2002-2012	yearly	census	Norway

Table A3.
(Continued.)

Region	Source	Year(s) of study	Resoluton	Method	Country
	Willebrand, T. unpubl.	1990-1992	mean	telemetry	Sweden
	Willebrand, 1988	1984-1987	yearly	telemetry	Sweden
British Isles	Baines, 1991	1989-1990	yearly	census	Scotland
	Baines, 1996	1991-1993	yearly	census	Scotland
	Bowker et al., 2006	2000-2003	yearly	telemetry	Wales
	Calladine et al., 2002	1996-2000	mean	census	England
	Summers et al., 2010	1991-2009	yearly	census	Scotland
	Warren & Baines, 2002	1998-2000	yearly	telemetry	England
	Watson, 2010	1957-1964	mean	census	Scotland
	Watson & Nethersole-Thompson, 2006	1934-1942	yearly	census	England
Continental Europe	Barnagaud et al., 2010	1990-2007	yearly	census	France
	Caizergues & Ellison, 2000	1991-1998	mean	census	France
	Colloque galliformes de montagne, 1987	1982-1987	yearly	census	France & Italy
	Ellison, 1978	1976-1977	yearly	census	France
	Ellison et al., 1982	1976-1980	yearly	census	France
	Ellison et al., 1984	1977-1981	yearly	census	France
	Marti & Pauli, 1983	1973-1983	yearly	census	Germany
	Miquet, 1988	1985-1987	yearly	census	France
	Zbinden & Salvioni, 2003	1981-2001	yearly	census	Switzerland
	Vith, 1974	1970-1973	mean	census	Estonia

Table A4.
Survival rates of adult females/both sexes combined.

Source	Species	Duration	Survival rate	Country
Semenow Tjan Shanskiy, 1979	capercaillie	1930-1957	0.52	Karelia
Semenow Tjan Shanskiy, 1979	capercaillie	1930-1957	0.41	Karelia
Helminen, 1963	capercaillie	1952-1961	0.53	Finland
Helminen, 1963	capercaillie	1952-1961	0.51	Finland
Helminen, 1963	capercaillie	1952-1961	0.48	Finland
Helminen, 1963	capercaillie	1952-1961	0.45	Finland
Lindén, 1981	capercaillie	1952-1971	0.71	Finland
Moss, 1987	capercaillie	1975-1984	0.66	Scotland
Wegge & Rolstad, 2011	capercaillie	1980-1990	0.64	Norway
Storch, 1993	capercaillie	1988-1992	0.65	Germany
Moss et al., 2000	capercaillie	1991-1997	0.63	Scotland
Catt et al., 1994	capercaillie	1992-1994	0.62	Scotland
Wegge & Rolstad, 2011	capercaillie	1996-2003	0.57	Norway
Åhlen et al., 2013	capercaillie	2000-2004	0.68	Sweden
Helminen, 1963	black grouse	1952-1961	0.5	Finland
Helminen, 1963	black grouse	1952-1961	0.44	Finland
Helminen, 1963	black grouse	1952-1961	0.42	Finland
Lindén, 1981	black grouse	1952-1971	0.53	Finland
Angelstam, 1984	black grouse	1977-1981	0.56	Sweden
Caizergues & Ellison, 1997	black grouse	1982-1988	0.66	France
Picozzi & Hepburn, 1986	black grouse	1984-1986	0.51	England
Willebrand, T. unpubl.	black grouse	1984-1987	0.5	Sweden
Caizergues & Ellison, 1997	black grouse	1990-1995	0.56	France
Wegge & Rolstad, 2011	black grouse	1996-2003	0.43	Norway
Warren & Baines, 2002	black grouse	1998-2000	0.72	England
Bowker et al., 2006	black grouse	1999-2003	0.39	Wales
Pekkola et al., 2014	black grouse	2005-2007	0.53	Finland
Pekkola et al., 2014	black grouse	2005-2007	0.69	Finland

Paper II

Title:

Impacts of voles and predators on nest predation in European boreal forest grouse

Jahren, Torfinn[1]

Torfinn.jahren@inn.no

Storaas, Torstein[1]

Torstein.storaas@inn.no

Willebrand, Tomas[1]

Tomas.willebrand@inn.no

Fossland Moa, Pål[2]

Pal.f.moa@nord.no

Hagen, Bjørn-Roar[2]

Bjorn-roar.hagen@nord.no

[1]Inland Norway University of Applied Sciences

Faculty of Applied Ecology and Agricultural Sciences

[2]Nord University

Faculty of Biosciences and Aquaculture

Abstract

To understand mechanisms behind increasing reproductive failure in sympatric woodland grouse it is necessary to identify nest predators and related processes. Using camera traps, we provide the first empirical identification of predation among 335 capercaillie and black grouse nests in the boreal forest. We evaluated nest predation patterns in relation to predators and voles via binomial and competing risk models. Daily rates amounted to 79 and 66 % losses to predation for capercaillie and black grouse nests respectively. Red fox and pine marten was responsible for 84 % of identified events whereas other predators were few and hens successfully defended their nest against corvids. Model rankings suggested that nest predation in black grouse followed pine marten and vole abundances as expected. Their interaction further showed that high pine marten abundances masked the relieving effect of voles. Red fox predation patterns on capercaillie nests supported the alternative prey hypothesis whereas pine marten predation was unaffected by voles and increased with pine marten abundance. We conclude that artificial nests are poor substitutes for real nests when aims are to identify and understand mechanisms regulating nest predation. We further suggest that woodland grouse nests are alternative prey for red foxes whereas pine martens are more efficient and specialized nest predators. Finally, legal control of pine martens can improve hatching success in both capercaillie and black grouse.

Keywords: *red fox, pine marten, nest predation, camera trap, capercaillie, black grouse, voles*

Introduction

Recruitment is an important driver of population dynamics in many ground-nesting birds, especially those with fast life-histories and a short life expectancy (Lack 1968; Newton 1998) and recent research has focused on predation as an important cause of nest failure. To advance the understanding of nest predation mechanisms, it is essential to identify the predator species responsible and obtain data on factors affecting their numerical and functional responses (Benson, Brown & Bednarz 2010).

Despite known limitations, artificial nests are often used to investigate these mechanisms because collecting data on active nests is difficult (Andren & Angelstam 1988; Major & Kendal 1996). Unlike artificial nests, active woodland grouse nests are protected by an incubating, cryptic-colored female, which is not only concealing the eggs from predators but is also releasing olfactory cues that can attract predators (Conover 2007). Females may also divert or deter predators (Montgomerie & Weatherhead 1988; Martin 1993). Studies using artificial nests often identify avian predators as the most important (Picozzi 1975; Storaas 1988; Willebrand & Marcström 1988), and the perceived importance of corvid predation of boreal woodland grouse nests originates from studies using artificial nests (e.g. Klaus 1985; Andren 1992; Summers *et al.* 2004).

Capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) are sympatric ground nesting woodland grouse in the forests of Fennoscandia (Seiskari 1962; Swenson & Angelstam 1993). In the boreal forest, they have similar associations to landscape characteristics and habitat diversity is important in explaining population fitness (Lande *et al.* 2014). Albeit population declines, their conservation status is of least concern at a global level (IUCN 2016) and several explanations for declining populations have been proposed. In contrast to populations in Britain and mainland Europe, habitat loss is not considered a detrimental driver in Fennoscandia. Instead, changes in land use, climate change (e.g. spring warming) and increasing populations of generalist predators are considered threats to Fennoscandian capercaillie and black grouse conservation (Jahren *et al.* 2016).

Knowledge about the importance of juvenile survival after brood breakup during fall as well as winter survival is largely lacking, but in the closely related willow ptarmigan (*Lagopus lagopus*), population models suggest juvenile survival to be of particular importance to future population persistence (Sandercock, Martin & Hannon 2005). Reproductive success in general and particularly early chick survival is mediated by several ultimate factors that predominantly predispose capercaillie and black grouse chicks to predation (e.g. weather and abundance of protein-rich food items (Moss 1986; Wegge & Kastdalen 2007)). Until hatching, nests of black grouse have higher probability of survival than those of capercaillie (Storaas & Wegge 1987; Jahren *et al.* 2016). In both species however, the vast majority of nest loss is due to predation, and differences in nesting success is therefore likely explained by nest detection probabilities mediated through a combination of female behavior and nesting habitat (e.g. Storaas et al. 1999).

Large annual variation in nest loss is common. Apparent nest losses vary from 0 to 84 % and 11 to 62 % for capercaillie and black grouse respectively (Myrberget & Hagen 1974; Spidsø, Wegge & Storaas 1984; Brittas & Willebrand 1991). However, over the past 80 years, nest loss in both capercaillie and black grouse has increased, with subsequent population declines. This is partly due to increased predation likely resulting from higher numbers of generalist predators (Jahren *et al.* 2016).

Annual variation in capercaillie and black grouse nest predation is inversely correlated with the vole cycle (Angelstam 1983; Wegge & Storaas 1990), which is consistent with the alterative prey hypothesis (Hagen 1952; Lack 1954; Angelstam, Lindström & Widén 1984). Since the 1980s when these studies were conducted, regional vole cycles have diminished or even disappeared (Ims, Henden & Killengreen 2008; Cornulier *et al.* 2013), although recent studies have suggested a return to cyclic fluctuations (Brommer *et al.* 2010; Korpela 2014) with reduced amplitude (Cornulier *et al.* 2013). Preceding and during the period of low-amplitude vole cycles, the red fox (*Vulpes vulpes*) population in Scandinavia was affected by an epizootic sarcoptic mange (*Sarcoptes scabiei*) (Mörner 1992). This revealed the importance of red fox as predator and possibly also competitor as population sizes in a number of small game species, notably also the pine marten (*Martes martes*) increased (Storch, Lindström & de Jounge 1990; Lindstrom *et al.* 1994; Lindström & Brainerd 1995; Smedshaug *et al.* 1999).

Nest predation in capercaillie and black grouse have also been described as incidental (Wegge & Storaas 1990; Saniga 2002) and predation rates could therefore also be explained by predator density and abundance of their main prey rather than phase-dependent predation rates dictated by the vole cycle. It therefore appears that mechanisms linking predation rates on woodland grouse nests to predators and their preferred prey are context dependent. We therefore expect that predation patterns described some 30 years ago have changed due to both increased populations of generalist predators (Krott & Lampio 1983; Helldin 2000a; Selås & Vik 2006) and distortion of the vole cycle (Hörnfeldt, Hipkiss & Eklund 2005).

No study has yet presented quantitative data of nest predators predating capercaillie and black grouse nests outside Scotland. In Scotland, pine marten was the only predator identified predating capercaillie nests, probably because it is protected and other potential nest predators are controlled (Summers, Willi & Selvidge 2009). In Fennoscandia, studies on active nests have shown that mammals are important nest predators (Storaas 1988; Willebrand & Marcström 1988) although the data has been limited.

In this study, we identify key predators of capercaillie and black grouse nests in the boreal forests of Norway. We further evaluate mechanisms behind predator-specific predation patterns, as well as predation in general, by linking nest predation to the vole cycle, vole abundance and red fox and pine marten abundances. We thereby attempt to evaluate principal hypotheses explaining nest predation patterns in precocial ground-nesting woodland grouse. We hypothesized that both mammals and birds would prey upon nests of capercaillie and black grouse but we expected mammals to be more frequent. We further anticipated that the previously strong and predictable relationship between predators, voles and alternative prey as predicted by the alternative prey hypothesis has changed, due to both increased populations of generalist predators and reduced cyclic amplitude in voles.

Methods

Study area

This study was carried out in the boreal forests of Hedmark (61° N 11° E, 27400 km^2, during 2009 – 2014) and Nord-Trøndelag (64° N 12° E, 22400 km^2, during 2010 – 2014) counties in southeast and central Norway. Forests (13000 and 6600 km^2) were dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) intermixed with birch (*Betula spp.*). Rowan (*Sorbus aucuparia*), alder (*Alnus incana*) and aspen (*Populus tremula*) were also present but at substantially lower densities (Moen 1999). The forests were commercially managed and most forested areas were accessible by forest roads. Capercaillie and black grouse were common and local (7 to 24 forest properties) density estimates from transect surveys (total 378 – 1373 km transects) showed large annual variation and prior to our study, combined August densities of both species varied between 1 - 26 birds km^{-2} (Solvang *et al.* 2009). Combined densities of 26 birds km^{-2} was estimated in 2006 and since then populations have fluctuated at lower levels. Potential nest predators included pine marten, red fox, European badger (*Meles meles*), common raven (*Corvus corax*), hooded crow (*Corvus cornix*), Eurasian jay (*Garrulus glandarius*), stoat (*Mustela erminea*), lynx (*Lynx lynx*), gray wolf (*Canis lupus*), brown bear (*Ursus arctos*), and wolverine (*Gulo gulo*).

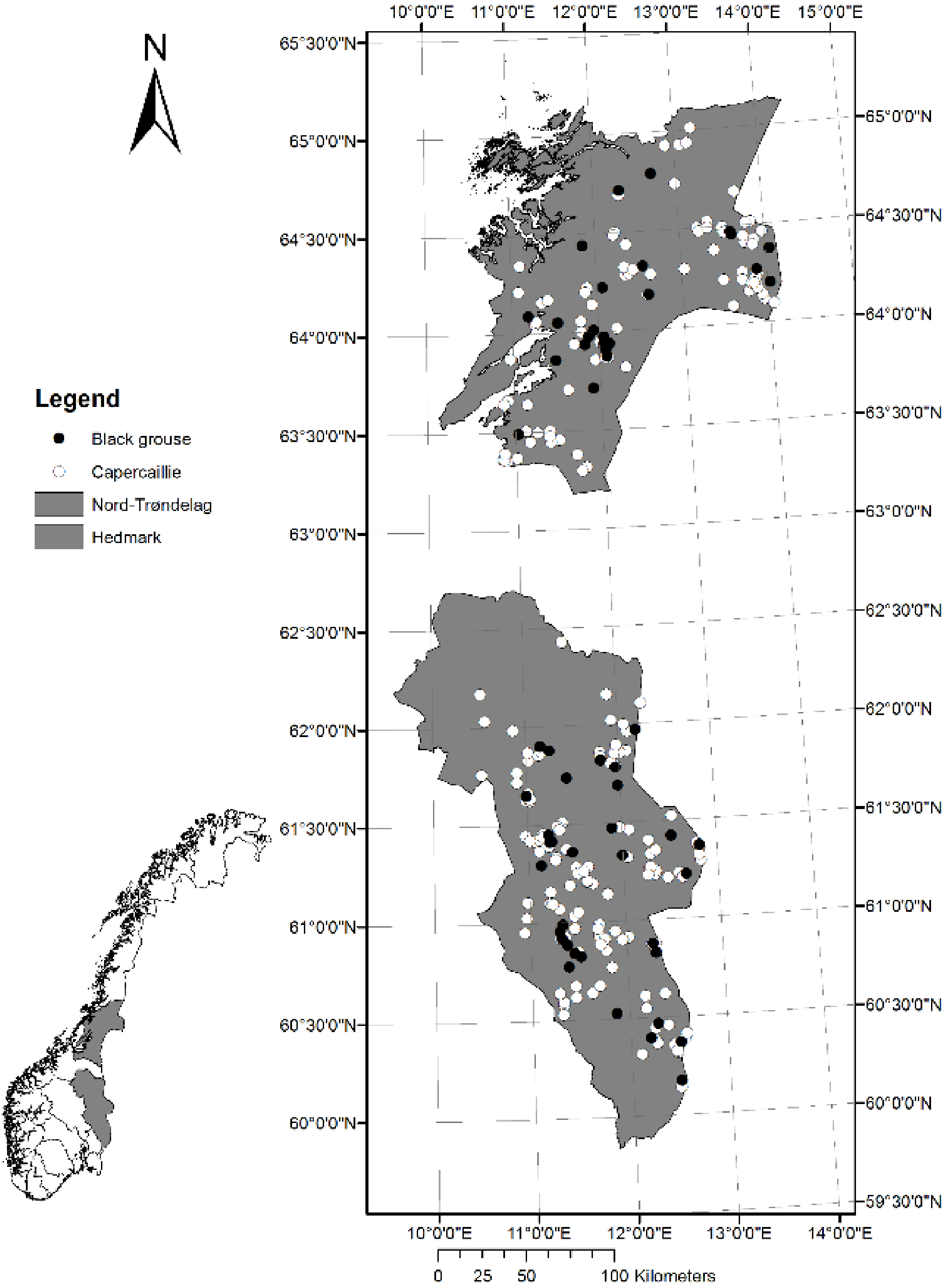

Figure 14 Nord-Trøndelag (north) and Hedmark (south) counties in Norway. Capercaillie (Tetrao urogallus) nests are white circles and black grouse (Lyrurus tetrix) nests are black circles.

Locating nests

Throughout spring in each year from 2009-2014 (2010-14 in Nord-Trøndelag), we invited the public and forest workers to report capercaillie and black grouse nests (see also Storaas and Wegge 1984). Each year, a few nests were also located using pointing dogs between May 10th and mid-June. Nests detected opportunistically have same survival as nests detected randomly (i.e. radio-tagged birds) (Storaas & Wegge 1984). For each nest, we recorded species and the UTM-position. Because we wanted to study predation, we excluded 25 nests (15 (5.32 %) and 10 (12.82 %) capercaillie and black grouse nests respectively) where female disappeared, leaving 267 capercaillie and 68 black grouse nests in the sample for predation analysis (Table 1). Two nest desertions were caused by flooding, one by human disturbance (i.e. shooting practice) and one by forest fire. Other potential causes may be predation of the female during off-bouts (Angelstam 1984; Wegge & Rolstad 2011), exhaustion or observer effects.

Dog handlers and most forestry workers had camera traps available and cameras were mounted immediately after they detected a nest. Most nests, in total 194 of 267 and 56 of 68 capercaillie and black grouse nests, respectively, were monitored with camera traps. For nests detected by the public, we mounted camera traps minimum one day after detection. After camera mounting, nests were not visited again for > three weeks. Nest fates were not always certain from photographs, and we then interpreted the remains of the eggshells to determine whether eggs hatched (neatly halved in cup and bowl with eggshell membrane attached) (e.g. Leopold 1937) or were predated (only fragments of eggshell or no remains were left). Camera traps were mounted on a tree or tree stump, 1-5 m away from the nest. If no natural feature was available, we considered longer mounting distances (< 10 m) but did not use artificial mounts. Initially (2009-12), we used camera traps with passive infrared (PIR) detection only, programmed to record three images when triggered and sleep-time of 1-10 minutes depending on the size of the memory card. Later (2013-14), we also used cameras with combined time-lapse (TL) and PIR. TL-cameras were, in addition to PIR, set to record three images every ten minutes to minimize false negatives. Camera models used were Moultrie Game Spy I-45™ (PIR) (http://www.moultriefeeders.com/), Bushnell Trophy Cam™ (PIR) (http://www.bushnell.com/) and WingCam II™ (PIR + TL) (http://www.wingevapen.no/).

Table 2 Details of sample size for capercaillie and black grouse nests

	Year	2009	2010	2011	2012	2013	2014	Total
	Vole cycle phase	Crash	Increase	Peak	Crash	Increase	Peak	
Capercaillie	Total sample[1]	16	68	60	50	35	53	282
	Deserted	0	5	2	5	0	3	15
	Complete capture history[2]	16	63	58	45	35	50	267
	Hatched	5	32	31	14	20	33	135
	Predated	11	31	27	31	15	17	132
Black grouse	Total sample[1]	0	29	24	15	4	6	78
	Deserted	0	5	4	1	0	0	10
	Complete capture history[2]	0	24	20	14	4	6	68
	Hatched	0	18	9	8	2	6	43
	Predated	0	6	11	6	2	0	25

[1] *Annual distribution of all the nests detected in this study.* [2] *Nests with complete capture histories (i.e. known dates of detection and end of incubation) used in predation analysis excluding nest desertions.*

Red fox and pine marten abundances

Indices of pine marten (PMA) and red fox (RFA) abundances were obtained from snow tracking along 899 predefined transects (Figure A1). Transect surveys were conducted in each county by volunteers surveying between 99 and 444 (mean = 294, SD = 120.03) transects of 3.5 (SD = 1.61) km length in late January or early February each year under favorable tracking conditions (i.e. 2-5 days after snowfall). On average, each transect was repeatedly surveyed 3.6 years (SD=1.57). Annual mean density of transects was one transect per 35.2 (29.7 – 51.6) km^2 forested area (i.e. capercaillie and black grouse habitat) and transect centroid points were spaced out 3800 (480-11000) m apart and were across contour lines, largely covering the entire forested area in each county.

For each transect we calculated annual RFA and PMA as crossing tracks/km/24 hrs. Red fox prevalence (i.e. proportion of transects with tracks) varied between 0.33 and 0.94 whereas pine marten prevalence varied between 0.17 and 0.49. Abundances varied between 0.40 and 0.67 for red fox and between 0.20 and 0.31 for pine marten (Table 2). Such indices reflect true densities of red fox and pine marten quite well (Thompson *et al.* 1989; Kurki *et al.* 1998), but they cannot discern predator density from predator activity. Therefore, they reflect relative predation pressure across space and time (Kurki *et al.* 1998) prior to nesting season. Annual predator-specific abundances were log-transformed and then attributed to the transects' centroid point. We further developed annual, county-wise spherical variogram models for each species to obtain models describing mean and spatial covariance. Variogram models were then fitted in ordinary kriging prediction models with leave one out cross validation and we predicted annual RFA and PMA for each county (Figure A2). Variogram and krige models were developed in the gstat library (Pebesma 2004) in program R (R Core Team 2016).

To capture spatial heterogeneity among home ranges, each nest was assigned a randomly-sized circular buffer corresponding to capercaillie or black grouse hens home range during incubation (capercaillie mean = 0.204 km^2, SE = 0.0183 and black grouse mean = 0.236 km^2, SE = 0.0774 (Kolstad, Wegge & Bø 1985; Wegge 1985)). Because generation of random numbers with the given parameters yield small as well as negative numbers, buffer size was restricted to minimum 0.1 km^2 for both species. Finally, each nest was assigned mean values of the predicted RFA and PMA the buffer included for the appropriate year.

Table 3 Annual transect data used for red fox (Vulpes vulpes) and pine marten (Martes martes) abundance indices in Hedmark and Nord-Trøndelag counties between 2009 and 2014. Prevalence is proportion of transects with red fox or pine marten tracks observed. Annual mean abundance is track crossings / transect length / days since last snowfall.

			2009	2010	2011	2012	2013	2014
Transects surveyed		Hedmark	429	444	406	371	400	280
		Nord-Trøndelag	-	215	203	215	173	99
Red fox	Hedmark	Prevalence	0.93	0.88	0.94	0.92	0.93	0.86
		Abundance	0.59	0.62	0.46	0.67	0.61	0.66
		2SE	0.053	0.060	0.039	0.065	0.054	0.089
	Nord-Trøndelag	Prevalence	-	0.45	0.46	0.55	0.36	0.33
		Abundance	-	0.40	0.52	0.70	0.51	0.53
		2SE	-	0.065	0.080	0.096	0.093	0.091
Pine marten	Hedmark	Prevalence	0.49	0.36	0.44	0.42	0.35	0.27
		Abundance	0.25	0.24	0.20	0.26	0.24	0.26
		2SE	0.034	0.042	0.028	0.037	0.034	0.046
	Nord-Trøndelag	Prevalence	-	0.22	0.28	0.35	0.18	0.17
		Abundance	-	0.23	0.24	0.31	0.24	0.22
		2SE	-	0.049	0.047	0.062	0.040	0.056

Vole cycle and vole abundance

Tengmalm's owl (*Aegolius funereus*) fecundity is dependent on vole fluctuations, which occur synchronously across large areas (Hornfeldt & Carlsson 1990; Sundell *et al.* 2004; Lehikoinen, Ranta & Pietiäinen 2011) and so we used annual, county-specific mean brood size of Tengmalm's owl (collected by Birdlife Norway) as an annual index of vole abundance (VA) (Table A 3). Because VA as a continuous predictor will not capture the temporal component of the alternative prey hypothesis (i.e. prey switching), we also specified annual dynamics in VA as phases in a population cycle. From the vole abundance index, we identified phases of the vole cycle (VC) as follows: annual vole indices were mean centered. We coded negative values as zero and positive values as one. Two consecutive years with either 0 (0 0) were defined as low (none detected) and two consecutive 1's (1 1) as peak phase. A 1 followed by 0 (1 0) was defined as crash, 0 followed by 1 (0 1) as an increase phase (Table 1).

Predation analysis

Prior to model building, predator abundances were checked for homoscedasticity by inspecting the residuals and then standardized to z-scores (mean/2SD) (Arm package; Gelman & Su 2016) to simplify interpretations of interactions between the quantitative predictors (González & Cox 2007). We also checked for collinearity between RFA and PMA.

Nest predation was analyzed in MCestimate (Etterson, Greenberg & Hollenhorst 2014), which is a standalone software for modelling the probability of nest failure in a binomial and competing risk (multi-fate) environment. MCestimate differ from classical survival analysis by modelling time as discrete and estimates are thereby probabilities of survival or failure across a fixed period of incremental time steps. This is in contrast to e.g. exponential or Weibull survival functions (i.e. instantaneous) in continuous time. The discrete-time logit-model in MCestimate is a generalization of the Mayfield method (Mayfield 1975; Dinsmore, White & Knopf 2002), with relaxed assumptions (e.g. daily monitoring not required). Daily probabilities of survival or failure are then calculated across transition matrices as a Markov chain. Thus, the probability of a nest surviving until day *i* is formalized as the product of probabilities per Markov transition matrix until day *i.*

Few observations of predators preying upon black grouse nests prevented us from partitioned analysis of those and so competing risk analysis were performed only for the fates of capercaillie nests. Competing events for capercaillie nest fates were hatched (n=135), red fox (n=28), pine marten (n=27) or unidentified predation (n=66). We left other identified predators (i.e. competing events) as constants because of few observations. When evaluating pooled predation (i.e. binomial fates), we included 135 hatched and 132 predated capercaillie nests and 42 hatched and 26 predated black grouse nests in the analysis.

We designed a set of simple candidate models to evaluate the support for the following hypotheses in explaining predator-specific and overall nest predation:

- Numerical response in predators (i.e. incidental)
- Functional response in predators (i.e. alternative prey)
- Predation patterns are predator-specific

To specifically address the different hypotheses, nest predation was formalized by a mixture of predictors including PMA, RFA, VA and VC (i.e. crash, increase or peak). Each modeled fate consisted of maximum two main effects and their interaction.

We did not fit red fox predation with PMA as main effect and vice versa, but they were fitted with the interaction between PMA and RFA. Parameterization of unidentified predation always mimicked the corresponding fit of red fox or pine marten (i.e. hypothesized to consist of both predator species). Therefore, each model fit for pine marten and red fox were repeated twice with unidentified predation hypothesized to be pine marten in the first case and red fox in the second. The candidate set for binary fates included 11 models whereas competing risk included 23 models.

Model evaluation and goodness of fit

We assessed goodness of fit by the Hosmer-Lemeshow χ^2-test (implemented in MCestimate) on the global model. No evidence for lack of fit was detected (Table 3).

Table 4 Hosmer-Lemeshow χ^2 goodness of fit assessment of the global models formalizing black grouse and capercaillie binomial fates and capercaillie competing risks.

	Groups	d.f.	χ^2	p-value
Black grouse	10	8	7.12	0.52
Capercaillie	10	8	6.33	0.61
Capercaillie comp. risks	10	68	42.40	0.99

Candidate models were ranked according to AICc (AIC corrected for small sample size). We inferred from the top ranking model as well as models within ΔAICc < 2 from the top ranking model. We exported the estimated regression coefficients and variance co-variance matrices from MCestimate to R (R Core Team 2016) for visualization.

Consequences of nest predation

To evaluate the potential impact of nest predation on population dynamics in black grouse and capercaillie, we regressed annual indices of capercaillie and black grouse populations against daily probabilities of predation at time$_t$ (DPP_t). Because capercaillie and black grouse density estimates were not available for both counties all years, we used relative change in hunter bag size between years (N_t/N_{t-1}) as population index (Figure A3). Annual bag size and number of hunters per county was retrieved from Statistics Norway (Statistics Norway 2016).

Results

Predator identification and daily predation rates

Of 132 and 26 predated capercaillie and black grouse nests, we identified the predator in 66 and 10 cases, accounting for 50 and 38.5 % of all predation events (details on camera trap performance further down). Mammals represented 98.5 % of identified capercaillie nest predators and 100 % of black grouse nest predators. Of identified predators red fox predated 42.4 % and 55.6 % of capercaillie and black grouse nests respectively, and corresponding pine marten predation was 41.0 % and 33.3 %. Of less importance were European badger (12.1 % and 11.1 %), domestic dog (1.5 % and 0 %), wolverine (1.5 % and 0 %) and golden eagle (1.5 % and 0 %) (Figure 2A).

From 267 capercaillie and 68 black grouse nests, we estimated daily predation rates of 0.0541 and 0.0425 respectively. These daily predation rates are equivalent to total predation of 0.79 and 0.66 when accounting for 28 (Summers, Willi & Selvidge 2009) and 25 (Ludwig *et al.* 2010) days of incubation for capercaillie and black grouse respectively. Estimates of daily probabilities of predation in capercaillie and black grouse nests overlapped (Figure 2B). Daily probabilities of unidentified predation was 0.028 and 0.028, red fox was 0.009 and 0.012 whereas pine marten predation was 0.005 and 0.012 for black grouse and capercaillie respectively (Figure 2C). Nest predation in capercaillie and black grouse explained 26 and 50 % of the variation in hunter bags between years (Figure A3).

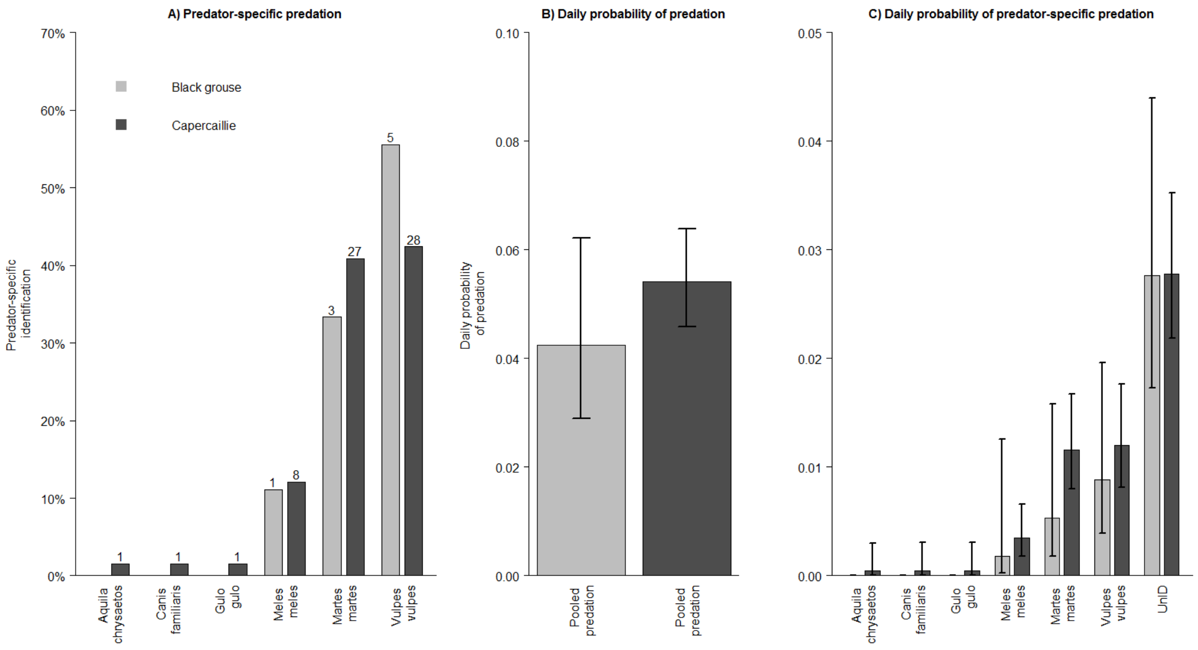

Figure 15 (A) Distribution (percentage) of camera-identified species predating black grouse (Lyrurus tetrix) (light) and capercaillie (Tetrao urogallus) (dark) nests. (B) Estimated daily probabilities of pooled predation (± 95 % CI) on black grouse and capercaillie nests and (C), estimated daily probabilities of species-specific predation (± 95 % CI) on black grouse and capercaillie nests.

Corvids

We did not observe corvid predation on active nests of neither capercaillie nor black grouse. In total, we observed corvids during four black grouse nest days and 14 capercaillie nest days. On active nests (i.e. female incubating), black grouse and capercaillie females confronted successfully defended their nest against hooded crow and raven attacks for all occasions (Figure 3). Eurasian jays and magpies (*Pica pica*) did not attack the active nests and were therefore not confronted (Table 4).

Figure 16 Female capercaillie (Tetrao urogallus) defending nest against hooded crow (Corvus cornix).

Table 5 Details of all corvid observations on capercaillie and black grouse nests.

County	Species	Year	Corvid Species	Minimum corvid group size	Number of days visited	Number of days confronted	Nest status at corvid visit	Nest fate
Nord-Trøndelag	Capercaillie	2010	Corvus cornix	3	1	1	Active	Red fox
	Capercaillie	2011	Corvus corax	1	1	1	Active	Unidentified predator
	Capercaillie	2013	Corvus cornix	1	1	1	Active	Red fox
	Capercaillie	2014	Corvus corax	1	1	1	Active	Red fox
	Black grouse	2010	Garrulus glandarius	1	3	0	Not active	Previously deserted
Hedmark	Capercaillie	2010	Corvus corax	1	1	0	Not active	Previously deserted
	Capercaillie	2010	Garrulus glandarius	1	1	0	Active	Unidentified predator
	Capercaillie	2013	Corvus corax	2	1	1	Active	Badger
	Capercaillie	2013	Corvus cornix	1	1	1	Active	Hatched
	Capercaillie	2013	Corvus cornix/Pica pica	1 & 3/1	4/1	4/0	Active	Unidentified predator
	Capercaillie	2014	Corvus corax	1 & 2	2	2	Active	Hatched
	Black grouse	2010	Corvus cornix	1	1	1	Active	Unidentified predator

Camera trap performance

We identified the predator in 76.7 and 71.4 % of possible cases on capercaillie and black grouse nests respectively. The predominant reason for unsuccessful identification of nest predators was that 67.7 and 60 % of predated capercaillie and black grouse nests were not camera monitored. Cameras stopped monitoring before predation took place (i.e. not operational) in 4.4 % and 6.7 % due to full memory card. False negatives (i.e. operational camera failed to record event) occurred in 23.3 and 28.6 % of cases for capercaillie and black grouse (Table 5).

Table 6 Overview of camera-trap performance on predated nests.

	Predated	**Predated & monitored**	**Identified of monitored§**	**False negative§**	**Memory card full**
Capercaillie	49.4% (132)	68.2% (90)	76.7% (66)	23.3% (20)	4.4% (4)
Black grouse	36.8% (26)	60% (15)	71.4% (10)	28.6% (4)	6.7% (1)
Total	47.2% (158)	66.5% (105)	76% (76)	24% (24)	4.8% (5)

§Cameras with full memory card (i.e. not operational) is not included.

Nest predation patterns in black grouse

Model ranking suggested PMA and VA as well as their interaction as the best models formalizing nest predation in black grouse (Table A1). As main effects, PMA was positively associated whereas VA was negatively associated with daily probability of predation (DPP) in black grouse (Figure 4). Their interaction however, showed that voles only relieved black grouse nests of predation when pine martens were at low or intermediate abundances. When pine martens were abundant, the relationship of voles to predation was positive but uncertain (Figure 5).

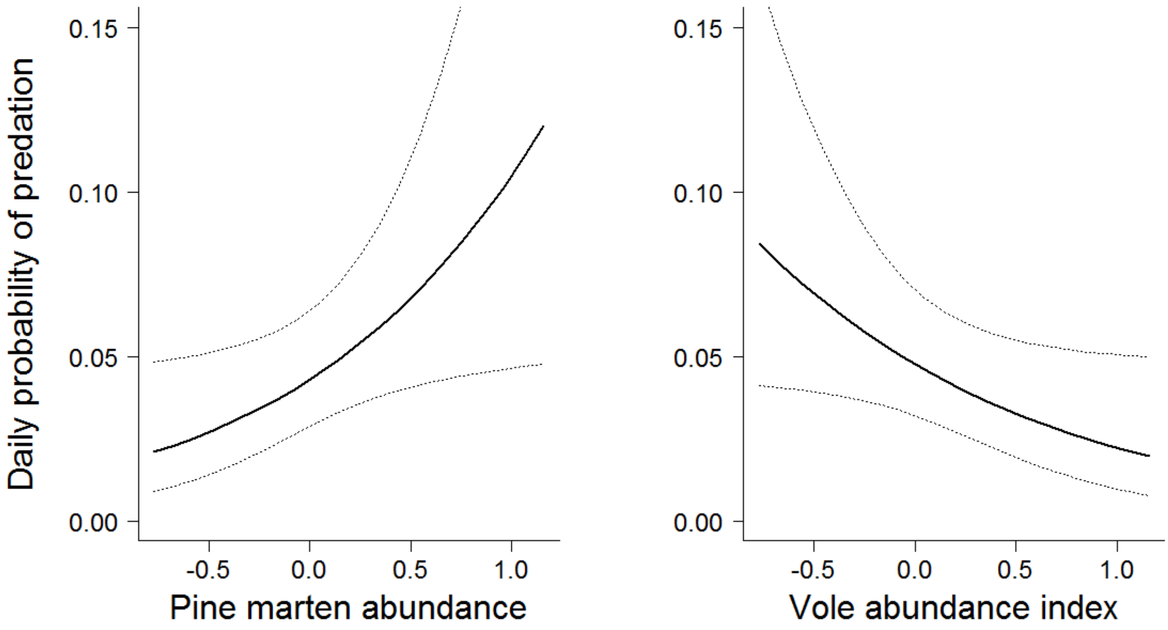

Figure 17 The relationships of pine marten abundance and vole abundance index to daily probability of pooled predation in black grouse.

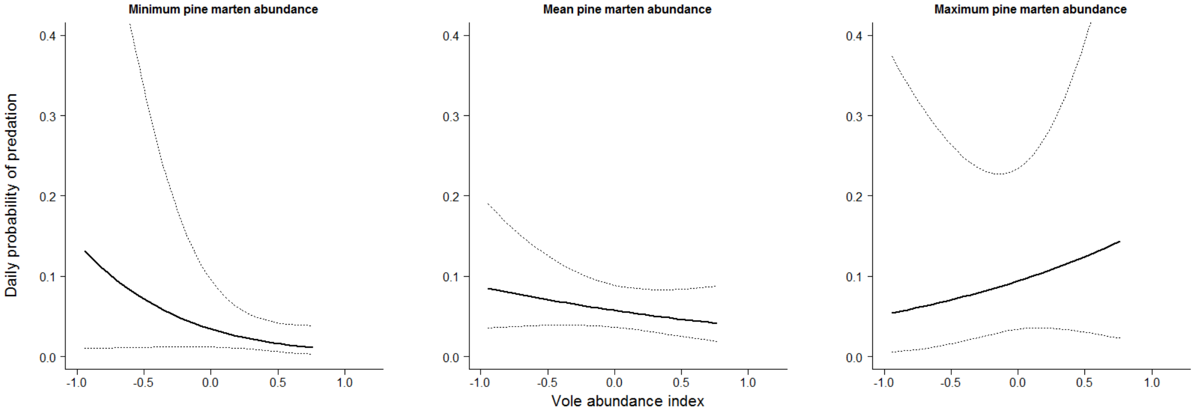

Figure 18 Estimated daily probability of pooled predation for black grouse nests as a function of vole abundance index under minimum, mean and maximum observed pine marten abundances.

Nest predation patterns in capercaillie

In general, daily probability of predation for capercaillie nests was highest in the crash phase of the vole cycle and subsequently decreased as the cycle progressed (Figure 6). Varying PMA did however disrupt the pattern of phase-dependent predation. As PMA increased, the increase phase in the vole cycle still relieved capercaillie nests of predation but during the peak phase, predation probabilities elevated at intermediate PMA and eventually exceeded those of the crash phase when PMA was high (Figure 7).

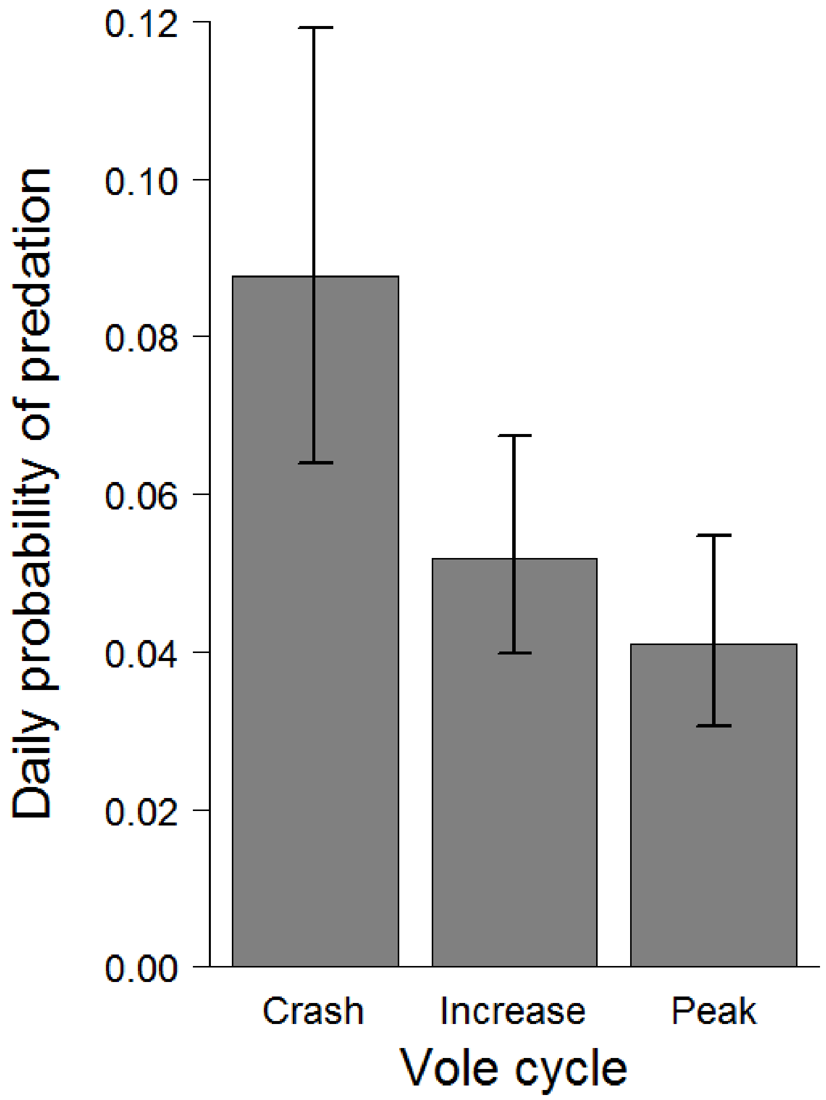

Figure 19 Estimated daily probability of pooled predation on capercaillie nests during the vole cycle

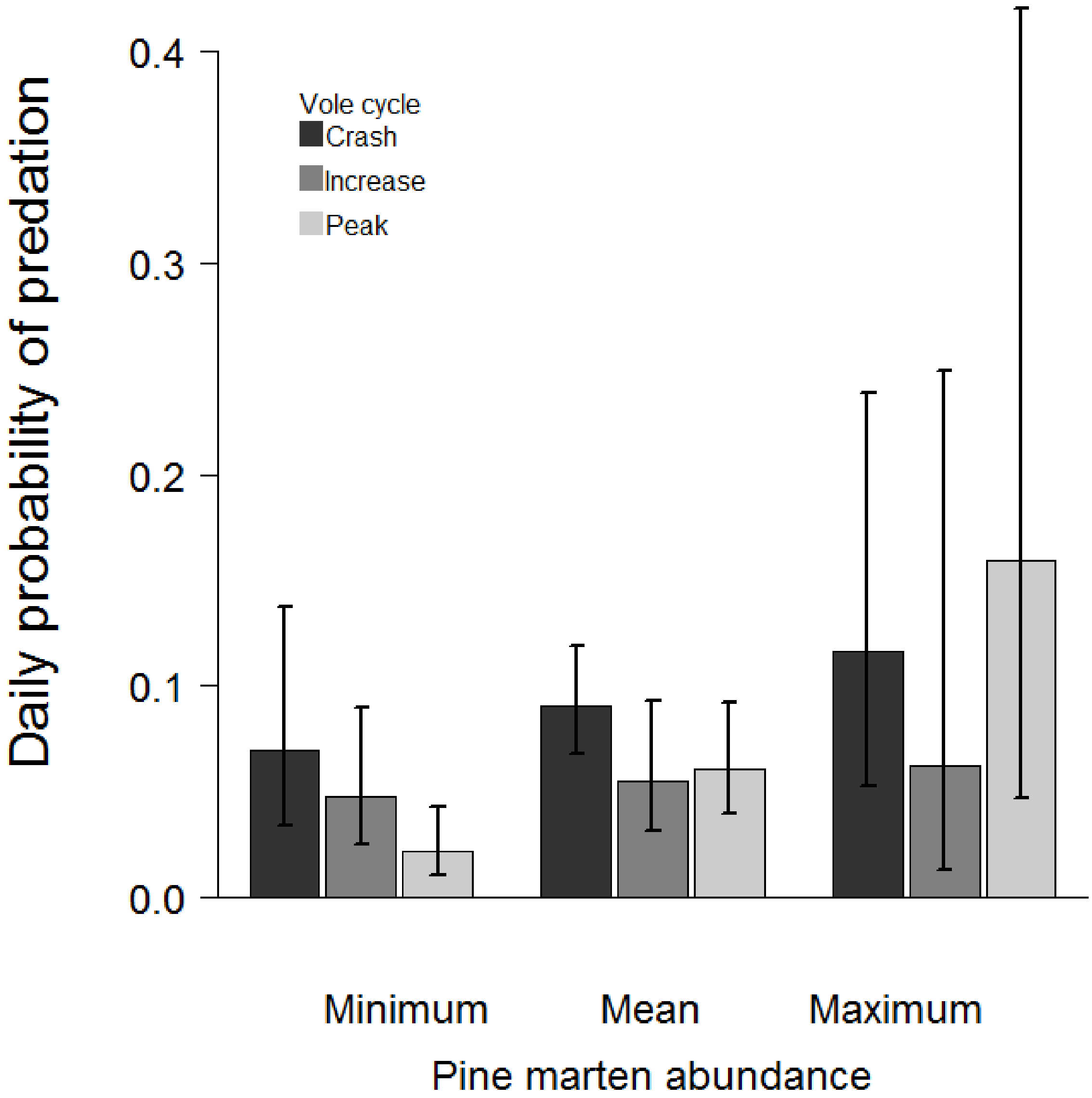

Figure 20 Estimated daily probability of pooled predation on capercaillie nests during the vole cycle with min, mean and max observed pine marten abundances.

Predator-specific predation patterns in capercaillie

The model best explaining partitioned predation on capercaillie nests was pine marten predation formalized as PMA with red fox and unidentified predation formalized as VC. Pine marten predation increased with PMA and both red fox and unidentified predation was highest in the crash phase of the VC and decreased as the VC progressed. Predation was generally higher and the phase-to-phase change in predation was more prominent for unidentified predators than for red fox (Figure 8).

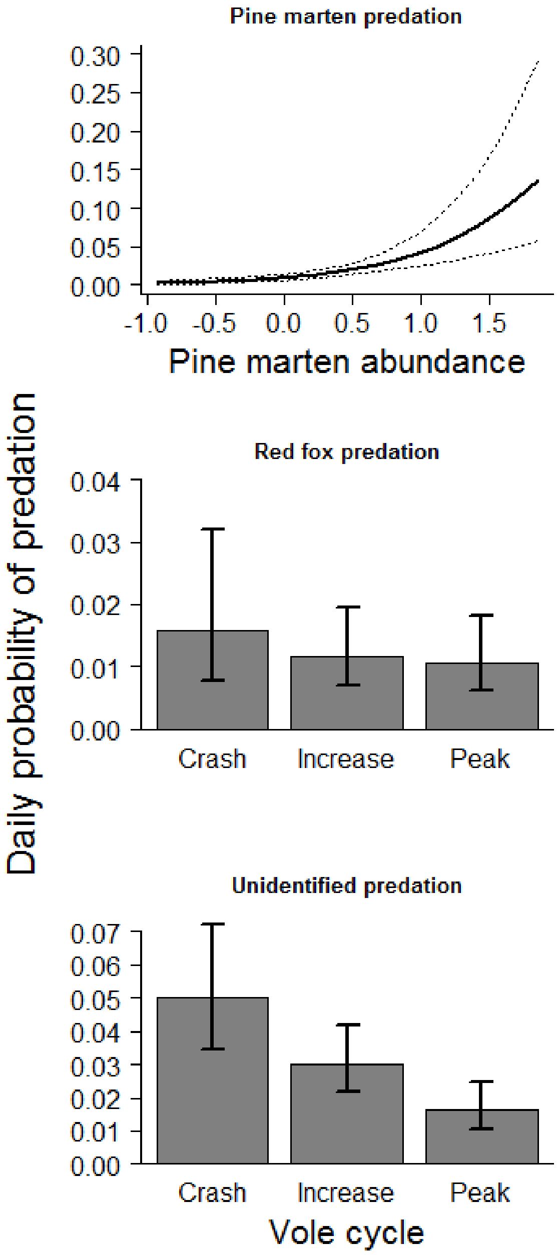

Figure 21 Estimated daily probability of predation on capercaillie nests by pine marten (top) as a function of pine marten abundance, red fox (middle) and unidentified (bottom) as a function of vole cycle.

Discussion

Here we show that red fox and pine marten are the most important predators of woodland grouse nests, and that previous studies identifying avian predators as significant are likely biased by their uncritical use of artificial nests (e.g. Moore & Robinson 2004). Pine marten and red fox were responsible for 84 % of all identified cases and European badger predated 12 %. Capercaillie and black grouse hens fought off both ravens and hooded crows and successfully defended their nests during all corvid visits. Eurasian jays and magpies were ignored. Overall nest predation in black grouse increased with PMA (pine marten abundance) and decreased with VA (vole abundance). The strength of the relationship to VA however, weakened as PMA increased. For capercaillie nests, overall predation rates were mediated by the VC (vole cycle) as predicted by the alternative prey hypothesis but only when pine martens were scarce. As PMA increased, peak years in the VC did not relieve capercaillie nests of predation. Pine marten predation on capercaillie nests increased with PMA. Conversely, red fox and unidentified predation was modified by the VC. Our results therefore confirm earlier reports that predation on boreal woodland grouse nests is mediated by vole and predator abundances (e.g. Angelstam, Lindström & Widén 1984; Wegge & Storaas 1990; Ludwig *et al.* 2010) but additionally, we shed light on nuances both with regards to interspecific variation in possible drivers as well as predator-specific responses to variable vole and predator abundances.

Empirical data presented here, on both number of corvids and behavior of incubating hens visited by corvids contradict earlier beliefs and seriously question the external validity of artificial nest studies promoting corvid predation on not only woodland grouse nests, but also nests of any sizeable ground nesting species in the boreal forest. Artificial nests mimicking e.g. grouse nests, lack the cryptic colored hen concealing the eggs and are therefore more easily detected by avian predators acting on visual cues (Storaas 1988; Willebrand & Marcström 1988). This bias increase further as hens protect and successfully defend the nest from corvid predation. Additionally, detection probabilities related to females escaping threats, and thereby revealing her eggs are lacking in such studies. Consequently, inference from artificial nests is ambiguous also due to species-specific differences in detection probabilities. Ravens have however been identified as a prominent predator on sage-grouse (*Centrocercus urophasianus*) nests in the sage-brush grasslands of North-America (Coates, Connelly & Delehanty 2008). There are obvious habitat properties favoring visually hunting predators in such landscapes compared to the conifer forests of Fennoscandia and indeed, sage-grouse nests well covered in shrubs were less likely to be detected by ravens (Coates & Delehanty 2010).

For approximately two to three out of ten cases, operational cameras failed to record the predation event (i.e. false negative). This number can be somewhat reduced by ensuring better camera mounting (e.g. camera tilts out of focus with time). Although these events remain unknown, we do not suspect species frequently predating capercaillie and black grouse eggs to have evaded detection altogether by our camera traps because within the same project, the range of nest predators identified predating willow ptarmigan (*Lagopus lagopus*) nests extends to a different predator guild including smaller species with presumed lower detectability (e.g. stoat). Thus, the camera set-up was capable of detecting potential differences in predator communities. Some nests were lacking camera trap monitoring due to camera availability. This led to low resolution in the capture histories (i.e. specific day of failure or success unknown) of non-monitored nests compared to nests with monitoring and so we could not sufficiently assess camera-effects on nest predation rates. Review studies of camera-effects on active nests however, suggest that camera presence tends to reduce predation rates (e.g. Richardson, Gardali & Jenkins 2009).

We wanted to study nest predation and we therefor did not include deserted nests. Stress from disturbance or from poor body condition may both cause nest abandonment. Hens may also be killed during off-bouts. Woodland grouse are staple food for goshawks (*Accipiter gentilis*) during spring (Angelstam 1984; Tornberg 2001) and goshawks were observed twice at capercaillie nests without predating eggs or hens. Adult black grouse hens do have lower survival than capercaillie (reviewed in Jahren *et al.* 2016) and so earlier day of nest abandonment is therefore expected if desertion is caused by mortality during off-bouts. For black grouse, the mean day of desertion after nest detection was day 3 and day 6 for capercaillie. Mean monitoring time for all nests was 10.23 and 10.45 days respectively. Additionally, we cannot rule out nest desertions triggered by observer effects. Although nest desertion rates caused by observer-effects in other precocial ground-nesters are generally low, they are higher during early stages of incubation and particularly during egg-laying (e.g. Livezey 1980) but individual variation in susceptibility to such stress is probably high. Nonetheless, according to estimated mortality rates for hens during spring (Wegge & Rolstad 2011), rates of abandonment detected here can be explained by mortality alone for capercaillie but not so for black grouse.

Contrary to expectation, we did not observe a statistical difference in daily probabilities of pooled predation between black grouse and capercaillie nests. This was largely due to substantial variation around the estimates rather than similar means and the lack of difference may relate to the relatively small sample of black grouse nests. Since their densities were rather similar (Solvang *et al.* 2009), we probably found more capercaillie nests because they are easier to detect than black grouse nests. It is likely that capercaillie hens flush relatively early (Storaas, Kastdalen & Wegge 1999) because the larger body size leads to a slower escape and higher expected adult survival make capercaillie hens favor own survival over the current reproductive attempt (Stearns 1992). Irrespective of sample size however, capercaillie and black grouse utilize and nest in different landscapes (Seiskari 1962; Storaas & Wegge 1987; Swenson & Angelstam 1993) and landscape-dependent predation pressure from red fox and pine marten (e.g. Kurki *et al.* 1998) may in part explain the unexpectedly high predation rates for black grouse nests.

Accounting for incubation duration (i.e. nest exposure), our estimates of 78.9 and 66.3 % predation of capercaillie and black grouse nests are higher than recent reports of apparent nest loss (Jahren *et al.* 2016). Estimates of nest loss accounting for exposure time are typically higher than apparent (i.e. proportional) estimates because failed nests are usually not found (Johnson 2007). Yet, the total loss in our sample of nests was higher still because we did not include nest failures other than predation. Despite high losses to predators, hens of both species may compensate and re-nest if the first nesting attempt fails (Willebrand 1992; Marjakangas & Törmälä 1997; Caizergues & Ellison 2000; Storaas, Wegge & Kastdalen 2000) and so annual re-nesting rates have likely mediated predation rates reported here but to an unknown degree.

Predation rates on black grouse nests were positively associated with PMA and negatively associated with VA. The relationship to voles however, leveled off in strength with increasing PMA. This suggests that incidental processes (e.g. numerical response in predators) are part of the mechanics governing nest predation in black grouse and that at certain levels of PMA, voles will not sufficiently buffer black grouse nests from predation. Furthermore, the lack of vole cycle phase-dependency in predation patterns also indicate that prey switching (i.e. type-III functional response) was not a mechanism dominating predation patterns on black grouse nests. Characteristic to incidental predation is the lack of reliability of the particular prey item to the predator and thus consumption of the particular prey item does not change predator behavior (Vickery, Hunter Jr. & Wells 1992). Incidental prey may be unreliable in terms of net energy gained from its consumption due to e.g. low detectability (McKinnon *et al.* 2010) and relative to capercaillie nests, nests of black grouse fits this description. Nonetheless, to confirm this pattern, predation rates need to be evaluated in relation to nest densities.

In contrast, predation patterns on capercaillie nests agree with those described by the alternative prey hypothesis (Hagen 1952; Lack 1954; Angelstam, Lindström & Widén 1984). This relationship however, was only consistent with the model when PMA was low. At higher PMA, a switch in predator foraging behavior from voles to capercaillie nests still took place when voles increased but vole peaks did no longer relieve capercaillie nests of predation and rates eventually exceeded those of crash years. This means that under elevated PMA, hatching success will not contribute to sequential years (i.e. vole-increase and peak) of population growth for capercaillie. Such a process may well be one of the underlying mechanisms driving the long-term population declines in boreal capercaillie (Jahren *et al.* 2016) additional to having a stabilizing effect on the population (Hanski, Hansson & Henttonen 1991). Nonetheless, this mechanism is likely ratio-dependent and may therefore also arise from low amplitude in vole peaks as well as from increased PMA (Arditit & Ginzburg 1989; Krebs *et al.* 2014).

Sympatric predators may exhibit different functional and numerical responses to variations in a shared prey species (Redpath & Thirgood 1999) and prey-switching during depletion of main prey may be towards different alternatives (O'Donoghue *et al.* 1998). Partitioned predation on capercaillie nests did indeed suggest different patterns for pine marten and red fox predation. Predation rates by pine marten was unaffected by voles and followed PMA, similar to findings in Finland where pine martens predate goldeneye (*Bucephala clangula*) nests with no apparent effect of vole fluctuations (Pöysä, Jalava & Paasivaara 2016). Capercaillie nests were relieved of red fox predation as the VC progressed irrespective of RFA (red fox abundance). Because we do not have information on nest densities, we cannot discern if pine martens predate capercaillie eggs incidentally or if they actively search them. Willebrand *et al.* (2017) however, showed that half of all dig events by pine martens during winter was for cached eggs and thereby suggested that eggs collected in spring can be important food for pine martens during winter.

The alternative prey hypothesis (Hagen 1952; Hörnfeldt 1978; Lindström *et al.* 1987) was developed during a period in which Scandinavian pine marten populations were recovering from eradication

(Helldin 2000a). Later, the alternative prey hypothesis' application to the woodland grouse system has been debated (e.g. Lindén 1988) but confirmed for other systems where red fox is the key predator (Hörnfeldt 1978; Danell & Hörnfeldt 1987; Angerbjörn 1989). Our results suggest that the effect of voles on nest predation is predictable according to the model when PMA is low. Additionally, the red fox appears as the moderator behind the classical relationship whereas pine marten predation is probably indirectly mediated by voles via a numerical response (e.g. Helldin 1999).

Conclusions

Nest survival is a pivotal part of reproductive output in woodland grouse and in order to reverse the negative population trends in Fennoscandia, implementation of measures to increase reproductive output is necessary (Jahren *et al.* 2016). By reducing pine marten abundances, overall nest success in black grouse can be improved. For capercaillie, measures can be taken to reduce red fox predation during the crash phase of the vole cycle. In contrast, pine marten predation can be reduced by reducing pine marten abundances. A reduction in pine marten numbers have both been suggested and demonstrated to increase reproductive output for capercaillie in other parts of their range (Moreno-Opo *et al.* 2015; Baines, Aebischer & Macleod 2016). However, whereas the reduction of e.g. red fox may reduce predation risk by red fox, this reduction can be compensated for by increased predation risk by other nest predators (Ellis-Felege *et al.* 2012).

We observed equal predation rates between red fox and pine marten but more red fox than pine marten tracks crossed our transects and relative densities indicated that pine martens were less abundant than red foxes in the boreal forest (Kurki *et al.* 1998). Consequently, future research can address potential differences in the efficiency of pine marten and red fox as nest predators. Additionally, investigations into the predation ratio-dependence between the amplitude in vole fluctuations and baseline population sizes of nest predators in the crash phase will possibly illuminate important mechanisms limiting nesting success in capercaillie and black grouse.

Acknowledgements

This study would not have been possible without the help of all the volunteers reporting nests, collecting data on owl broods, conducting snow tracking and organizing field work locally. We also want to thank the Trygve Gotaas Foundation, The Norwegian Wildlife Fund and County Administrations in Hedmark and Nord-Trøndelag for financial support. Finally, we wish to thank two anonymous reviewers for constructive comments improving the manuscript.

Data Accessibility:

Not clarified yet.

References

Andersen, R., Fagerheim, W.I. & Solheim, J. (2009) *Hjorteviltforvaltning. Hvordan Forvalte Store Beitedyr. Tre Scenarier.* Trondheim - In Norwegian.

Andren, H. (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology*, **73**, 794–804.

Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*.

Andren, H. & Angelstam, P. (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology*, **69**, 544–547.

Angelstam, P. (1983) *Population Dynamics of Tetraonids Especially the Black Grouse* Tetrao Tetrix L. *in Boreal Forests*. Uppsala University, Uppsala, Sweden.

Angelstam, P. (1984) Sexual and seasonal differences in mortality of the black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scandinavica*, **15**, 123–134.

Angelstam, P. (2004) Habitat Thresholds and Effects of Forest Landscape Change on the Distribution and Abundance of Black Grouse and Capercaillie. *Ecological Bulletins*, 173–187.

Angelstam, P., Lindström, E. & Widén, P. (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, **62**, 199–208.

Angerbjörn, A. (1989) Mountain hare populations on islands: effects of predation by red fox. *Oecologia*, **81**, 335–340.

Arditit, R. & Ginzburg, L.R. (1989) Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology*, **139**, 311–326.

Baddeley, A., Rubak, E. & Turner, R. (2015) Spatial point patterns: methodology and applications with R.

Baines, D., Moss, R. & Dugan, D. (2004) Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology*, **41**, 59–71.

Baines, D., Richardson, M. & Warren, P. (2017) The invertebrate diet of Black Grouse Tetrao tetrix chicks: a comparison between northern England and the Scottish Highlands. *Bird Study*, **64**, 117–124.

Baines, D., Aebischer, N.J. & Macleod, A. (2016) Increased mammalian predators and climate change predict declines in breeding success and density of capercaillie *Tetrao urogallus*, an old stand specialist, in fragmented Scottish forests. *Biodiversity and Conservation*, **25**, 2171–2186.

Bartoń, K. & Zalewski, A. (2007) Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography*, **16**, 281–289.

Benson, T., Brown, J. & Bednarz, J. (2010) Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology*, **79**, 225–234.

Berryman, A. & Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos*, **92**, 265–270.

Bogdziewicz, M. & Zwolak, R. (2013) Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review. *European Journal of Forest Research*, **133**, 1–11.

Brainerd, S.M., Helldin, J.O., Lindstrom, E.R., Rolstad, E., Rolstad, J. & Storch, I. (1995) Pine marten (Martes martes) selection of resting and denning sites in Scandinavian managed forests. *Annales Zoologici Fennici*, **32**, 151–157.

Brinchmann, A. (1926) Coccidiosen hos lirype. *Bergens Museums Årbok*, p. Bergen Museum, Bergen, Norway - In Norwegian.

Brittas, R. & Willebrand, T. (1991) Nesting habitats and egg predation in Swedish black grouse.

Ornis Scandinavica, **22**, 261–263.

Brommer, J.E., Pietiäinen, H., Ahola, K., Karell, P., Karstinen, T. & Kolunen, H. (2010) The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through ‘climatic forcing’. *Global Change Biology*, **16**, 577–586.

Burnham, K. & Anderson, D. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer.

Cagnacci, F., Lovari, S. & Meriggi, A. (2003) Carrion dependence and food habits of the red fox in an Alpine area. *Italian Journal of Zoology*, **70**, 31–38.

Caizergues, A. & Ellison, L.N. (2000) Age-specific reproductive performance of black grouse *Tetrao tetrix* females. *Bird Study*, **47**, 344–351.

Carricondo-Sanchez, D., Samelius, G., Willebrand, O. & Willebrand, T. (2016) Spatial and temporal variation in the distribution and abundance of red foxes in the tundra and taiga of northern Sweden. *Eur J Wildl Res*.

Cavallini, P. & Lovari, S. (1991) Environmental factors influencing the use of habitat in the red fox, Vulpes vulpes. *Journal of Zoology*, **223**, 323–339.

Christiansen, E. (1979) Skog- og jordbruk, smågnagere og rev. *Tidsskrift for skogbruk*, **87**, 115–119.

Coates, P.S., Connelly, J.W. & Delehanty, D.J. (2008) Predators of greater sage-grouse nests identified by video monitoring. *Journal of Field Ornithology*, **79**, 421–428.

Coates, P.S. & Delehanty, D.J. (2010) Nest predation of greater sage-grouse in relation to microhabitat factors and predators. *Journal of Wildlife Management*, **74**, 240–248.

Conover, M. (2007) *Predator-Prey Dynamics: The Role of Olfaction*. CRC Press, Boca Raton, FL.

Cornulier, T., Yoccoz, N.G., Bretagnolle, V., Brommer, J.E., Butet, A., Ecke, F., Elston, D.A., Framstad, E., Henttonen, H., Hornfeldt, B., Huitu, O., Imholt, C., Ims, R.A., Jacob, J., Jedrzejewska, B., Millon, A., Petty, S.J., Pietiainen, H., Tkadlec, E., Zub, K. & Lambin, X. (2013) Europe-wide dampening of population cycles in eystone herbivores. *Science*, **340**, 63–66.

Dahl, K. (1924) Norges Jeger og Fiskerforbunds Tidsskrift - In Norwegian. *Norges Jeger og Fiskerforbunds Tidsskrift - In Norwegian*, pp. 169–189.

Danell, K. & Hörnfeldt, B. (1987) Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. *Oecologia*, **73**, 533–536.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, Or, the Preservation of Favoured Races in the Struggle for Life*. J. Murray, London, UK.

DeVault, T., Jr, O.R. & Shivik, J. (2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, **102**, 225–234.

Dinsmore, S.J., White, G.C. & Knopf, F.L. (2002) Advanced techniques for modeing avian nest survival. *Ecology*, **83**, 3476–3488.

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.

Elmhagen, B., Kindberg, J., Hellström, P. & Angerbjörn, A. (2015) A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio*, **44**, 39–50.

Englund, J. (1980a) Population dynamics of the red fox (Vulpes vulpes L., 1758) in Sweden. *The Red Fox*.

Englund, J. (1980b) Yearly variations of recovery and dispersal rates of fox cubs tagged in Swedish coniferous forests. *Biogeographica*.

Erikstad, K. & Spidsø, T. (1982) The influence of weather on food intake, insect prey selection and feeding behaviour in willow grouse chicks in northern Norway. *Ornis Scandinavica*.

Erlinge, S., Goransson, G., Hogstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylven, M. (1983) Can vertebrate predators regulate their prey? *The American Naturalist*, **123**, 125–133.

Erlinge, S., Goransson, G., Hogstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylven, M. (1988) More Thoughts on Vertebrate Predator Regulation of Prey. *The American Naturalist*, **132**, 148–154.

Erlinge, S., Göransson, G. & Hansson, L. (1983) Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos*, **40**, 36–52.

Erlinge, S., Agrell, J., Nelson, J. & Sandell, M. (1991) Why are some microtine populations cyclic while others are not? *Acta Theriologica*.

Errington, P. (1946) Predation and vertebrate populations. *The Quarterly Review of Biology*.

ESRI INC. (2011) ArcGIS.

Etterson, M.A., Greenberg, R. & Hollenhorst, T. (2014) Landscape and regional context differentially affect nest parasitism and nest predation for wood thrush in central Virginia, USA. *The Condor*, **116**, 205–214.

Etterson, M., Nagy, L., Robinson, T. & Johnson, D. (2007) Partitioning risk among different causes of nest failure. *The Auk*.

Fletcher, Q.E., Boutin, S., Lane, J.E., Lamontagne, J.M., Mcadam, A.G., Krebs, C.J. & Humphries, M.M. (2010) The functional response of a hoarding seed predator to mast seeding. *Ecology*, **91**, 2673–2683.

Flint, P.L. & Grand, J.B. (1997) Survival of Spectacled Eider Adult Females and Ducklings during Brood Rearing. *The Journal of Wildlife Management*, **61**, 217–221.

Foley, J.A. (2005) Global Consequences of Land Use. *Science*, **309**, 570–574.

Formosof, A.N. (1933) The Crop of Cedar Nuts, Invasions Into Europe of the Siberian Nutcracker (Nucifraga caryocatactes macrorhynchus Brehm) and Fluctuations in Numbers of the Squirrel (Sciurus vulgaris L.). *The Journal of Animal Ecology*, **2**, 70.

Frafjord, K., Becker, D. & Angerbjörn, A. (1989) Interactions between arctic and red foxes in Scandinavia—predation and aggression. *Arctic*.

Gelman, A. & Su, Y.-S. (2016) Data Analysis Using Regression and Multilevel/Hierarchical Models - R package version 1.9-3.

Gomo, G., Mattisson, J., Hagen, B.R., Moa, P.F. & Willebrand, T. (2017) Scavenging on a pulsed resource: quality matters for corvids but density for mammals. *BMC Ecology*, **17**, 22.

González, A. de & Cox, D. (2007) Interpretation of interaction: A review. *The Annals of Applied Statistics*, **1**, 371–385.

Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M. & Nilsen, E.B. (2012) Habitat heterogeneity and mammalian predator-prey interactions: Predator-prey interactions in a spatial world. *Mammal Review*, **42**, 55–77.

Goszczyński, J. (2002) Home ranges in red fox: territoriality diminishes with increasing area. *Acta Theriologica*.

Graf, R.F., Bollmann, K., Suter, W. & Bugmann, H. (2005) The importance of spatial scale in habitat models: Capercaillie in the Swiss Alps. *Landscape Ecology*, **20**, 703–717.

Güthlin, D., Storch, I. & Küchenhoff, H. (2013) Landscape variables associated with relative abundance of generalist mesopredators. *Landscape Ecology*, **28**, 1687–1696.

Hagen, Y. (1952) *Rovfuglene Og Viltpleien*, 1st ed. Gyldendal, Oslo, Norway (in Norwegian).

Halpin, M. & Bissonette, J. (1988) Influence of snow depth on prey availability and habitat use by red fox. *Canadian Journal of Zoology*, **66**, 587–592.

Hanski, I. (1990) Density Dependence, Regulation and Variability in Animal Populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **330**, 141–150.

Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *The Journal of Animal Ecology*, **60**, 353–367.

Hansson, L. (1988) The domestic cat as a possible modifier of vole dynamics. *Mammalia*, **52**, 159–164.

Hansson, L. (1992) Landscape ecology of boreal forests. *Trends in ecology & evolution*, **7**, 299–302.

Hansson, L. & Henttonen, H. (1988) Rodent dynamics as community processes. *Trends in ecology & evolution*, **3**, 195–200.

Hedwall, P. & Brunet, J. (2013) Changes in the abundance of keystone forest floor species in response to changes of forest structure. *Journal of vegetation Science*, **24**, 296–306.

Heiberg, G. (1995) *Essays Og Artikler*. Grøndahl og Dreyer, Oslo, Norway.

Helldin, J.-O. (1999) Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography*, **22**, 324–336.

Helldin, J.O. (2000a) Population trends and harvest management of pine marten *Martes martes* in Scandinavia. *Wildlife Biology*, **6**, 111–120.

Helldin, J.O. (2000b) Seasonal diet of pine marten Martes martes in southern boreal Sweden. *Acta Theriologica*, **45**, 409–420.

Helle, P. & Ikonen, K. (2015) Wildlife monitoring in Finland - on-line information to game administration, hunters and wider public, http://www.metla.fi/life/lifedata/pdf/Helle_IBFRA_2015.pdf

Henden, J., Ims, R. & Yoccoz, N. (2009) Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. *Journal of Animal Ecology*.

Henden, J., Ims, R., Yoccoz, N. & Hellström, P. (2010) Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. *Oikos*.

Henden, J., Stien, A. & Bårdsen, B. (2014) Community-wide mesocarnivore response to partial ungulate migration. *Journal of Applied Ecology*, **51**.

Henttonen, H. (1989) Does an increase in the rodent and predator densities, resulting from modern forestry, contribute to the long-term decline in Finnish tetraonids? *Suomen Riista*, **35**, 83–90.

Herman-Brunson, K.M., Jensen, K.C., Kaczor, N.W., Swanson, C.C., Rumble, M.A. & Klaver, R.W. (2009) Nesting ecology of greater sage-grouse Centrocercus urophasianus at the eastern edge of their historic distribution. *Wildlife Biology*, **15**, 395–404.

Hersteinsson, P. & MacDonald, D.W. (1992) Interspecific Competition and the Geographical Distribution of Red and Arctic Foxes Vulpes Vulpes and Alopex lagopus. *Oikos*, **64**, 505–515.

Hijmans, R.J. (2016) raster: Geographic Data Analysis and Modeling.

Hjeljord, O. (2015) *INA Fagrapport 30: Ryper Før Og Nå*. Fakultet for miljøvitenskap og teknologi Institutt for naturforvaltning, Ås, Norway - In Norwegian.

Holling, C. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385–398.

Hone, J. (1999) On rate of increase(r): patterns of variation in Australian mammals and the implications for wildlife management. *Journal of Applied Ecology*.

Hornfeldt, B. & Carlsson, B. (1990) Effects of cyclic food supply on breeding performance in Tengmalm's owl (Aegolius funereus). *Canadian Journal of Zoology*, **68**, 522–530.

Hudson, P.J. (1992) *Grouse in Space and Time : The Population Biology of a Managed Gamebird*. Game Conservancy Ltd.

Huhta, E., Helle, P., Nivala, V. & Nikula, A. (2017) The effect of human-modified landscape structure on forest grouse broods in two landscape types. *Ecosphere*, **8**, e01950.

Höglund, N. (1953) Vem tar tjäderns egg? *Svensk Jakt - In Swedish*, **91**, 416–420.

Höglund, N. (1960) Studies of the winter diet of pine marten *(Martes m. martes)* in County Jämtland. *Viltrevy (Swedish Wildlife)*, **1**, 319–337.

Hörnfeldt, B. (1978) Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia*, **32**, 141–152.

Hörnfeldt, B., Hipkiss, T. & Eklund, U. (2005) Fading out of vole and predator cycles? *Proceedings of the Royal Society*, **272**, 2045–2049.

Ims, R., Henden, J. & Killengreen, S. (2008) Collapsing population cycles. *Trends in Ecology & Evolution*, **23**, 79–86.

IUCN. (2016) IUCN, http://www.iucnredlist.org

Jahren, T., Storaas, T., Willebrand, T., Fossland Moa, P. & Hagen, B.-R. (2016) Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years. *Animal Biology*, **66**, 363–400.

Johnson, D.H. (2007) Methods for estimating nest success: An historical tour. *Studies in Avian Biology*, **34**, 1–12.

Josefsson, T., Gunnarson, B., Liedgren, L., Bergman, I. & Östlund, L. (2010) Historical human influence on forest composition and structure in boreal Fennoscandia. *Canadian Journal of Forest Research*, **40**, 872–884.

de Jounge, J. (1981) *Predation of the Pine Marten* (Martes Martes) *in Relation to Habitat Selection* *and Food Abundance during Winter in Central Sweden*.

Jędrzejewski, W. & Jędrzejewska, B. (1992) Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Biatowieza National Park, Poland. *Ecography*, **15**, 212–220.

Kauhala, K., Helle, P. & Helle, E. (2000) Predator Control and the Density and Reproductive Success of Grouse Populations in Finland. *Ecography*, **23**, 161–168.

Kelly, C. & Price, T.D. (2005) Correcting for Regression to the Mean in Behavior and Ecology. *The American Naturalist*, **166**, 700–707.

Kidd, N.A.C. & Lewis, G.B. (1987) Can Vertebrate Predators Regulate Their Prey? A Reply. *The American Naturalist*, **130**, 448.

Killengreen, S.T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N.G. & Ims, R.A. (2011) The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. *Journal of Animal Ecology*, **80**, 1049–1060.

Kjellén, N. & Roos, G. (2000) Population trends in Swedish raptors demonstrated by migration counts at Falsterbo, Sweden 1942–97. *Bird Study*, **47**, 195–211.

Klaus, S. (1985) Predation among capercaillie in a reserve in Thuringia. *Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. World Pheasant Association, Reading, UK.

Kolstad, M., Wegge, P. & Bø, T. (1985) *The Habitat Ecology of Black Grouse (*Tetrao Tetrix L.*) during Spring and Summer in East Norway*. Direktoratet for Vilt og Ferskvannsfisk, Trondheim, Norway (in Norwegian).

Korpela, K. (2014) *Biological Interactions in the Boreal Ecosystem Under Climate Change - Are the Vole and Predator Cycles Disappearing?* University of Jyväskylä.

Krebs, C.J., Bryant, J., Kielland, K., O'Donoghue, M., Doyle, F., Carriere, S., DiFolco, D., Berg, N., Boonstra, R., Boutin, S., Kenney, A.J., Reid, D.G., Bodony, K., Putera, J., Timm, H.K., Burke, T., Maier, J.A.K. & Golden, H. (2014) What factors determine cyclic amplitude in the snowshoe hare (*Lepus americanus*) cycle? *Canadian Journal of Zoology*, **92**, 1039–1048.

Krott, P. & Lampio, T. (1983) Naadan esiintymisesta Suomessa 1900-luvulla. (In Finnish with English summary: occurrence of the pine marten *(Martes martes)* in Finland in the 1900s). *Suomen riista*, **30**, 60–63.

Kurki, S., Nikula, a, Helle, P. & Linden, H. (1998) Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology*, **67**, 874–886.

Kämmerle, J.-L., Coppes, J., Ciuti, S., Suchant, R. & Storch, I. (2017) Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. *Ecosphere*, **8**, e01934.

Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford, Uk.

Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen press, London, UK.

Lakka, J. & Kouki, J. (2009) Patterns of field layer invertebrates in successional stages of managed boreal forest: Implications for the declining Capercaillie Tetrao urogallus L. population. *Forest Ecology and Management*, **257**, 600–607.

Lande, U., Herfindal, I., Willebrand, T., Fossland Moa, P. & Storaas, T. (2014) Landscape characteristics explain large-scale variation in demographic traits in forest grouse. *Landscape Ecology*, **29**, 127–139.

Lehikoinen, A., Ranta, E. & Pietiäinen, H. (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia*, **165**, 349–355.

Leopold, A. (1933) *Game Management*. Charles Scribner's Sons, New York.

Leopold, A. (1937) Pheasant Nesting Study. *The Wilson Bulletin*, **49**, 91–95.

Leopold, A. (1949) *A Sand County Almanac - and Sketches Here and There*. Oxford University Press.

Lesley, A.. & Shipley, A.E. (1912) *Grouse in Health and in Disease*. Smith, Elder & Company, London, UK.

Lindén, H. (1981) Estimation of juvenile mortality in capercaillie, Tetrao urogallus and the black grouse, Tetrao tetrix from indirect evidence. *Finnish Game Research*, **39**, 35–51.

Lindén, H. (1988) Latitudinal gradients in predator-prey interactions, cyclicity and synchronism in voles and small game populations in Finland. *Oikos*, **52**, 341–349.

Lindén, H. & Helle, P. (2003) The rise and fall of Black Grouse populations in Finland since 1860s. *Proceedings of the European Conference Black Grouse – Endangered Species of Europe* (eds P. Málková & P. Procházka), pp. 113–114. Journal of Ornithology, Prague, Czech Republic.

Lindstrom, E.R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., Lemnell, P.A., Martinsson, B., Skold, K. & Swenson, J.E. (1994) Disease reveals the predators: Sarcoptic mange, red fox predation, and prey populations. *Ecology*, **75**, 1042–1049.

Lindström, E. (1982) *Population Ecology of the Red Fox (Vulpes Vulpes L.) in Relation to Food Supply*. University of Stockholm.

Lindström, E. & Brainerd, S. (1995) Pine marten—red fox interactions: a case of intraguild predation? *Annales Zoologici Fennici*, **32**, 123–130.

Lindström, J., Ranta, E., Lindén, M. & Lindén, H. (1997) Reproductive Output, Population Structure and Cyclic Dynamics in Capercaillie, Black Grouse and Hazel Grouse. *Journal of Avian Biology*, **28**, 1–8.

Lindström, E., Angelstam, P., Widén, P. & Andrén, H. (1987) Do predators synchronize vole and grouse fluctuations? An experiment. *Oikos*, **48**, 121–124.

Linnell, J.D.C., Broseth, H., Odden, J. & Nilsen, E.B. (2010) Sustainably harvesting a large carnivore? Development of eurasian lynx populations in Norway during 160 years of shifting policy. *Environmental Management*, **45**, 1142–1154.

Linnell, J.D.C., Fiske, P., Odden, J., Brøseth, H., Herfindal, I. & Andersen, R. (2007) An evaluation of structured snow-track surveys to monitor Eurasian lynx Lynx lynx populations. *Wildlife Biology*, **13**, 456–466.

Linnell, J.D.C., Odden, J., Pedersen, V. & Andersen, R. (1998) Records of intra-guild predation by Eurasian lynx, *Lynx lynx*. *Canadian Field Naturalist*, **112**, 707–708.

Linnell, J.D.C., Swenson, J.E. & Anderson, R. (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, **4**, 345–349.

Livezey, B.C. (1980) Effects of selected observer-related factors on fates of duck nests. *Wildlife Society Bulletin*, **8**, 123–128.

Loison, A. & Langvatn, R. (1998) Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia*, **116**, 489–500.

Lovel, T. (ed). (1979) Woodland Grouse Symposium., p. 180pp. WPA, Inverness, Scotland.

Ludwig, G. (2007) *Mechanisms of Population Declines in Boreal Forest Grouse*. University of Jyväskylä.

Ludwig, G., Alatalo, R. V, Helle, P. & Siitari, H. (2010) Individual and environmental determinants of daily black grouse nest survival rates at variable predator densities. *Annales Zoologici Fennici*, **47**, 387–397.

Magnússon, K., Brynjarsdóttir, J. & Nielsen, O. (2004) *Population Cycles in Rock Ptarmigan* Lagopus Muta*: Modelling and Parameter Estimation*. University of Iceland, Division of

Applied Mathematics and Computer Science / Icelandic Institute of Natural History, Reykjavik, Iceland.

Major, R. & Kendal, C. (1996) The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*, **138**, 298–307.

Marcström, V. (1960) Studies on the Physiological and Ecological Background to the Reproduction of the Capercaillie, Tetrao Urogallus Lin.(Reprinted from Viltrevy.)[A Thesis. With.

Marcström, V., Keith, L.B., Engren, E. & Cary, J.R. (1989) Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Canadian Journal of Zoology*, **67**, 658–668.

Marcström, V., Kenward, R. & Engren, E. (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *The Journal of Animal Ecology*, **57**, 859–872.

Marjakangas, A. & Törmälä, L. (1997) Female age and breeding performance in a cyclic population of black grouse *Tetrao tetrix*. *Wildlife Biology*, **3**, 195–203.

Martin, T. (1993) Nest predation and nest sites. *BioScience*, **43**, 523–532.

Mayfield, H.F. (1975) Suggestions for calculating nest success. *The Wilson Bulletin*, **87**, 456–466.

McElreath, R. (2016) *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. CRC-Press.

McKinney, M. (2002) Urbanization, biodiversity, and conservation the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population. *BioScience*, **52**, 883–890.

McKinnon, L., Berteaux, D., Gauthier, G. & Bêty, J. (2013) Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos*, **122**, 1042–1048.

McKinnon, L., Smith, P. a, Nol, E., Martin, J.L., Doyle, F.I., Abraham, K.F., Gilchrist, H.G., Morrison, R.I.G. & Bêty, J. (2010) Lower predation risk for migratory birds at high latitudes. *Science*, **327**, 326–327.

Messmer, T.A., Brunson, M.W., Reiter, D. & Hewitt, D.G. (1999) United States Public Attitudes regarding Predators and Their Management to Enhance Avian Recruitment. *Wildlife Society Bulletin*, **27**, 75–85.

Miljødirektoratet & Naturdata. (2016) Hjorteviltregisteret, www.hjorteviltregisteret.no

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Csanyi, S. & Stenseth, N.C. (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology*, **43**, 721–734.

Moen, A. (1999) *Vegetation* (ed A. Lillethun). National Mapping Authority, Hønefoss, Norway.

Montgomerie, R.D. & Weatherhead, P.J. (1988) Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology*, **63**, 167.

Moore, R.P. & Robinson, W.D. (2014) Artificial bird nests ,external validity, and bias in ecological field studies. *Ecology*, **85**, 1562–1567.

Moran, P.A.P. (1950) Notes on Continuous Stochastic Phenomena. *Biometrika*, **37**, 17–23.

Moreno-Opo, R., Afonso, I., Jiménez, J., Fernández-Olalla, M., Canut, J., García-Ferré, D., Piqué, J., García, F., Roig, J., Muñoz-Igualada, J., González, L.M. & López-Bao, J.V. (2015) Is it necessary managing carnivores to reverse the decline of endangered prey species? Insights from a removal experiment of mesocarnivores to benefit demographic parameters of the pyrenean capercaillie. *PLoS ONE*, **10**, 1–17.

Moss, R. (1986) Rain, breeding success and distribution of capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* in Scotland. *Ibis*, **128**, 65–72.

Moss, R., Storch, I. & Müller, M. (2010) Trends in grouse research. *Wildlife Biology*, **16**, 1–11.

Myrberget, S. (ed). (1977) Foredrag fra Nordisk Skogsfuglsymposium 1976. *Nordisk Skogsfuglsymposium 1976*, p. 94. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway - In Norwegian.

Myrberget, S. & Hagen, Y. (1974) Reproduksjon hos lirype og skogsfugl i Setesdalen 1919-1934. *Sterna - In Norwegian*, **13**, 23–33.

Mörner, T. (1992) Sarcoptic mange in Swedish wildlife. *Revue Scientifique et Technique (International Office of Epizootics)*, **11**, 1115–1121.

Naturresursinstitutet. (2017) Luke, http://stat.luke.fi/sv/tilasto/4481

Needham, R., Odden, M., Lundstadsveen, S. & Wegge, P. (2014) Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. *Acta theriologica*.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. & Dickman, C.R. (2015) The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, **24**, 1–11.

Newton, I. (1998) *Population Limitation in Birds*. Academic Press, New York.

Novoa, C., Desmet, J.-F., Brenot, J.-F., Muffat-Joly, B., Arvin-Bérod, M., Resseguier, J. & Tran, B. (2011) Demographic traits of two alpine populations of Rock Ptarmigan. *Ecology conservation and management of grouse* (eds B. Sandercock, K. Martin, & G. Segelbacher), pp. 267–280. University of California Press, Los Angeles, United States.

Nur, N. (1984) The Consequences of Brood Size for Breeding Blue Tits I. Adult Survival, Weight Change and the Cost of Reproduction. *The Journal of Animal Ecology*, **53**, 479–496.

O'Donoghue, M., Boutin, S., Krebs, C. & Zuleta, G. (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208.

Odden, J., Linnell, J.D.C. & Andersen, R. (2006) Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research*, **52**, 237–244.

Ordiz, A., Milleret, C., Kindberg, J., Månsson, J., Wabakken, P., Swenson, J.E. & Sand, H. (2015) Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere*, **6**, art284.

Panek, M. & Bresiński, W. (2002) Red foxVulpes vulpes density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. *Acta Theriologica*.

Panzacchi, M., Linnell, J.D.C., Melis, C., Odden, M., Odden, J., Gorini, L. & Andersen, R. (2010) Effect of land-use on small mammal abundance and diversity in a forest-farmland mosaic landscape in south-eastern Norway. *Forest Ecology and Management*, **259**, 1536–1545.

Panzacchi, M., Linnell, J.D.C., Odden, J., Odden, M. & Andersen, R. (2008a) When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. *Canadian Journal of Zoology*, **86**, 116–126.

Panzacchi, M., Linnell, J.D.C., Odden, M., Odden, J. & Andersen, R. (2009) Habitat and roe deer fawn vulnerability to red fox predation. *Journal of Animal Ecology*, **78**, 1124–1133.

Panzacchi, M., Linnell, J.D.C., Serrao, G., Eie, S., Odden, M., Odden, J. & Andersen, R. (2008b) Evaluation of the importance of roe deer fawns in the spring-summer diet of red foxes in southeastern Norway. *Ecological Research*, **23**, 889–896.

Pasanen-Mortensen, M., Pyykönen, M. & Elmhagen, B. (2013) Where lynx prevail, foxes will fail – limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography*, **22**, 868–877.

Pebesma, E. (2004) Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, **30**, 683–691.

Pianka, E.R. (1974) Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*, **71**, 2141–5.

Picozzi, N. (1975) Crow predation on marked nests. *The Journal of Wildlife Management*, **39**, 151–155.

Picozzi, N., Moss, R. & Kortland, K. (1999) Diet and survival of capercaillie Tetrao urogallus chicks in Scotland. *Wildlife Biology*.

Prugh, L.R., Stoner, C.J., Clinton, W.E., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The Rise of the Mesopredator. *BioScience*, **59**, 779–791.

Pulliainen, E. (1980) Food and feeding habits of the pine marten in Finnish Forest Lapland forest in winter. *Proceedings of the Worldwide Furbearer Conference*, p. Frostburg, Md.

Pulliainen, E. (1981) A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish Forest Lapland over 13 winters. *Annales Zoologici Fennici*.

Pöysä, H., Jalava, K. & Paasivaara, A. (2016) Generalist predator, cyclic voles and cavity nests: testing the alternative prey hypothesis. *Oecologia*, **182**, 1083–1093.

R Core Team. (2016) R: A Language and Environment for Statistical Computing.

Rajala, P. (1974) The Structure and Reproduction of Finnish Populations of Capercaillie, Tetrao Urogallus, and Black Grouse, Lyrurus Tetrix, on the Basis of Late Summer Census Data from 1963-66. *Finnish Game Research*, 1–51.

Ranta, E., Helle, P. & Lindén, H. (2004) Forty years of grouse monitoring in Finland. *Suomen Riista*.

Ranta, E., Lindstrom, J. & Linden, H. (1995) Synchrony in tetraonid population dynamics. *Journal of Animal Ecology*.

Redpath, S. & Thirgood, S. (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology*, **68**, 879–892.

Richardsen, K. (2012) *Den Store Rovviltkrigen - En Undersøkelse Av Lov Om Udrydding Af Rovdyr Og Om Freding Af Andet Vildt (1845)*. University of Tromsø (In Norwegian).

Richardson, T.W., Gardali, T. & Jenkins, S.H. (2009) Review and meta-analysis of camera effects on avian nest success. *Journal of Wildlife Management*, **73**, 287–293.

Rosalino, L., Sousa, M., Pedroso, N. & Basto, M. (2010) The influence of food resources on red fox local distribution in a mountain area of the western Mediterranean. *Vie et milieu*.

Sandercock, B.K., Martin, K. & Hannon, S.J. (2005) Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. *Oecologia*, **146**, 13–24.

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

Seiskari, P. (1962) On the winter ecology of the capercaillie, *Tetrao urogallus*, and the black grouse, *Lyrurus tetrix*, in Finland. *Papers on Game Research*, **22**, 1–119.

Selås, V., Johnsen, B. & Eide, N. (2010) Arctic fox Vulpes lagopus den use in relation to altitude and human infrastructure. *Wildlife Biology*.

Selås, V., Sonerud, G.A., Framstad, E., Kalas, J.A., Kobro, S., Pedersen, H.B., Spidso, T.K. & Wiig, O. (2011) Climate change in Norway: warm summers limit grouse reproduction. *Population Ecology*, **53**, 361–371.

Selås, V. & Vik, J.O. (2006) Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897-1976. *Journal of Zoology*, **269**, 299–308.

Semenow Tjan Shanskiy, O.I. (1979) *Ecology of Tetraonids* (ed T. from R. by A.A.C. for S. Translations). U.S. Department of Agriculture and National Science Foundation, Whashington D.C., USA.

Sibly, R. & Hone, J. (2002) Population growth rate and its determinants: an overview. *of the Royal*

Society B: Biological ....

Sidorovich, V., Sidorovich, A. & Izotova, I. (2006) Variations in the diet and population density of the red fox Vulpes vulpes in the mixed woodlands of northern Belarus. *Mammalian Biology-Zeitschrift*, **71**, 74–89.

Siivonen, L. (1953) On the destruction of gallinaceous birds. *Suomen Riista*, **8**, 46–48.

Siivonen, L. (1957) The problem of the short-term fluctuations in numbers of tetraonids in Europe. *Papers on Game Research*, **19**, 1–44.

Silverman, B.W. (1986) *Density Estimation for Statistics and Data Analysis*. Chapman and Hall.

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

Sirkiä, S., Nikula, A., Helle, P., Lindén, H., Norrdahl, K., Suorsa, P. & Valkeajärvi, P. (2011) Contemporary mature forest cover does not explain the persistence of Capercaillie (Tetrao urogallus) lekking areas in Finland. *Ornis Fennica*, **88**, 208–216.

Skara, A.B. & Steinset, T.A. (2016) Statistics Norway, https://www.ssb.no/jord-skog-jakt-og-fiskeri/statistikker/elgjakt

Small, R., Marcström, V. & Willebrand, T. (1993) Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography*, **16**, 360–364.

Smedshaug, C., Selås, V., Lund, S. & Sonerud, G. (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biology*, **5**, 157–166.

Smith, C.C. & Reichman, O.J. (1984) The Evolution of Food Caching by Birds and Mammals. *Annual Review of Ecology and Systematics*, **15**, 329–351.

Solomon, M.E. (1949) The Natural Control of Animal Populations. *The Journal of Animal Ecology*,

18, 1.

Solvang, H., Pedersen, H.C., Storaas, T. & Hagen, B.R. (2009) *Rapport for Skogsfugltaksering 2005-2008*. Høgskolen i Hedmark, Elverum, Norway (in Norwegian).

Spence, J. (2001) The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology & Evolution*, **16**, 591–593.

Spidsø, T., Wegge, P. & Storaas, T. (1984) Renesting in capercaillie in southern Norway. *The Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. York, UK.

Statistics Norway. (1934) *Pelsdyrtellingen I Norge*. H Aschehoug & Co. - In Norwegian, Oslo, Norway - In Norwegian.

Statistics Norway. (2016) Statistics Norway, https://www.ssb.no/statistikkbanken/selectvarval/Define.asp?subjectcode=&ProductId=&MainTable=Smaavilt2&nvl=&PLanguage=0&nyTmpVar=true&CMSSubjectArea=jord-skog-jakt-og-fiskeri&KortNavnWeb=srjakt&StatVariant=&checked=true

Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, Uk.

Stigler, S.M. (1997) Regression towards the mean, historically considered. *Statistical methods in medical research*, **6**, 103–14.

Storch, I. (1993) Habitat selection by capercaillie in summer and autumn: Is bilberry important? *Oecologia*, **95**, 257–265.

Storch, I. (1994) Habitat and survival of capercaillie Tetrao urogallus nests and broods in the Bavarian Alps. *Biological Conservation*, **70**, 237–243.

Storch, I. (2002) On spatial resolution in habitat models: Can small-scale forest structure explain capercaillie numbers? *Conservation Ecology*.

Storch, I. (2007) *Grouse: Status Survey and Conservation Action Plan 2006-2010* (ed I. Storch).

WPA, IUCN and Fordingbridge, UK, Gland, Switzerland.

Storch, I. (2015) Conservation status and threats to grouse worldwide: an update. *Oral presentation - International Grouse Symposium*, p. Reykjavik, Iceland.

Storch, I., Lindström, E. & de Jounge, J. (1990) Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriologica*, **35**, 311–320.

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

Storaas, T., Kastdalen, L. & Wegge, P. (1999) Detection of forest grouse by mammalian predators: A possible explanation for high brood losses in fragmented landscapes. *Wildlife Biology*, **5**, 187–192.

Storaas, T. & Wegge, P. (1984) High nest losses in capercaillie and black grouse in Norway. *The Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. York, UK.

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

Storaas, T., Wegge, P. & Kastdalen, L. (2000) Weight-related renesting in capercaillie *Tetrao urogallus*. *Wildlife Biology*, **6**, 299–303.

Stubsjøen, T., Sæther, B.-E., Solberg, E.J., Heim, M. & Rolandsen, C.M. (2000) Moose (*Alces alces*) survival in three populations in northern Norway. *Canadian Journal of Zoology*, **78**, 1822–1830.

Summers, R.W., Green, R.E., Proctor, R., Dugan, D., Lambie, D., Moncrieff, R., Moss, R. & Baines, D. (2004) An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *Journal of Applied Ecology*, **41**, 513–525.

Summers, R.W., Willi, J. & Selvidge, J. (2009) Capercaillie *Tetrao urogallus* nest loss and attendance at Abernethy Forest, Scotland. *Wildlife Biology*, **15**, 319–327.

Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology*, **73**, 167–178.

Sundell, J., O'hara, R., Helle, P., Hellstedt, P. & Henttonen, H. (2013) Numerical response of small mustelids to vole abundance: delayed or not? *Oikos*.

Swenson, J. & Angelstam, P. (1993) Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Canadian Journal of Zoology*, **71**, 1303–1310.

Søilen, E. (1995) *Sportsmenn I Veideland - Norges Jeger- Og Fiskerforbund*. StikkaTrykk, Billingstad, Norway (In Norwegian).

The Norwegian Mapping Authority. (2017) The Norwegian Mapping Authority, http://kartverket.no/en/

Thompson, I.D., Davidson, I.J., O'Donnell, S. & Brazeau, F. (1989) Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Canadian Journal of Zoology*, **67**, 1816–1823.

Thorson, J., Skaug, H., Kristensen, K. & Shelton, A. (2015) The importance of spatial models for estimating the strength of density dependence. *Ecology*.

Tjernberg, M. (1981) Diet of the golden eagle *Aquila chrysaetos* during the breeding season in Sweden. *Ecography*, **4**, 12–19.

Tonteri, T., Salemaa, M., Rautio, P., Hallikainen, V., Korpela, L. & Merilä, P. (2016) Forest management regulates temporal change in the cover of boreal plant species. *Forest Ecology and Management*, **381**, 115–124.

Tornberg, R. (2001) Pattern of goshawk *Accipiter gentilis* predation on four forest grouse species in northern Finland. *Wildlife Biology*, **7**, 245–256.

Tovmo, M., Mattisson, J., Kleven, O. & Brøseth, H. (2016) *Overvaking Av Kongeørn I Noreg 2015. Resultat Frå 12 Intensivt Overvaka Område*, NINA Rappo. Trondheim - In Norwegian.

Trewhella, W., Harris, S. & McAllister, F. (1988) Dispersal distance, home-range size and population density in the red fox (Vulpes vulpes): a quantitative analysis. *Journal of Applied Ecology*.

Tryjanowski, P., Hartel, T., Báldi, A. & Szymański, P. (2011) Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. *Acta Ornithologica*.

Turchin, P. (2003) *Complex Population Dynamics : A Theoretical/empirical Synthesis*. Princeton University Press.

Vanha-Majamaa, I. & Jalonen, J. (2001) Green Tree Retention in Fennoscandian Forestry. *Scandinavian Journal of Forest Research*, **16**, 79–90.

Vickery, P., Hunter Jr., M. & Wells, J. (1992) Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos*, **63**, 281–288.

Viltdata. (2017) Viltdata, https://rapport.viltdata.se/statistik/

Vos, A. (1995) Population dynamics of the red fox (Vulpes vulpes) after the disappearance of rabies in county Garmisch-Partenkirchen, Germany, 1987—1992. *Annales Zoologici Fennici*, **32**, 93–97.

Vuorisalo, T., Talvitie, K., Kauhala, K., Bläuer, A. & Lahtinen, R. (2014) Urban red foxes (Vulpes vulpes L.) in Finland: A historical perspective. *Landscape and Urban Planning*, **124**, 109–117.

Walther, G., Post, E., Convey, P., Menzel, A. & Parmesan, C. (2002) Ecological responses to recent climate change. *Nature*.

Walton, Z., Samelius, G., Odden, M. & Willebrand, T. (2017) Variation in home range size of red foxes Vulpes vulpes along a gradient of productivity and human landscape alteration. *PLoS ONE*, **12**.

Watanabe, S. (2010) Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, **11**, 3571–3594.

Wegge, P. (1985) *The Sociobiology, Reproduction, and Habitat of Capercaillie Tetrao Urogallus L. in Southern Norway*. University of Montana.

Wegge, P. & Grasaas, T. (1977) Bestandsstudier av storfugl på Sørlandet. *Viltrapport 5* (ed S. Myrberget), pp. 22–39. Direktoratet for vilt og ferskvannsfisk - In Norwegian, Trondheim, Norway - In Norwegian.

Wegge, P. & Kastdalen, L. (2007) Pattern and causes of natural mortality of capercaille, *Tetrao urogallus*, chicks in a fragmented boreal forest. *Annales Zoologici Fennici*, **44**, 141–151.

Wegge, P. & Kastdalen, L. (2008) Habitat and diet of young grouse broods: resource partitioning between Capercaillie *(Tetrao urogallus)* and Black Grouse *(Tetrao tetrix)* in boreal forests. *Journal of Ornithology*, **149**, 237–244.

Wegge, P. & Rolstad, J. (2011) Clearcutting forestry and Eurasian boreal forest grouse: Long-term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix* reveals unexpected effects on their population performances. *Forest Ecology and Management*, **261**, 1520–1529.

Wegge, P. & Storaas, T. (1990) Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway. *Oecologia*, **82**, 527–530.

Willebrand, T. (1992) Breeding and age in female black grouse Tetrao tetrix. *Ornis Scandinavica*, **23**, 29–32.

Willebrand, T. & Marcström, V. (1988) On the danger of using dummy nests to study predation. *Auk*, **105**, 378–379.

Willebrand, T., Willebrand, S., Jahren, T. & Marcström, V. (2017) Snow tracking reveals different foraging patterns of red foxes and pine martens. *Mammal Research*, **In print**, 1–10.

Wood, S.N. (2006) *Generalized Additive Models : An Introduction with R*. Chapman & Hall/CRC.

Zwickel, F.C. & Bendell, J.F. (1967) Early mortality and the regulation of numbers in blue grouse. *Canadian Journal of Zoology*, **45**.

Östlund, L., Zackrisson, O. & Axelsson, A. (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, **27**, 1198–1206.

Åhlen, P.-A., Willebrand, T., Sjöberg, K. & Hörnell-Willebrand, M. (2013) Survival of female capercaillie Tetrao urogallus in northern Sweden. *Wildlife Biology*, **19**, 368–373.

Appendix

Model ranking

Table A 1 Overview of candidate models parameterizing nest predation in black grouse (top) and capercaillie (bottom) ranked according to AICc. Covariate abbreviations are as follows: PMA is pine marten abundance, RFA is red fox abundance, VA is vole abundance index and VC is phase in the vole cycle. *For models with interaction terms (e.g. χ_1: χ_2), main effects are included but not shown. Constant survival is highlighted bold. Log(L) is the log likelihood of the respective model. ΔAICc, w_i and K are AICc distance from respective model to best ranking model, model weight and number of parameters in the model respectively.*

	Model	**log(L)**	**AICc**	**ΔAICc**	**w_i**	**K**
Black grouse	PMA	101.01	206.03	0.00	0.29	2
	VA	101.54	207.11	1.07	0.17	2
	VA:PMA	99.86	207.79	1.76	0.12	4
	RFA:PMA	99.99	208.05	2.02	0.10	4
	VC	101.13	208.30	2.26	0.09	3
	Constant	103.41	208.82	2.79	0.07	1
	VA:RFA	100.52	209.10	3.07	0.06	4
	RFA	102.99	209.99	3.96	0.04	2
	VA:VC	99.30	210.75	4.72	0.03	6
	VC:PMA	99.49	211.12	5.09	0.02	6
	VC:RFA	100.51	213.17	7.14	0.01	6
Capercaillie	VC	506.91	1019.82	0.00	0.39	3
	VC:PMA	504.44	1020.92	1.10	0.23	6
	VA:PMA	507.18	1022.38	2.56	0.11	4
	PMA	509.27	1022.54	2.72	0.10	2
	VA	509.52	1023.04	3.22	0.08	2
	VA:VC	506.45	1024.93	5.11	0.03	6
	VC:RFA	506.58	1025.19	5.37	0.03	6
	RFA:PMA	508.87	1025.75	5.93	0.02	4
	VA:RFA	509.42	1026.87	7.05	0.01	4
	RFA	512.29	1028.59	8.77	0.00	2
	Constant	513.40	1028.80	8.98	0.00	1

Table A 2 Overview of candidate models parameterizing competing risk nest predation in capercaillie ranked according to AICc. All other predators besides pine marten, red fox and unidentified are kept constant. Covariate abbreviations are as follows: PMA is pine marten abundance, RFA is red fox abundance, VA is vole abundance index and VC is phase in the vole cycle. For models with interaction terms (e.g. χ_1: χ_2*), main effects are included but not shown. Constant survival for all events is highlighted bold. Log(L) is the log likelihood of the respective model. ΔAICc,* w_i *and K are AICc distance from respective model to best ranking model, model weight and number of parameters in the model respectively.*

Model							
Pine marten	**Red fox**	**Unidentified**	**log(L)**	**AICc**	**ΔAICc**	w_i	**K**
PMA	VC	VC	667.36	1358.85	0.00	0.71	12
PMA	VA	VA	671.19	1362.47	3.62	0.12	10
PMA	RFA	PMA	671.97	1364.03	5.18	0.05	10
PMA	RFA	RFA	672.18	1364.45	5.59	0.04	10
VC:PMA	VC:RFA	VC:RFA	661.01	1366.43	7.58	0.02	22
VA:PMA	VA:RFA	VA:RFA	667.26	1366.75	7.90	0.01	16
VC	RFA	VC	671.50	1367.13	8.28	0.01	12
VA:PMA	VA:RFA	VA:PMA	667.58	1367.39	8.53	0.01	16
PMA	VA	PMA	673.81	1367.71	8.86	0.01	10
PMA	VA	RFA	674.00	1368.09	9.23	0.01	10
PMA	VC	PMA	673.62	1369.36	10.50	0.00	11
VC:PMA	VC:RFA	VC:PMA	662.48	1369.38	10.53	0.00	22
PMA	VC	RFA	673.81	1369.73	10.88	0.00	11
VA	RFA	VA	675.25	1370.59	11.74	0.00	10
VC	VC	VC	673.11	1372.36	13.51	0.00	13
RFA:PMA	RFA:PMA	RFA:PMA	670.48	1373.18	14.33	0.00	16
VA	VA	VA	677.08	1374.26	15.40	0.00	10
VA	RFA	PMA	677.96	1376.01	17.16	0.00	10
VA	RFA	RFA	678.12	1376.32	17.47	0.00	10
VC	RFA	PMA	677.78	1377.68	18.82	0.00	11
VC	RFA	RFA	677.94	1377.99	19.13	0.00	11
Constant	**Constant**	**Constant**	682.49	1379.02	20.17	0.00	7
VA:VC	VA:VC	VA:VC	670.13	1384.68	25.83	0.00	22

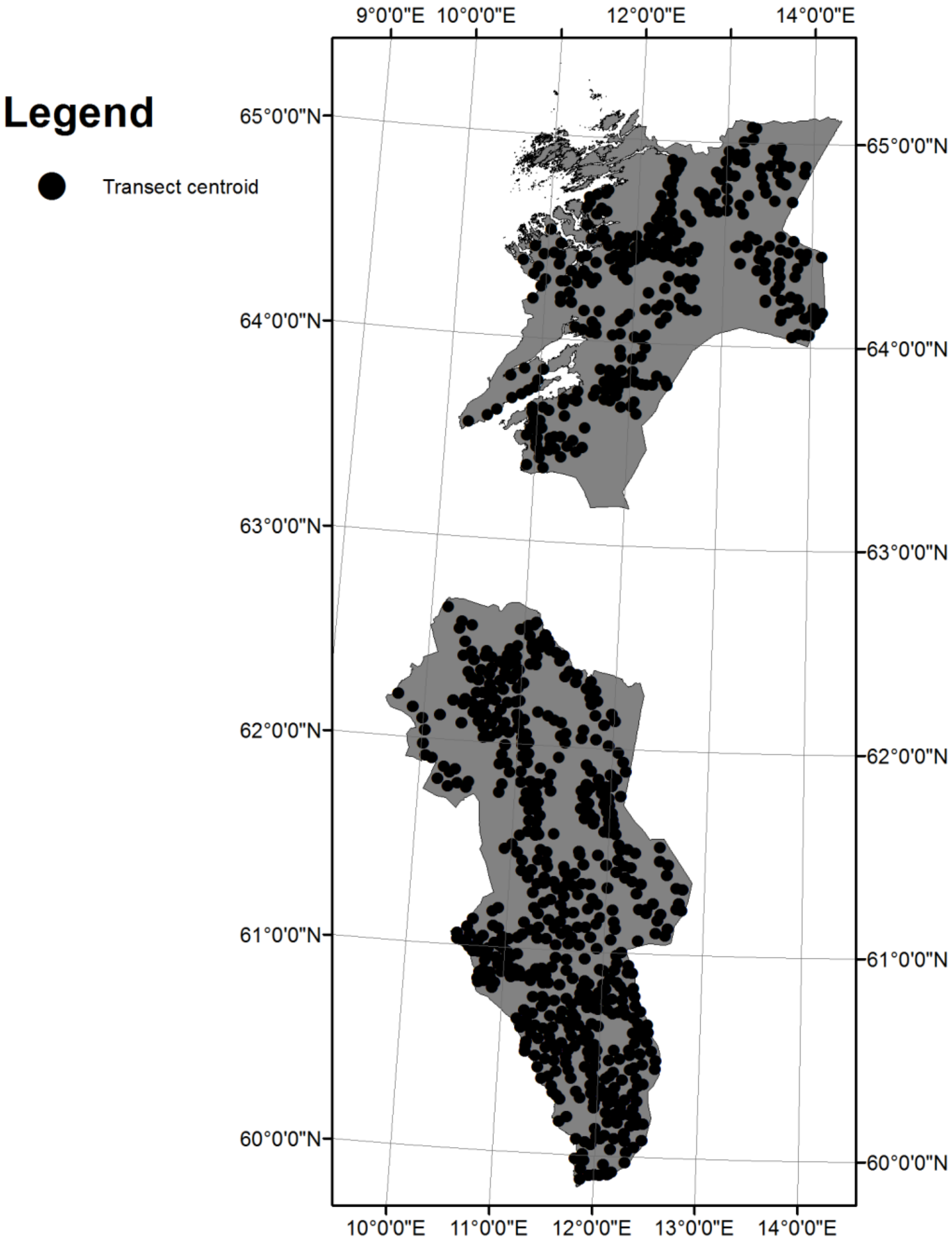

Figure A 1 Location of transects (centroids) used for snow track indices of red fox (Vulpes vulpes) and pine marten (Martes martes) in Nord-Trøndelag (top) and Hedmark (bottom) counties between 2009 (2010) and 2014.

Table A 3 Data on tengmalm's owl (Aegolius funereus) reproduction used as proxy for voles

	Year	Mean brood size	Number of nest boxes w/reproduction attempt	Centered value (VAI)	Binary coding	VC
Hedmark	2008	4.24	250	0.21	1	
	2009	3.46	202	-0.57	0	Crash
	2010	5.66	639	1.63	1	Increase
	2011	5.8	2331	1.77	1	Peak
	2012	0	28	-4.03	0	Crash
	2013	4.22	571	0.19	1	Increase
	2014	4.81	1367	0.78	1	Peak
	Mean	4.03				
Nord-Trøndelag	2009	0	0	-2.94	0	
	2010	7	6	4.06	1	Increase
	2011	3.41	41	0.47	1	Peak
	2012	0	0	-2.94	0	Crash
	2013	4.25	10	1.31	1	Increase
	2014	3	3	0.06	1	Peak
	Mean	2.94				

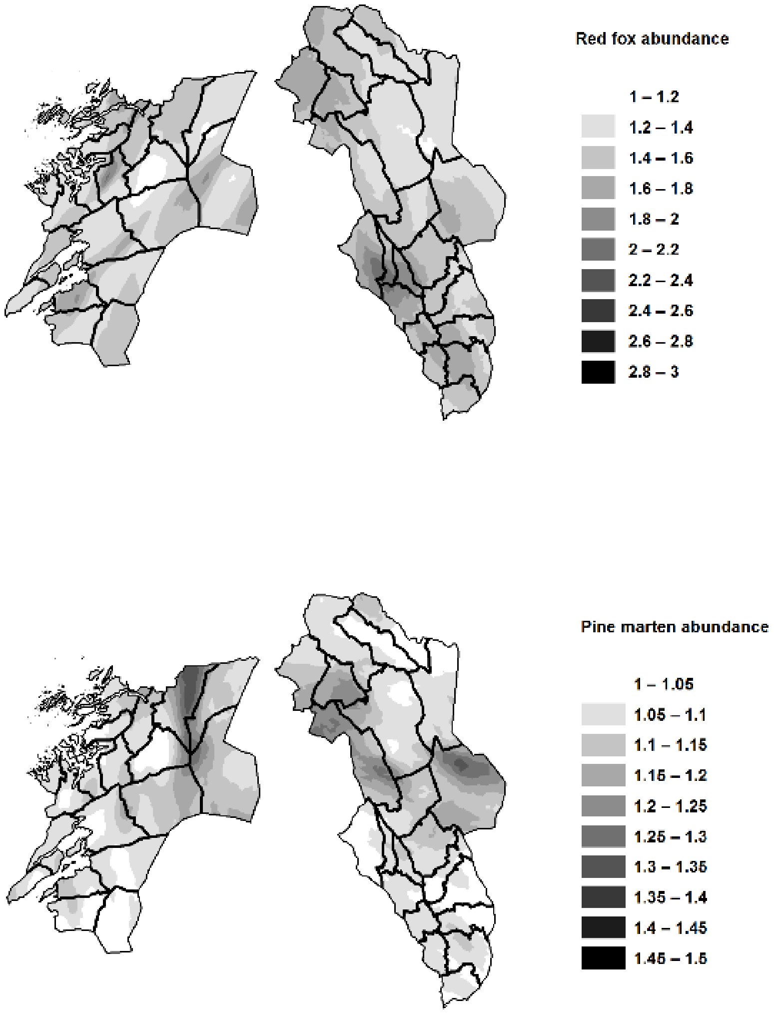

Figure A 2 Kriging maps of mean red fox (Vulpes vulpes) (top) and pine marten (Martes martes) (bottom) abundance in Nord-Trøndelag (left) and Hedmark (right) between 2009 (2010) and 2014.

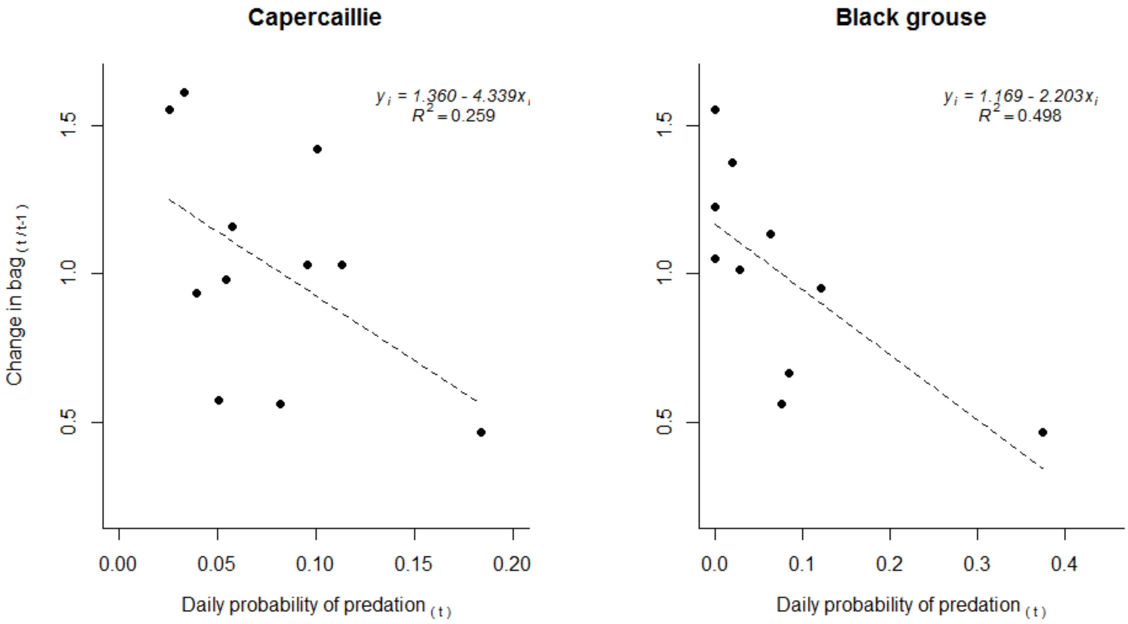

Figure A 3 From left to right: The relationship between daily probability of predation and rate of change in annual bag per hunter for capercaillie (Tetrao urogallus) and black grouse (Lyrurus tetrix) in Hedmark and Nord-Trøndelag between 2009 and 2014. Trend lines are fitted values from linear models. In upper, right-hand corner are respective linear model equation (Y = a+bx) and goodness of fit (R^2) for the respective model.

Paper III

Mamm Res
DOI 10.1007/s13364-017-0332-2

ORIGINAL PAPER

Snow tracking reveals different foraging patterns of red foxes and pine martens

Tomas Willebrand[1] · Sofia Willebrand[1] · Torfinn Jahren[1] · Vidar Marcström[2]

Received: 14 May 2017 / Accepted: 1 August 2017

Abstract Red fox (*Vulpes vulpes*) shares similar prey preferences and co-occurs with several other carnivores, and is together with pine marten (*Martes martes*), the most common mesocarnivore in the northern boreal forest. Voles are important prey for both species, but it is unclear to what extent they compete for the same food resources in winter. Here, we use 2139 km and 533 km of meticulous snow tracking of red foxes and pine martens to evaluate their food niches. We measured hunting and digging behaviour, whether successful or not, and the effect of snow depth and temperature. Pine martens were restricted to forested habitats, whereas red foxes used a wide range of habitats. Red foxes were found to dig more often than pine martens, 0.67 vs. 0.39 digging events per kilometre. Hunting was less common and similar in both species, about 0.1 hunting event per kilometre. Pine martens were more efficient in hunting and finding food remains compared to red foxes. Increasing snow depth reduced hunting success and also reduced dig success of red foxes. Food niche overlap was small. Red foxes used mostly voles and carrion remains of ungulates, whereas pine martens used cached eggs and small birds. We suggest that caching eggs is an important strategy for pine martens to survive winter in northern latitudes. Snow depth was important for capturing voles, and thick snow cover appeared to mask the effect of vole peaks. Intensified land use, as clear-cutting and leaving slaughter remains from harvest, will benefit red foxes on the expense of pine martens. The ongoing climate change with warmer winters and less snow will likely further benefit the red fox.

Keywords Niche · Competition · Red fox · Pine marten · Carcass · Egg · Voles

Introduction

Many medium-sized mammalian carnivores overlap in prey preferences, and the relative abundance of competing species is likely affected by interspecific competition (Holt 1977; Pianka 1981). Intraguild predation may further enhance the outcome of competition, even if it is only a small proportion of the predators' diet (Palomares et al. 1999). Red fox (*Vulpes vulpes*) shares partly similar prey preferences and co-occurs with several other carnivores (Brangi 1995; Kauhala et al. 1998; Carvalho and Gomes 2001; Elmhagen and Tannerfeldt 2002; Mitchell and Banks 2005; Lanszki et al. 2006; Sidorovich et al. 2010; Murdoch et al. 2010; Bassi et al. 2012). Increased competition from red foxes is proposed as an important factor eliminating the arctic fox (*V. lagopus*) from large parts of the Scandinavian tundra (Hersteinsson et al. 2003).

Red foxes and pine martens (*Martes martes*) are common mesopredators in the boreal conifer forests of northern Scandinavia (Kurki et al. 1998). At the turn of the last century, both species had been harvested down to substantially lower densities than today because of their valuable winter fur and as part of extensive predator control programs (Helldin 2000a; Selas and Vik 2006). Pine martens became completely protected during the 1930s in Sweden (Helldin 2000a), but the red foxes appear to have better sustained the intensive harvest programs and were never protected. Today, there is

Communicated by: Andrzej Zalewski

✉ Tomas Willebrand
tomas.willebrand@inn.no

[1] Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, N-2480 Koppang, Norway

[2] Uppsala University, 752 36 Uppsala, Sweden

an open, but restricted season for both species, although the interest for population control and fur harvest is limited.

The red foxes are highly adaptable and found in a wide range of landscapes, including pine marten habitat, which is mostly restricted to the conifer forest (Storch et al. 1990). Only a few density estimates are available on red foxes and pine martens in Sweden: A range of 0.2–0.8 red fox km^{-2} was estimated from south and central parts of Sweden (Lindström et al. 1987), and winter densities of 0.2–0.4 km^{-2} were reported from a conifer-dominated area in northern Sweden (Willebrand 1988). The latter study recorded pine marten densities of 0.3–0.4 km^{-2}, which is similar to the 0.3 km^{-2} estimated by Helldin (1999). Both red foxes and pine martens show functional and numerical responses to the variation in vole (subfamily *Arvicolinae*) abundance (Englund 1970; Hanski et al. 1991; Helldin 2000b), which often exhibit geographically synchronized multiannual cyclic fluctuations (Hornfeldt et al. 1986; Marcstrom et al. 1990). Woodland grouse (subfamily *Tetranoinae*) and mountain hares (*Lepus timidus*) are alternative prey when voles are scarce (Small et al. 1993), and a negative effect of increased predation from red foxes and pine martens has been shown experimentally (Marcstrom et al. 1988a; Marcstrom et al. 1988b; see also Jahren et al. 2016).

Little is known about the interaction between red foxes and pine martens in the boreal forest, but predation by red foxes on pine martens has been recorded (Lindstrom et al. 1995). Bag records of pine martens also increased dramatically during the severe outbreak of sarcoptic mange in red foxes in Sweden (Storch et al. 1990), although Kurki et al. (1998) suggested that the long-term effect on the pine marten population from red fox competition was limited. In addition, there are reported cases of predation by pine martens on red fox cubs (Brzeziński et al. 2014). It has been proposed that winter severity limits the distribution of red foxes (Bartoń and Zalewski 2007), when prey availability is at its minimum in northern Sweden. Abundance of birds is greatly reduced due to southward migration, and snow can make it difficult to hunt remaining potential prey. Especially the voles are protected by occupying the subnivean space, and Lindstrom and Hornfeldt (1994) showed that the amount of small rodents in fox stomachs declined with increasing snow depths. Studies using camera traps and scat analysis have shown that remains of ungulate carcasses are an important food source for red foxes (Lund 1962; Englund 1965; Jedrzejewski and Jedrzejewska 1992; Needham et al. 2014; Selas and Vik 2006). Pine martens also appear to be a generalist predator with a winter diet similar to the red fox. Pine marten will also catch prey in trees, and red squirrels (*Sciurus vulgaris*) can be a regular finding in pine marten scats, but it is rarely found in red fox scats or stomachs from the same area (Storch et al. 1990; Helldin 2000b).

Here, we use data from extensive snow tracking of red foxes and pine martens in northern Sweden to evaluate whether red foxes are more limited by snow than pine martens and expect that red foxes should utilize carrion more than pine martens. Registering events, frequency and success during tracking were compared to snow depth and temperature. We expect red foxes and pine martens to have only partial overlap in food niche, and red foxes should be more opportunistic and use a broader range of habitat and food niche compared to pine martens.

Methods

Study area

This study was done in the coastal area of Gulf of Bothnia in northern Sweden (65.717 lat., 22.83 long.), and data were collected as part of the large-scale predator removal experiment described in Marcstrom et al. (1988a, b). Most tracking was done on the islands of Bergön (18.0 km^2) and Rånön (23.5 km^2) between 3 and 4 km from the mainland. Red foxes and pine martens were also tracked on the mainland north of Bergön and Rånön close to Kalix municipality.

The average winter temperature was − 10 °C, and the sea ice was frozen between November and early June. The ground was snow-covered between 160 and 180 days. The large part of the study area, including the islands, was commercially managed boreal conifer forest with clear-cutting and replanting practices. Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*) were the most common tree species, with less than 10% birch (*Betula* spp.). Other deciduous trees, mostly along the coastline, were alder (*Alnus incana*) and willow (*Salix* spp.). Open bogs were only present in low proportions (Elveland 1976).

Density of red fox and pine marten were 0.2–0.6 and 0.1–0.3 km^{-2} respectively (Marcstrom et al. 1988a,b). Moose (*Alces alces*) were common in the area and regulated by hunting to minimize the risk of extensive forest damages. Capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), hazel grouse (*Tetrastes bonasia*) (hereafter grouse) and mountain hare were common small game species. Voles showed a 3–4-year fluctuation pattern, with peaks in 1977, 1980 and 1984. Goshawks (*Accipter gentilis*) were rare in the area. There were no permanent settlements on the islands, but small villages and boat landings could be found on the mainland. The islands did not have any roads, but the mainland was transversed both by public and forest roads. The communities in this part of Sweden utilize both fish and wildlife as a contribution to their subsistence. Entrails, including lungs and heart, from harvested moose were left at the kill sites.

Snow tracking

Tracks were followed 1–4 days after snowfall depending on wind and temperature. There were 436 (330 red fox and 107 pine marten) tracking events between the winters of 1975–1981 and 1985–1987; 293 of these occurred on Bergön and Rånön. Tracking and data recording were done by three to six experienced trappers in different years. The trappers were hired through the predator removal project and had several years' experience of trapping and shooting red foxes and pine martens. Areas of the island that were subjected to predator control were excluded from our tracking dataset. Each trapper followed a prescribed route until a track of a red fox or a pine marten was located. On Bergön and Rånön, line transects for estimating mountain hare density were used. On the mainland, snowmobiles were used to find tracks by travelling on unploughed forest roads, clear-cut edges and bogs. This probably resulted in somewhat more fox encounters on the mainland than the islands, 86 vs. 70% fox tracks. Each track was followed in both directions. All events were recorded carefully as (1) hunting attempts (successful/unsuccessful chase) and (2) dig sites to find voles, cached food or scavenging on different remains under the snow. Pounces through the snow with no subsequent digging were categorized as a hunting attempt. Tracks in the snow from hunting and potentially killing prey, presence of blood, remains at dig sites, hair, bones and feathers were all recorded. It was possible to differentiate hunting attempts on grouse from small birds. It is possible that small items or a vole kill occasionally could go undetected.

Habitat was recorded during tracking, and the following habitat classes were used: (1) conifer forest; (2) clear-cuts, bogs and young pine plantations (< 1.5 m); (3) ice-covered lakes and sea; (4) shoreline (within 75 m from water edge); and (5) rock outcrops with scattered trees. We have no information on the overall landscape composition and therefore only compare relative habitat use of the species. Temperature and snow depth were recorded at each tracking event.

Data analysis

We evaluated the difference between the foraging behaviour of red foxes and pine martens and to what extent snow depth and air temperature affected the foraging. The frequencies of hunting and digs, as well as whether these attempts were successful or not, were used as response variables in a negative binomial and binomial regression models respectively. We used a Bayesian approach to model our data, because it provides a full posterior distribution, and the credible interval of the parameters shows the chance that it has captured the correct value. The four models were developed in the JAGS language (Plummer 2003), and R2Jags (Su and Yajima) was used as an interface to R (R Core Team 2017). Year was used as a random intercept in all models. Snow depth and temperature were standardized by subtracting the mean and dividing with twice the standard deviation. Temperature and snow depth were not significantly correlated, Pearsons $r = -0.009$ ($t = -0.190$, df = 433, p value = 0.849). We ran three chains, with a thinning rate of three and a burn-in of 6000. Only non-informative priors were used. The full models are presented in Appendix 1. The number of iterations was increased until convergence, R-hat < 1.1 (Gelman et al. 2013). Trace plots were used to visually evaluate the mixing of the chains. A posterior predictive check (i.e. a Bayesian p value) was used to evaluate if the model fit was acceptable (Hooten and Hobbs 2014). The squared residuals of the data points were compared to the squared residuals of a randomly generated data set from the fitted distribution. A value less than 0.05 or larger than 0.95 was considered a poor fit that required another distribution and/or additional parameters. For each model, we explored four alternative covariate sets: (1) intercept only, (2) species only, (3) species, snow and temperature and (4) species interaction with snow and temperature in addition to 3. The *leave-one-out cross-validation* (Vehtari et al. 2016) was used to explore the four models by calculating the loo information criteria and its standard error. The function logdensity.*foo* in JAGS was used to extract the posterior log likelihood for each data point and joined into a matrix that was parsed to the loo function. The difference between the highest ranking models was larger than 2.7 except in one case. The model of hunting success with only species effect was favoured by a difference of 1.1 compared to including snow depth and temperature, but we choose to present the latter model. We did not consider model averaging (Cade 2015).

The frequency of hunting and digs was initially analysed using a Poisson distribution with a log link and distance tracked (logged) as an offset variable. Results revealed a large over-dispersion, and both zero-inflated Poisson and negative binomial models were explored as alternatives. The Bayesian p value was 0 for the zero-inflated Poisson models but was within the acceptable range for the negative binomial models. The potential success of digs and hunting events following a track was modelled using a binomial distribution and a logit link. Dig success showed large over-dispersion and an initial Bayesian p value < 0.05, and we therefore added the individual observation as a random variable (Harrison 2014).

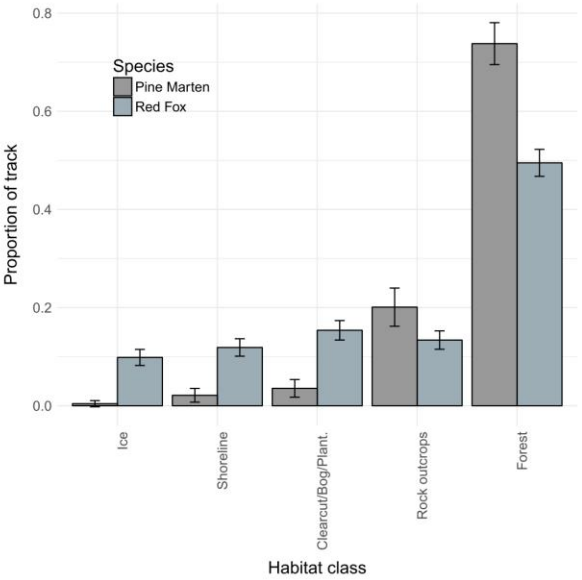

Fig. 1 The proportion of different habitat classes along the tracks of red fox and pine marten summarized for all tracks. The ± 1 standard error is included at top of each bar

Frequencies of prey species and scavenging objects for pine martens and red foxes were tested by Fischer exact test and computing *p* values by Monte Carlo simulations with 2000 replicates. The proportions of the five habitat classes for each tracking event were calculated, and the average and standard error were presented. The general niche concept has multidimensional properties, but here, we used it to describe the number of different food items utilized. We calculated Pianka's standardized index for niche breadth and overlap (Krebs 1999) for digs and hunting for red foxes and pine martens respectively. All calculations were made using R (R Core Team 2017).

Results

The total distance tracked was 2139 and 533 km for red foxes and pine martens respectively. The average length of each followed track was longer for red foxes compared to pine martens, 6.5 vs. 5.0 km respectively (Student's *t* test (two-sided), $t = -4.03$, df = 199, $P < 0.001$). The majority of tracks were followed between rest sites. A larger proportion of the pine martens tracks went through forest and tree covered rock outcrops (94%) compared to red foxes (63%). Red foxes used shorelines and sea ice to about 20% (Fig. 1).

Figure 2 shows the density plots of the predictions for red fox and pine marten foraging behaviour from the four different final models (Table 1) at average snow depth and temperature. The posterior distributions of the model parameters were used to calculate predictions (Table 1), which then were back transformed using the appropriate link function. Red foxes were more often engaged in digs (0.67 km^{-1}) compared to pine martens (0.39 km^{-1}). Snow depth had a negative effect on dig frequency by red foxes but not for pine martens. Parameter values were − 0.39

Fig. 2 Density plots of the model estimates for red fox and pine marten digging (**a**) and hunting (**b**) frequency and digging (**c**) and hunting (**d**) success rates, assuming average snow depth and temperature. The predictions were based on the posterior distribution of the model parameters (Table 1), back transformed using the appropriate link function

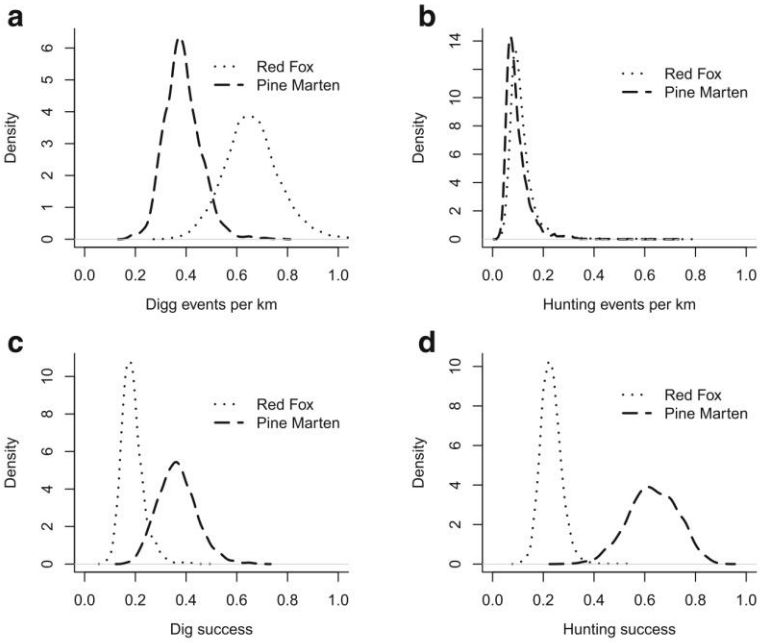

Table 1 Parameter values of the four selected models of dig and hunting events, and their probability of success

	Intercept	Species	Snow depth	Temperature	Snow + species	Temp. + species	SD year	BP	Loo
Dig events	− 0.969 (− 1.336, − 0.615)	0.541 (0.307, 0.783)	0.066 (− 0.354, 0.481)	− 0.641 (− 1.015, − 0.252)	− 0.455 (− 0.898, − 0.010)	0.270 (− 0.179, 0.420)	0.484 (0.254, 0.914)	0.927	1955.7 (51.4)
Dig success	− 0.556 (− 1.206, 0.128)	− 0.950 (− 1.479, − 0.426)	0.759 (0.350, 1.188)	0.475 (0.080, 0.896)	–	–	0.641 (0.272, 1.304)	0.267	889.8 (27.2)
Hunting events	− 2.424 (− 3.093, − 1.465)	0.181 (− 0.310, 0.649)	− 0.554 (− 0.888, − 0.229)	− 0.209 (− 0.569, 0.152)	–	–	0.917 (0.390, 1.953)	0.498	754.2 (39.0)
Hunting success	0.567 (− 0.240, 1.442)	− 1.788 (− 2.715, − 0.930)	− 0.196 (− 0.770, 0.372)	0.462 (− 0.201, 1.120)	–	–	0.306 (0.108, 1.120)	0.323	229.1 (19.4)

Events were analysed using negative binomial model with logarithmic link. Success was analysed using a binomial model with a logit link. The loo information criterion was used to rank the models. The 95% credible interval of the parameter values is shown in parenthesis. SD year shows the random effect of year on the intercept. BP is the Bayesian probability, and Loo is the information criteria and associated standard error in parenthesis

and 0.07 respectively (Table 1). Increasing temperature had a negative effect on the frequency of digs by both species, − 0.37 and − 0.64 respectively. Note that the positive interaction parameter (0.27) for red foxes had a wide credible 95% interval including zero effect. Hunting events occurred at a similar rate for both species, 0.11 and 0.09 hunting events per kilometre for red foxes and pine martens respectively (Fig. 2b). Snow depth and temperature reduced the number of hunting events, − 0.55 and − 0.21 respectively. Not that the 95% credible interval for temperature includes zero effect.

Pine martens were more successful than red foxes in both digs and hunting (Fig. 2c, d). Pine martens were successful in 0.39 of the dig events, whereas the corresponding value for red foxes was 0.18. The success of digs was positively affected by both snow depth and temperature with parameter values of 0.76 and 0.48 respectively. The difference in successful hunting attempts was large, 0.64 vs. 0.23 successful attempts for pine martens and red foxes respectively. The parameter value was − 0.20 for snow depth and 0.46 for temperature, but the credible interval included zero effect in both cases.

Red fox successful digs (n = 261) prey items contained voles (37%), ungulate remains (26%) and mountain hares (11%), whereas pine marten successful digs (n = 77) prey items contained eggs (48%), small birds (22%) and voles (21%) (Table 2). Prey proportion in successful hunting also showed differences between red foxes (n = 54) and pine martens (n = 17). Voles (48%) and mountain hare (22%) dominated red fox successful hunting events, whereas pine marten hunts contained principally small birds (54%), although the sample size was low. The contingency tables of both digs and hunting showed a significant difference between red fox and pine marten (Fisher's exact test, $P < 0.001$).

The pooled number of all vole catches in different years showed a peak in 1977 and 1978 but was lower in the other years of the study (Fig. 3a). More captures of voles were registered at shallow snow depths, and 23 of 26 occasions when red foxes captured voles by pounces occurred when snow depth was below 25 cm. Pine martens were never registered to catch voles on snow or by pouncing through the snow as red foxes. Red foxes showed a wider niche breadth than pine martens, that was wider for digs than for hunting events. Niche overlap between red foxes and pine martens was low for both digs (0.14) and hunting (0.11) events.

Discussion

Our results suggest several differences in winter foraging strategies between red foxes and pine martens, when

Table 2 The proportion of different prey and remains identified from successful digs and hunting events of red fox and pine marten tracked in northern Sweden during winter

Activity	Species	Vole	Hare	Small birds	Ungulate	Grouse	Egg	Other	Niche breadth	Niche overlap
Digging	Red fox (261)	37%	11%	8%	26%	–	8%	8%	0.54	0.14
	Pine marten (77)	21%	–	22%	1%	–	48%	8%	0.34	
Hunting	Red fox (54)	48%	22%	6%	–	20%	–	6%	0.34	0.11
	Pine marten (17)	–	24%	59%	–	12%	–	6%	0.23	

Values are presented as proportion of total number of successful events for each species. The total number is given in parenthesis. Pianka's niche breadth and overlap was calculated according to Krebs (1999)

prey availability is at its lowest and potential competition for food is high. As shown earlier by Storch et al. (1990), pine martens almost exclusively used forested habitat, whereas the red foxes can be found in all types of habitats.

Several studies have shown the importance of scavenging and use of cached food for both pine martens and red foxes. In Norway, Lund (1962) found 0.56 digs km^{-1} by red foxes similar to this study, whereas Halpin and Bissonette (1988) found on average 1.8 digs per kilometre in eastern Maine, USA. In southern Norway, red foxes dug for ungulate carrion 0.35 times per kilometre (Needham et al. 2014). In this study, digs resulted in finding food more often than at hunting attempts, and both species would on average find food from digs 3 out of 4 days. Compared to red foxes, digs appeared less opportunistic by pine martens because of fewer digs but with higher success. We lack estimates of the probability to miss an attempt to dig or kill a prey, but we do not believe our estimates of time between kills and digs to be significantly over-estimated.

Pine martens were about three times more successful in chasing and killing prey compared to red foxes, although hunting events were only recorded about once every 10 km in both species. Red foxes are larger than pine martens, and it is possible that a smaller size is advantageous to approach potential prey undetected. Using the average distance between rest sites to estimate time between kills resulted in about 3 days for pine martens but more than 6 days for red foxes. Similar to our results, Jędrzejewski et al. (1993) found that pine martens were successful in 65% of hunting attempts on small rodents. Other studies on hunting success of red foxes in winter are unfortunately not available.

Niche breadth of red foxes was higher for digs (0.54) than hunting (0.34), and similar to other studies: 0.36–0.6 (Kauhala et al. 1998; Brangi 1995; Cagnacci et al. 2003). Low values (0.03–0.16) have been reported in two studies (Lanszki et al. 2006; Lanszki et al. 2007), where the diet was dominated by small mammals. Niche breadths can also vary greatly among seasons and years in the same area (Murdoch et al. 2010; Sidorovich et al. 2010), supporting an opportunistic feeding. We did not observe tracks of red foxes killing pine martens or smaller mustelids as has been reported earlier (Lindstrom et al. 1995; Dell'Arte et al. 2007). In our study, pine martens had lower niche breadths in digs and hunting compared to red foxes, and previous studies have shown a wide range of niche breadths, 0.2–0.7 (Jędrzejewski et al. 1993; Helldin 2000b). The low overlap could indicate a strategy by pine martens to avoid foraging competition with red foxes. Voles are an important food source for both red foxes (Englund 1970) and pine martens

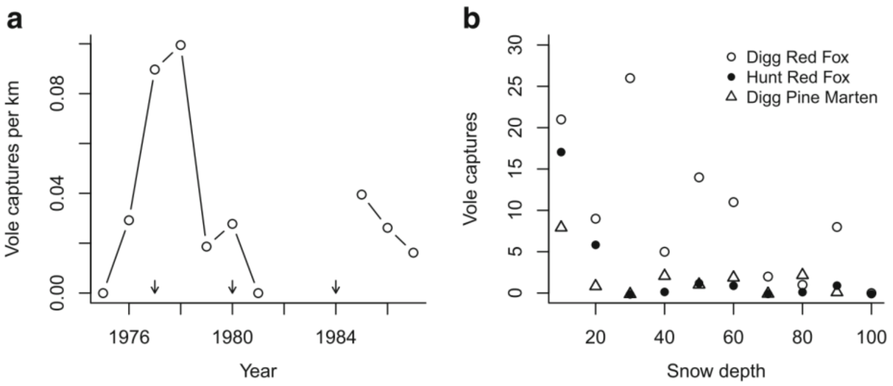

Fig. 3 **a** Pooled vole captures per kilometre for red foxes and pine martens during different years of the study. The *arrows* indicate the peaks of the vole cycle. **b** The sum of vole captures by red fox (digs and hunting) and pine marten (digs) at different snow depth intervals (5–15, 15–25, 25–35 cm, etc.)

(Pulliainen and Ollinmaki 1996; Helldin 1999), although the latter author suggested that pine martens were less affected than red foxes by the variation in vole abundance probably because pine martens prey less on voles in winter.

The suggestion that the common behaviour of caching eggs (Hoglund 1960; Storch et al. 1990) is an important alternative resource in winter for pine martens is in agreement with our findings. In an unpublished pilot study, one of the authors cached frozen chicken eggs at 16 points in 1 × 1 km grid with camera traps in central Norway. The eggs were hidden just under the topsoil when temperature was constantly below 0°, about a week before the ground was snow-covered. Throughout the winter, all cached eggs were found and removed. At 15 points, the eggs were removed by pine martens and one by wolverine. Red foxes were only observed investigating the dig sites after the eggs had been removed. Further south, where winters are fairly mild and short, the food overlap between pine marten and red fox was substantially larger than in this study (Sidorovich et al. 2000; Sidorovich et al. 2010). In these studies, both red foxes and pine martens were found to use a wide range of food items in winter, for example, fruits and beetles. We expect both species to have a different foraging behaviour in our study area during summer and likely show a larger overlap. The difference in foraging efficiency between the two could then be insignificant or even reversed.

Increasing snow depth reduced the number of hunting attempts and their probability of success for both species. Snow depth affected the relative high frequency of dig events for red foxes negatively but did not affect pine martens. Snow conditions are important for the consumption of voles by pine martens (Storch et al. 1990) and red foxes (Lindstrom and Hornfeldt 1994) and probably explain why only the first of the three vole peaks was revealed in the amount of voles captured in different years. Red foxes pounced through the snow to capture voles up to about 25 cm, but the negative effect of snow depth on digs for voles was less pronounced. The biomass of voles in the stomachs of red foxes decreased with snow depth (Lindstrom and Hornfeldt 1994), and they found a substantially lower vole biomass below 70 cm of snow. The proportion of birds in the diet of pine martens in autumn/winter has been found to increase with latitude (Jędrzejewski et al. 1993), and we propose that birds become important for pine martens as snow depth increases and impedes the killing of voles. Unlike red foxes, pine marten can capture prey in trees. Several woodpeckers (*Dendrocopos major*) were caught in trees, but we only found one case of a killed red squirrel, probably due to the lack of suitable red squirrel habitat as old spruce stands (Andren and Delin 1994).

Small birds and cached eggs were common food of pine marten, a likely competitive advantage in relation to red fox in undisturbed conifer forests at northern latitudes in winter. Pine martens were efficient in killing prey and finding food under the snow. It seems that the smaller size of pine martens compared to red foxes is an advantage that makes it possible to catch prey in trees and search for voles under stones and stumps. We speculate that pine martens prefer to cache eggs from capercaillie and black grouse nests to use the subsequent winter; these eggs are larger and more abundant compared to eggs of other birds in the boreal conifer forest. The declining populations grouse (Jahren et al. 2016) would then likely affect pine martens more than red foxes. In addition, ongoing human land use probably favours red foxes. Clear-cutting practices reduce the preferred habitat for pine marten but increase the grassy habitat preferred by the field vole (*Microtus agrestis*), which is a common prey for red foxes (Lindstrom 1992; Dell'Arte et al. 2007). Sidorovich et al. (2010) showed that red fox consumption of field vole increased after clear-cutting but less so for pine martens. Large populations of moose regulated through hunting provide entrails at kill sites, and sometimes whole carcasses of moose and domestic reindeer (Henden et al. 2010; Gomo et al. 2017), that will support the scavenging red foxes.

Long winters and deep snow probably limit red foxes more than pine martens that are more adapted to soft dry snow and more easily move on the snow surface compared to red foxes. One pine marten used the soft snow to approach a capercaillie male by moving under the snow the last few meters. The ongoing climate change has already resulted in warmer and more humid winters with less snow. This will further benefit red foxes and increase their importance in the northern boreal forest ecosystem at the expense of pine marten. However, the long-term effects of climate change is difficult to predict because the species composition of the ecosystem will gradually change and individual species will adapt at different speeds forming new biotic communities (Pecl et al. 2017).

Acknowledgements We are grateful to Erik Engren for organizing the field work and selecting trappers for the tracking. The field work was financed by the National Swedish Environment Protection Board and the Swedish Hunter's Association, with permission to work on the islands by Svenska Cellulosa AB. Additional support was provided by Inland Norway University of Applied Sciences. We thank two anonymous reviewers for many helpful suggestions

Appendix 1.

a) Model code in jags for running negative binomial regression with year as random intercept. Log link was used and the logged values for kilometre were added as an offset. Code shows the full model with interaction.

```
model
{
  # Priors
  alpha1 ~ dnorm(0, 0.001)
  beta1 ~ dnorm(0, 0.001)
  beta2 ~ dnorm(0, 0.001)
  beta3 ~ dnorm(0, 0.001)
  beta12 ~ dnorm(0, 0.001)
  beta13 ~ dnorm(0, 0.001)
  r ~ dunif(0, 50)

  for (y in 1:Nyear){ a[y]~dnorm(0, tau.year) }
  tau.year<-1/(sigma.year*sigma.year)
  sigma.year ~dunif(0,18)

#Likliehood
   for (y in 1:Nyear){
    for (i in 1:n[y]) {

      D[i,y] ~ dnegbin(p[i,y], r)
      log(mu[i,y]) <- a[y]+logA[i,y]+alpha1 +
beta1*x1[i,y]+beta2*x2[i,y]+beta3*x3[i,y]+beta12*x1[i,y]*x2[i,y]+beta
13*x1[i,y]*x3[i,y]

    # Transforms mu into p,
    p[i,y] <- r/(r + mu[i,y])

# Bayesian p-value and likelihood to loo
    ExpY[i,y] <- mu[i,y]
    E[i,y]    <- pow((D[i,y] - ExpY[i,y]),2)
    Y2[i,y] ~ dnegbin(p[i,y], r)
    E2[i,y]    <- pow((Y2[i,y] - ExpY[i,y]),2)
    loglik[i,y]<-logdensity.negbin(D[i,y],p[i,y],r)
    }
       fit1[y]<-sum(E[1:n[y],y])
       fit1.new[y]<-sum(E2[1:n[y],y])
     }
      # Add up discrepancy measures
      fit <- sum(fit1[1:10])
      fit.new <- sum(fit1.new[1:10])
}
```

b) Model code in jags for running logistic regression with logit link, and year as a random intercept. Code shows the full model with interaction.

```
model {
# Priors
  alpha1 ~ dnorm(0,0.001)
  beta1 ~ dnorm(0,0.001)
  beta2 ~ dnorm(0,0.001)
  beta3 ~ dnorm(0,0.001)
  beta12 ~ dnorm(0,0.001)
  beta13 ~ dnorm(0,0.001)

for (y in 1:Nyear){ a[y]~dnorm(0, tau.year) }
tau.year<-1/(sigma.year*sigma.year)
sigma.year ~dunif(0,18)

# Likelihood
for (y in 1:Nyear){
  for (i in 1:n[y]) {
    C[i,y] ~ dbin(p[i,y], N[i,y])
logit(p[i,y]) <-
alpha1+a[y]+beta1*x1[i,y]+beta2*x2[i,y]+beta3*x3[i,y]+
beta13*x3[i,y]*x1[i,y] + beta12*x2[i,y]*x1[i,y]+ind[i,y]

#  Bayesian p-value and likelihood to loo
   pred[i,y]<-N[i,y]*p[i,y]
   Presi[i,y] <- (C[i,y]-pred[i,y]) / sqrt(N[i,y]*p[i,y]*(1-p[i,y]))
   C.new[i,y] ~ dbin(p[i,y], N[i,y])
   Presi.new[i,y] <- (C.new[i,y]-pred[i,y]) / sqrt(N[i,y]*p[i,y]*(1-
p[i,y]))
   loglik[i,y] <- logdensity.bin(C[i,y], p[i,y], N[i,y])
 }
 fit1[y]<-sum(Presi[1:n[y],y])
 fit1.new[y]<-sum(Presi.new[1:n[y],y])
}
 fit <- sum(fit1[1:10])
 fit.new <- sum(fit1.new[1:10])
}
```

References

Andren H, Delin A (1994) Habitat selection in the Eurasian red squirrel, Sciurus vulgaris, in relation to forest fragmentation. Oikos 70:43

Bartoń KA, Zalewski A (2007) Winter severity limits red fox populations in Eurasia. Global Ecol Biogeography 16:281–289

Bassi E, Donaggio E, Marcon A, Scandura M, Appolonio M (2012) Trophic niche overlap and wild ungulate consumption by red fox and wolf in a mountain area in Italy. Mamm Biol 77:369–376

Brangi A (1995) Seasonal changes of trophic niche overlap in the stone marten (Martes foina) and the red fox (Vulpes vulpes) in a mountainous area of the Northern Apennines (N-Italy). Hystrix 7:1–2

Brzeziński M, Rodak Ł, Zalewski A (2014) “Reversed” intraguild predation: red fox cubs killed by pine marten. Acta Theriol 59:473–477

Cade BS (2015) Model averaging and muddled multimodel inferences. Ecology 96:2370–2382

Cagnacci F, Lovari S, Meriggi A (2003) Carrion dependence and food habits of the red fox in an Alpine area. Italian Journal of Zoology 70: 31–38

Carvalho JC, Gomes P (2001) Food habits and trophic niche overlap of the red fox, European wild cat and common genet in the Peneda-Gerês National Park. Galemys 13:39–48

Dell’Arte GL, Laaksonen T, Norrdahl K, Korppimaki E (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecologia 31:276–281

Elmhagen B, Tannerfeldt M (2002) Food-niche overlap between arctic and red foxes. Can J Zool 80:1274–1285

Elveland J (1976) Myrar på Storön vid norrbottenskusten. Wahlenbergia, Scripta Botanica Umensia (in Swedish)

Englund J (1965) Studies on food ecology of the red fox (Vulpes v.) in Sweden. Swedish Wildlife 3:377–485

Englund J (1970) Some aspects of reproduction and mortality rates in Swedish foxes (Vulpes vulpes), 1961-63 and 1966-69. Swedish Wildlife 8:1–78

Gelman A, Carlin JB, Stern HS et al (2013) Bayesian data analysis. CRC Press, Third Edition

Gomo G, Mattisson J, Hagen BR, Moa PF, Willebrand T (2017) Scavenging on a pulsed resource: quality matters for corvids but density for mammals. BMC Ecol 17:22

Halpin MA, Bissonette JA (1988) Influence of snow depth on prey availability and habitat use by red fox. Can J Zool 66:587–592

Hanski I, Hansson L, Henttonen H (1991) Specialist predators, generalist predators, and the microtine rodent cycle. J Anim Ecol 60:353–367

Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:1:19

Helldin J-O (1999) Diet, body condition, and reproduction of Eurasian pine Martens Martes Martes during cycles in microtine density. Ecography 22:324–336

Helldin J (2000a) Population trends and harvest management of pine marten Martes martes in Scandinavia. Wildl Biol 6:111–120

Helldin J-O (2000b) Seasonal diet of pine marten Martes martes in southern boreal Sweden. Acta Theriol 45:409–420

Henden J-A, Ims RA, Yoccoz NG et al (2010) Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. Oikos 119:27–34

Hersteinsson P, Angerbjorn A, Frafjord K, Kaikusalo A (2003) The arctic fox in fennoscandia and Iceland: management problems. Biol Conserv 49:67–81

Hoglund NH (1960) Studies on the winter diet of pine marten (Martes martes L.) in Jämtland province. Sweden 14:319–337 (in Swedish)

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theor Popul Biol 12:197–229

Hooten MB, Hobbs NT (2014) A guide to Bayesian model selection for ecologists. Princeton University Press

Hornfeldt B, Löfgren O, Carlsson BG (1986) Cycles in voles and small game in relation to variations in plant production indices in northern Sweden. Oecologia 68:496–502

Jahren T, Storaas T, Willebrand T (2016) Declining reproductive output in capercaillie and black grouse–16 countries and 80 years. Anim Biol 66:363–400

Jędrzejewsk W, Jędrzejewsk B (1992) Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Biatowieza National Park, Poland. Ecography 15:212–220

Jędrzejewski W, Zalewski A, Jędrzejewska B (1993) Foraging by pine marten Martes martes in telation to food resources in Białowieża National Park, Poland. Acta Theriol 38:405–426

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

Krebs CJ (1999) Ecological methodology, 2nd edn Benjamin/Cummings

Kurki S, Nikula A, Helle P, Lindén H (1998) Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. J Anim Ecol 67:874–886

Lanszki J, Heltai M, Szabó L (2006) Feeding habits and trophic niche overlap between sympatric golden jackal (Canis aureus) and red fox (Vulpes vulpes) in the Pannonian ecoregion (Hungary). Can J Zool 84:1647–1656

Lanszki J, Zalewski A, Horvath G (2007) Comparison of red fox Vulpes vulpes and pine marten Martes martes food habits in a deciduous forest in Hungary. Wildl Biol 13:258–271

Lindstrom ER (1992) Diet and demographics of the red fox (*Vulpes vulpes*) in relation to population density — the sarcoptic mange event in Scandinavia. In: Wildlife 2001: Populations. Springer Netherlands, Dordrecht, pp 922–931

Lindström E, Angelstam P, Widén P, Andrén H (1987) Do predators synchronize vole and grouse fluctuations?: An Experiment. Oikos 48:121

Lindstrom ER, Brainerd SM, Helldin J-O, Overskaug K (1995) Pine marten—red fox interactions: a case of intraguild predation? Ann Zool Fennici 32:123–130

Lindstrom ER, Hornfeldt B (1994) Vole cycles, snow depth and fox predation. Oikos 70:156–160

Lund MK (1962) The red fox in Norway II:: the feeding habits of the red fox in Norway. Meddelelser fra Statens viltundersøkelser. Oslo: Statens viltundersøkelser 2 ser nr 12. 79 pp.

Marcstrom V, Hoglund N, Krebs C (1990) Periodic fluctuations in small mammals at Boda, Sweden from 1961 to 1988. J Anim Ecol 59: 753–761

Marcstrom V, Kenward R, Engren E (1988a) The impact of predation on boreal tetraonids during vole cycles—an experimental study. J Anim Ecol 57:859–872

Marcstrom V, Keith LB, Engren E, Cary RJ (1988b) Demographic responses of arctic hares (Lepus timidus) to experimental reductions of red foxes (Vulpes vulpes) and martens (Martes martes). Can J Zool 67:658–668

Mitchell BD, Banks PB (2005) Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. Austral Ecology 30:581–591

Murdoch JD, Munkhzul T, Buyandelger S, Reading RP, Sillero-Zubiri C (2010) Seasonal food habits of corsac and red foxes in Mongolia and the potential for competition. Mamm Biol 75:36–44

Needham R, Odden M, Lundstadsveen SK, Wegge P (2014) Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. Acta Theriol 59: 391–398

Palomares F, Caro TM, Holt RD (1999) Interspecific killing among mammalian carnivores. Am Nat 153:492–508

Pecl GT, Araujo MB, Bell J, Blanchard J, Bonebrake TC, Chen I, Clark TD, Colwell RK, Danielsen F, Evengard B, Robinson S et al (2017)

Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355:1–9

Pianka ER (1981) Competition and niche theory. Theoretical ecology principles and applications 8:67–196

Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling http://www.ci.tuwien.ac.at/Conferences/DSC-2003/. Accessed 15 April 2017

Pulliainen E, Ollinmaki P (1996) A long-term study of the winter food niche of the pine marten Martes martes in northern boreal Finland. Acta Theriol 41:337–352

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for statistical computing, Vienna. (https://www.R-project.org)

Selas V, Vik J (2006) Possible impact of snow depth and ungulate carcasses on red fox (Vulpes vulpes) populations in Norway, 1897-1976. J Zool 269:299–308

Sidorovich VE, Polozov AG, Lauzhel GO, Krasko DA (2000) Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog Nyctereutes procyonoides on native predators in northern Belarus. Zeitschrift fur Saeugetierkunde 65:271–285

Sidorovich VE, Sidorovich AA, Krasko DA (2010) Effect of felling on red fox (Vulpes vulpes) and pine marten (Martes martes) diets in transitional mixed forest in Belarus. Mamm Biol 75:399–411

Small RJ, Marcström Y, Willebrand T (1993) Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. Ecography 16:360–364

Storch I, Lindström E, de Jounge J (1990) Diet and habitat selection of the pine marten in relation to competition with the red fox. Acta Theriol 35:311–320

Su Y-S, Yajima M R2jags: Using R to Run "JAGS." R package version 0.5–7. In: cran.r-project.org. https://CRAN.R-project.org/package=R2jags. Last accessed 15 April 2017

Willebrand T (1988) Demography and ecology of a black grouse (*Tetrao tetrix* L.) population. PhD thesis, Uppsala University, Sweden, p 148

Vehtari A, Gelman A, Gabry J (2016) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat Comput 26:744–772

Paper IV

The impact of human land use and landscape productivity on the abundance and dynamics of red fox in southeastern Norway

Torfinn Jahren[1], Morten Odden[1], John D. C. Linnell[2], Manuela Panzacchi[2]

[1]Inland Norway University of Applied Sciences

Faculty of Applied Ecology and Agricultural Sciences

[2]Norwegian Institute for Nature Research

Abstract

In the boreal forest, the red fox (*Vulpes vulpes*) is a key species due to its many strong food web linkages and its exploitation of niches that form in the wake of human activities. Recent altitudinal range expansion and a perceived population increase have become topics of concern in Scandinavia, primarily due to the potential impacts of red foxes on both prey and competitor species. However, despite it being a common species there is still surprisingly little knowledge about the temporal and spatial characteristics of its population dynamics. In this study, we synthesized 12 years of snow-track transect data covering a 27.000 km^2 study area to identify factors associated with red fox distribution and population dynamics. Using Bayesian hierarchical regression models, we evaluated the relationships of landscape productivity and climate gradients as well as anthropogenic subsidies with an index of red fox population size and growth rates. We found that landscapes with high human settlement density and large amounts of gut piles from moose (*Alces alces*) hunting were associated with higher red fox abundances. Population dynamics were characterized by direct density dependent growth, and the structure of density dependence was best explained by the amount of agricultural land in the landscape. Population equilibrium levels increased and populations were more stable in areas with a higher presence of agricultural lands, whereas density dependent population growth was more prominent in areas of low agricultural presence. We conclude that human land-use is a dominant driver of red fox population dynamics in the boreal forest, and we suggest that reducing anthropogenic subsidization preceding and during winter may reduce predation pressure on species inhabiting the agriculture-forest matrix in the southern boreal forest.

Introduction

Human land use has dramatically altered the structure and dynamics of natural habitats in biomes across the world (Walther *et al.* 2002; Foley 2005). Effects of human land use on species distribution and abundance vary in their complexity and direction. Direct effects of human influence may be inevitable outcomes of habitat change (Andren 1994) and resource management (e.g. Milner *et al.* 2006), or indirect consequences mediated through changes in community structure (e.g. Prugh *et al.* 2009). A matter of concern is an observed large-scale and long-term increase in the number and distribution of generalist predators, for example the red fox (*Vulpes vulpes*) in Europe (e.g. Vos 1995; Prugh *et al.* 2009; Selås *et al.* 2011; Baines, Aebischer & Macleod 2016). Several ultimate explanations for the increase in generalist predator populations have been discussed, and in the context of our paper, findings about the potential role of land use practices are especially relevant (Christiansen 1979; Henttonen 1989; Selås & Vik 2006). Additionally, the role of climate change and mesopredator release have received attention (e.g. Bartoń & Zalewski 2007; Prugh *et al.* 2009; Elmhagen *et al.* 2015). These are complementary hypotheses and they have been used to explain increased carrying capacity of red fox populations due to increased resource availability or less intra-guild predation.

Opportunistic and facultative species like the red fox may successfully exploit niches that form in the wake of human activities, and this may subsequently have detrimental effects on competitor- and prey species (Hersteinsson & MacDonald 1992; Lindstrom *et al.* 1994; Smedshaug *et al.* 1999; Kämmerle *et al.* 2017). Diverse and strong food-web linkages of red foxes in the boreal forests have been demonstrated via both experimental and correlative predation studies on roe deer (*Capreolus capreolus*) and several other prey species (Marcström, Kenward & Engren 1988; Frafjord, Becker & Angerbjörn 1989; Lindstrom *et al.* 1994; Kauhala, Helle & Helle 2000; Panzacchi *et al.* 2009).

The red fox is a very successful habitat generalist, and its distribution range is the largest among carnivores (Hersteinsson & MacDonald 1992). Locally, however, red foxes can turn into specialists and select mosaic landscapes (Pulliainen 1981; Kurki *et al.* 1998; Güthlin, Storch & Küchenhoff 2013) with relatively high prey densities (Cavallini & Lovari 1991; Panzacchi *et al.* 2008a; Henden, Stien & Bårdsen 2014; Carricondo-Sanchez *et al.* 2016) and such landscapes are often modified by humans. Human settlements will primarily provide red foxes with increased scavenging opportunities (McKinney 2002; Vuorisalo *et al.* 2014). Secondary (i.e. indirect) effects from anthropogenic land use may be modulated via forestry and agricultural practices as they create habitats for preferred prey (i.e. voles) (Christiansen 1979; Henttonen 1989; Panzacchi *et al.* 2010; Güthlin, Storch & Küchenhoff 2013; Bogdziewicz & Zwolak 2013), and increase predation success by increasing the amount of habitat edges (Gorini *et al.* 2012 and references therein). The secondary effects of human land use distribute uniformly throughout the year and are therefore likely to increase overall carrying capacity. Additionally, a marked increase in ungulate abundances in Scandinavia during the last decades has increased the availability of gut piles form big game hunting during autumn hunting season and natural mortality (Loison & Langvatn 1998; Stubsjøen *et al.* 2000; Gomo *et al.* 2017). These are pulsed, but substantial, food resources that increase in abundance particularly preceding and during winter (Halpin & Bissonette 1988; Cagnacci, Lovari & Meriggi 2003; DeVault, Jr & Shivik 2003; Sidorovich, Sidorovich & Izotova 2006; Needham *et al.* 2014; Gomo *et al.* 2017).

Red fox population densities in the boreal forest vary considerably among years according to the multi-annual population cycles of its main prey, microtine voles (Lindström 1982). This pattern is more profound with increasing latitude and altitude (Englund 1980a; Lindén 1988), and the degree of stability in the red fox population probably relates to both the availability of alternative prey in the low phase of the vole cycle as well as density dependent, negative feedback mechanisms from predation on voles (Erlinge, Göransson & Hansson 1983). Such negative feedback mechanisms may result from alternative prey sustaining high red fox population densities that, in turn, increase predation pressure on voles in the crash phase of the cycle.

Studies investigating red fox population performance rarely incorporate spatiotemporal variability and are therefore limited to either temporal or spatial inference. Whereas such studies are often valuable in identifying ecological factors and mechanisms in the dimension under study, they often fail to identify the complexity of spatiotemporal heterogeneity which is essential in understanding population and community dynamics (Thorson *et al.* 2015). We therefore aim to investigate factors potentially involved in the regulation of spatiotemporal variation in red fox abundance and population growth across a gradient of human influence on the landscape. To do this, we contrast potential effects of anthropogenic subsidies and land use to natural productivity gradients on red fox abundance and temporal variability in population growth structure. The bulk of literature on red fox spatial and temporal performance suggests that we can expect red fox population abundance to relate positively to human land use and that human land use should stabilize the variability in population growth. Finally, we discuss potential mechanisms underlying the observed patterns as well as potential consequences of anthropogenic subsidization of generalist predators on the boreal forest ecosystem.

Methods

Study area

This study was conducted in Hedmark County, Norway between 2003 and 2014 (Figure 1). Hedmark (27400 km^2, of which 13000 km^2 is forest) has marked latitudinal productivity gradients. In the south, there are relatively high productivity agricultural lowlands intermixed with large forested areas on low hills. Further north there are deeper valleys, forest ridges and mountains. In the north, agriculture and human settlements are confined to strips along the valley bottoms and the landscape is less productive. Similarly, the continental climate is milder in the south (annual mean temperature 4.76 °C) than in the north (annual mean temperature 1.68 °C) (www.no.climate-data.org) and winter severity (i.e. snow depth and temperature) increases with a latitudinal as well as an altitudinal gradient. Forests are primarily made up of conifers, dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but intermixed with deciduous species such as rowan (*Sorbus aucuparia*), grey alder (*Alnus incana*), aspen (*Populus tremula*), birch (*Betula pubescens* and *B. pendula*) and willow (*Salix caprea*). Municipality-wise, human population densities vary from 0.6 to 86 people km^{-2}, with the lowest densities in the north. Red foxes are common throughout the county and annual hunting bags varied between 2160 and 4170 foxes during the study period (Statistics Norway 2016). Potential predators of the red fox e.g. Eurasian lynx (*Lynx lynx*) (Linnell *et al.* 1998) and golden eagle (*Aquila chrysaetos*) (Tjernberg 1981) occur throughout the county, whereas the grey wolf (*Canis lupus*) population is concentrated in the east and southeast (Odden, Linnell & Andersen 2006; Ordiz *et al.* 2015; Tovmo *et al.* 2016).

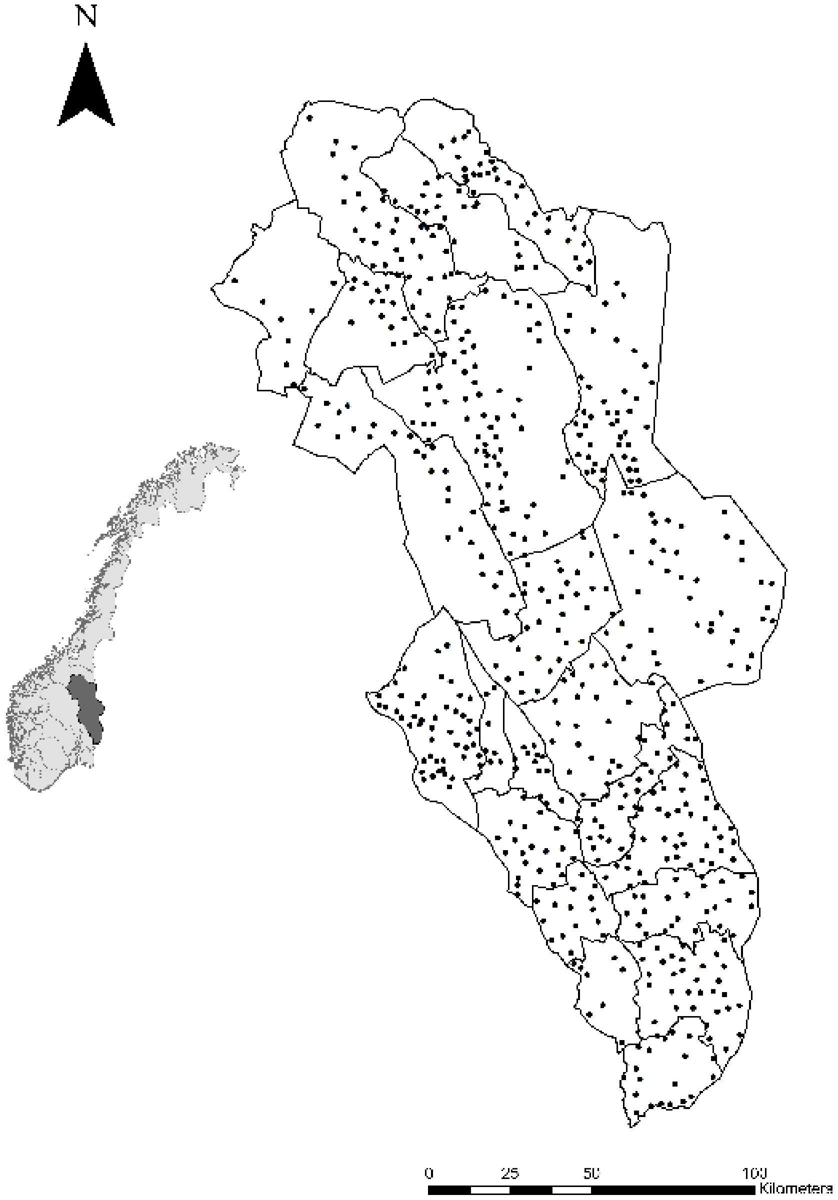

Figure 22 Hedmark County in southeastern Norway with transect centroid points depicted as dots.

Red fox abundance

Snow tracking along 613 predefined transects averaging 2.95 km in length (SD = 0.54) was organized by the Hedmark chapter of the Norwegian Association for Hunters and Anglers. Experienced volunteers conducted the fieldwork under favorable conditions (i.e. from 2 to 5 days after snowfall) in late January or early February each year between 2003 and 2014. The number of surveyed transects varied among years (mean = 391.7), with the highest number in 2006 (n=472) and the lowest in 2014 (n= 268, Table 1). Transect layout was originally designed to monitor Eurasian lynx family groups, and transects were therefore situated below the timberline and across contour lines (Linnell *et al.* 2007). Along each transect, the number of crossing red fox tracks, transect length (km) and days since last snowfall were reported during each transect survey. Transect density within the whole study area varied between 0.98 (2014) and 1.72 (2006) transects per 100 km^2 whereas the density per 100 km^2 forested area varied between 2.06 and 3.63 (Table 1). In total, 21.675 fox crossings were observed along 13.746 km of transect during the 12-year survey. Annual abundance estimates were calculated for each transect. Here, abundance was an index of relative density and was expressed as crossing tracks km^{-1} $24hrs^{-1}$. In total, we obtained abundance estimates for 4700 transect-years. Snow-track surveys may reflect actual density quite well (Thompson *et al.* 1989; Kurki *et al.* 1998), but they cannot distinguish between red fox density and activity. Hence, the transect data better reflect predation pressure by red fox as perceived by prey-species across the landscape (Kurki *et al.* 1998).

Red fox temporal variation

Not all individual transects were complete 12-year time-series because of zero observations or they were not surveyed. The presence of zero-observations constitutes a problem when doing time-series analysis because of e.g. logarithmic transformations and calculation of population growth rates. To amend both zero-observations and years not surveyed, individual transects were pooled into 300 transect-groups based on proximity by using the spatstat and raster libraries in R (Baddeley, Rubak & Turner 2015; Hijmans 2016). These transect-groups then constituted new individual time series for investigations of temporal variation in the red fox population. Consequently, after grouping, transect-groups had longer sequences of monitoring and fewer zero-observations. For zero counts (not to be confused with not surveyed) still remaining after grouping (n=97) we added the smallest observable entity possible (Turchin 2003), which in our case was 1 crossing red fox track. Finally, because red fox populations in the southern boreal forest have previously been described as cyclic with a length of 3-4 years, each time series should cover minimum one potential cycle. We therefore discarded segments of < 4 years of consecutive monitoring and remaining segments were treated as 255 individual, complete time-series with 1781 time-steps of abundance estimates (Figure A 1).

Table 7 Annual number of transects surveyed and transect density

Year	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**
Number of transects	360	434	459	472	367	347
Transects per 100km^{-2} total area	1.31	1.58	1.68	1.72	1.34	1.27
Transects per 100km^{-2} forested area	2.77	3.34	3.53	3.63	2.82	2.67
Year	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**

Number of transects	415	430	403	354	391	268
Transects per 100km^{-2}	1.51	1.57	1.47	1.29	1.43	0.98
Transects per 100km^{-2} forested area	3.19	3.31	3.10	2.72	3.01	2.06

Habitat data

Transects were related to predictor variables via the transect centroid point. These predictors included elevation, latitude, relative settlement density and relative agricultural density (Figure 2). Transect altitude was assessed via a digital terrain model (DTM) from The Norwegian Mapping Authority (The Norwegian Mapping Authority 2017). We expressed latitude as the UTM-north coordinate of the transect centroid point. Land-use maps (N250) (The Norwegian Mapping Authority 2017) were the basis for relative settlement and agricultural density estimates. We transformed houses to a point layer that was subsequently used to predict a planar kernel density map from which we extracted kernel values for each transect centroid point. Kernel bandwidth was estimated by Gaussian approximation (Silverman 1986). For relative density of agricultural land, we calculated the geometrical center of agriculture fields and predicted planar kernel density by using agricultural-field size as z-value. Again, kernel density values were extracted to the transect centroid points.

The only predictor with spatiotemporal variation was moose culled per hectare productive forest. This variable (hereafter "offal") was calculated for each municipality (351 to 3180 km^2 large), as this was the smallest scale from which culling data was available. The annual number of moose culled per municipality was retrieved from Statistics Norway (Skara & Steinset 2016) and Hjorteviltregisteret (Miljødirektoratet & Naturdata 2016), whereas the extent of productive forest was derived from digital land-use maps (N250) (The Norwegian Mapping Authority 2017). Transect-group predictors were the means of the transect predictor values prior to grouping. Development of planar kernel density predictions was done in ArcGIS (ESRI INC 2011).

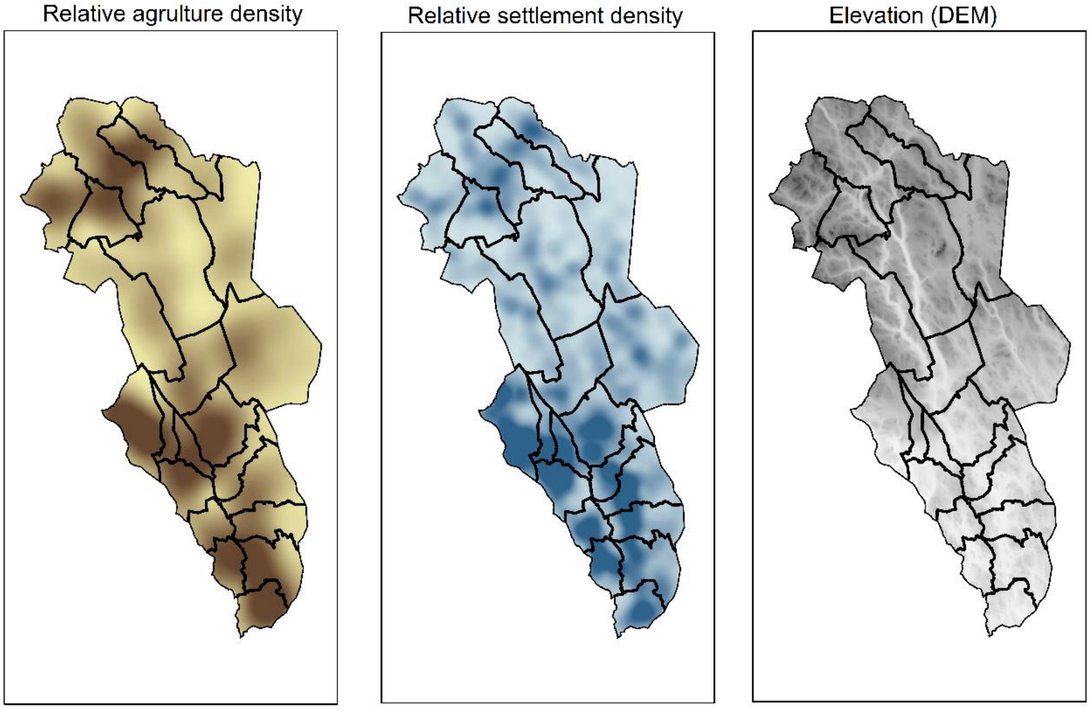

Figure 23 From left to right: Relative density of agricultural land, relative settlement density and the digital elevation model used as predictors. From light to dark color indicate low to high values of the respective parameter.

Statistical analyses

We evaluated environmental and anthropogenic relationships to red fox abundance by modeling red fox abundance (tracks km^{-1} 24hrs^{-1}) as a dependent variable in a hierarchical Bayesian linear model framework via the rethinking library (McElreath 2016) in R (R Core Team 2016). Red fox abundance was formalized as a Gamma-Poisson distribution with a log-link function. The linear predictor was offset with the log of transect length (km) and log of days since last snowfall, and we fitted municipality as a random effect (See appendix for details on model components).

To describe and specify temporal variation in the red fox population we first detrended all time-series with the fitted values from a linear model of the respective time-series. Then, each transect-group with > 10 time-steps (n=58) was checked for cyclicity in the negative feedback processes via the partial rate correlation function (PRCF). The PRCF is quite similar to the partial auto correlation function, but it regresses the instantaneous rate of increase ($r_t = \ln(\frac{N_t}{N_{t-1}}$) on lagged population abundances (Berryman & Turchin 2001). We did not detect any cyclic pattern in the negative feedback processes of population regulation by using Bartlett's criteria of significance. Furthermore, lag 1 from the partial rate correlation function (PRCF[1]) was the dominating order of feedback-delay indicating that direct density dependence was the dominating pattern in growth structure of the red fox population. Henceforth we used the instantaneous rate of increase (*r*) as a dependent variable in the model framework investigating spatiotemporal variation in population growth. These models were formalized as a Gaussian distribution with an identity-link (See appendix for details on model components).

We modeled both abundance and density dependent growth as functions of linear terms. Each model of instantaneous rate of increase included red fox abundance at time t_{-1} as part of an interaction with each predictor. This allowed us to investigate spatial variation in density dependence. Red fox abundance at time t_{-1} however, was formalized as a second order polynomial due to its curvilinear relationship to the instantaneous rate of increase. We fitted 20 and 11 *a priori* models for each dependent variable (abundance and *r* respectively). We specified simple models aiming at obtaining factor-specific information relating red fox abundance and density dependent growth to anthropogenic activity and natural productivity gradients.

Relative -settlement and -agricultural density, as well as elevation and latitude were not paired in the same model due to collinearity ($r > 0.6$). All predictors were scaled to z-scores (x - mean/2SD), and thus, intercepts and interactions were simpler to interpret (Gelman & Su 2016). Markov chain Monte Carlo sampling (MCMC) was specified to run at four chains across 6000 iterations and burn-in was set to 4000 iterations. We detected spatial autocorrelation in our data via the Moran's I test (Moran 1950). Spatial autocorrelation was handled by modelling varying intercepts as a function of squared distances between the random effects (i.e. between municipalities and transect groups for abundance and growth models respectively).

Model evaluation and selection

We visually inspected Markov chains for failure to converge and no convergence issues were detected. All $\hat{R}$ values were between 1 and 1.01. Relative model parsimony was assessed by WAIC (widely applicable information criterion) (Watanabe 2010) based on posterior likelihoods. We followed an information-theoretic approach when evaluating models, and hence, a combination of model weights and relative distance to the top model were criteria of inference. Parameter posterior predictions were averaged across models based on model weights, keeping all other fixed effects constant, and reported parameter predictions henceforth incorporate parameter uncertainty.

Results

Temporal variation in abundance of red fox in the study area varied between 2003 and 2014 with more variation earlier than later in the period (Figure 2).

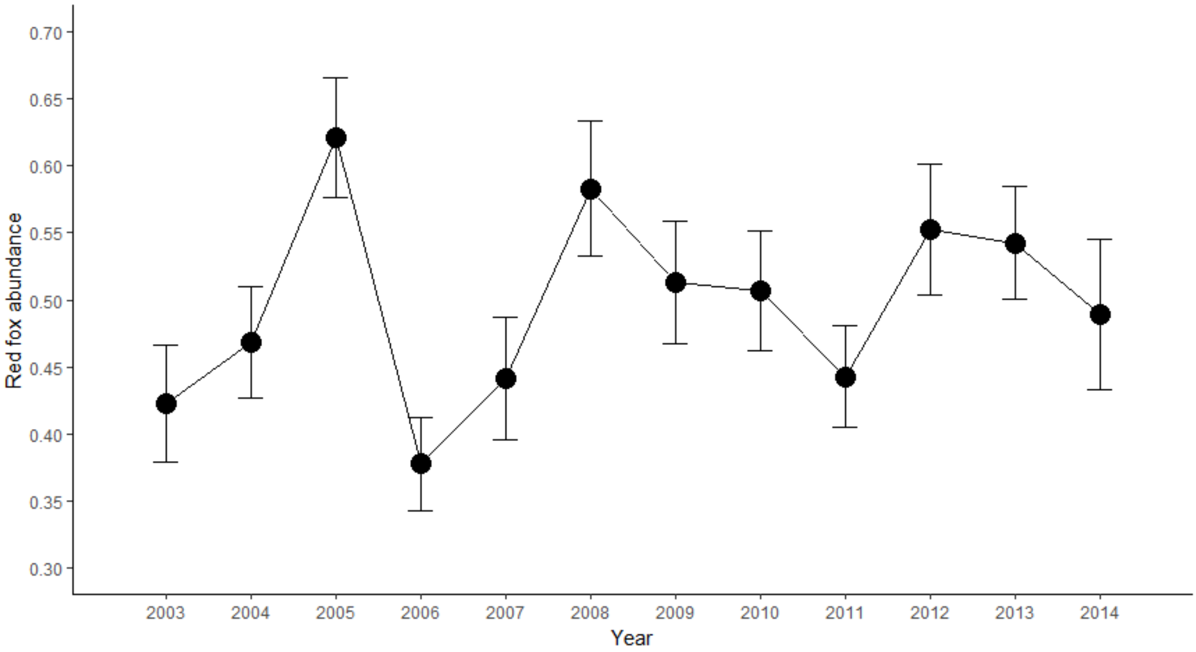

Figure 24 Mean red fox abundance (tracks km^{-1} 24 hrs^{-1}) ± 2SE across transects in the study area (2003-2014)

Evaluation of the abundance models showed that the additive effect of settlement density and offal performed markedly better than any other model ($WAIC_w = 0.82$) (Table A 1). The positive effect of settlement density on red fox abundance was quite strong, whilst the weaker, but positive, effect of offal included a slope of zero (Table A 3). Adding offal to settlements greatly improved the model parsimony as compared to settlements alone (Figure 4).

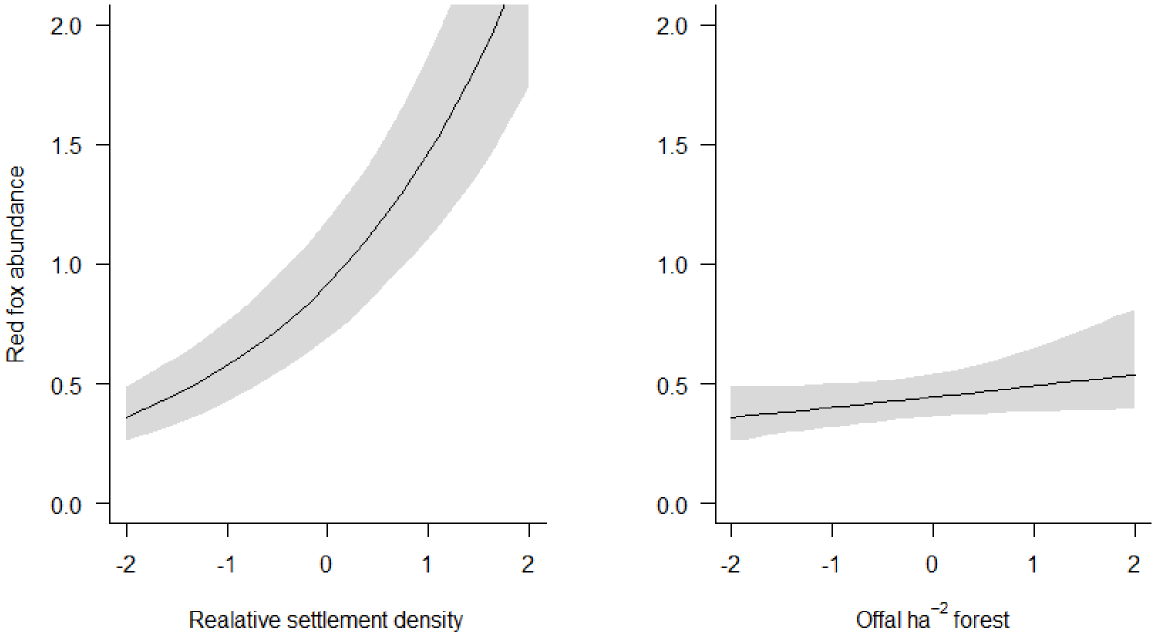

Figure 25 Model weighted predictions of red fox abundance as a function of settlements (left) and offal ha^{-2} productive forest (right) whilst holding the other fixed effect constant. Shaded areas are 95% highest posterior density intervals.

Whereas the mean abundance from transect-groups was generally concentrated around a few hotspots, absolute values of instantaneous rate of increase were more heterogeneously distributed (Figure 5). The first order (i.e. annual) density dependent structure indicated a relatively strong degree of density dependence ($\beta = -1.33$) (Figure 6). Median instantaneous rate of increase was 0.045 (Mean = 0.027, SD = 0.025) and ranged between -3.62 and 3.68 (Figure 7).

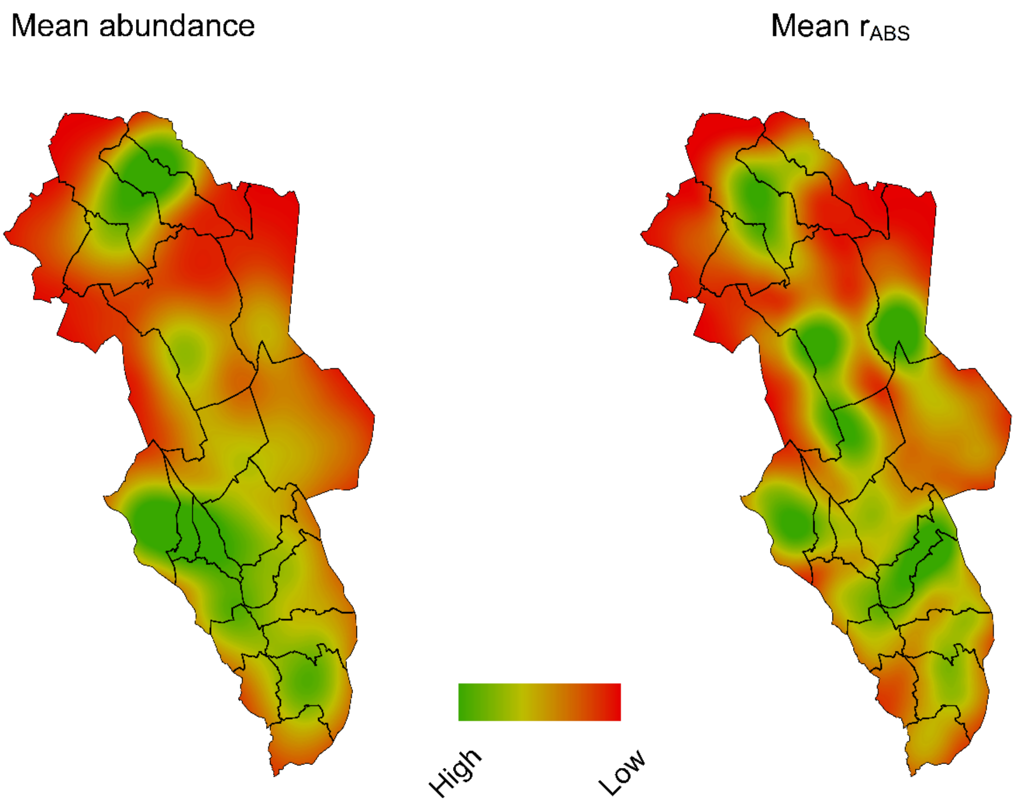

Figure 26 Spatial variation in mean abundance (2003-14) and instantaneous rate of increase (mean of absolute values 2003-14) from the transect-groups in Hedmark county.

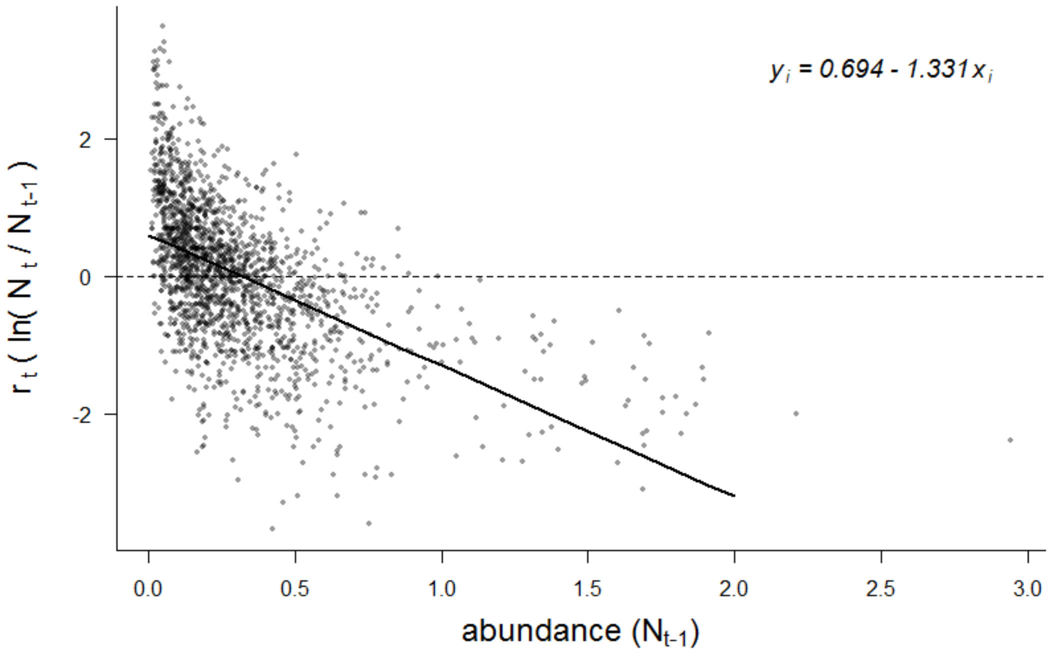

Figure 27 First order density dependent structure ($r_t = f(N_{t-1}) + \epsilon_t$) in the red fox population.

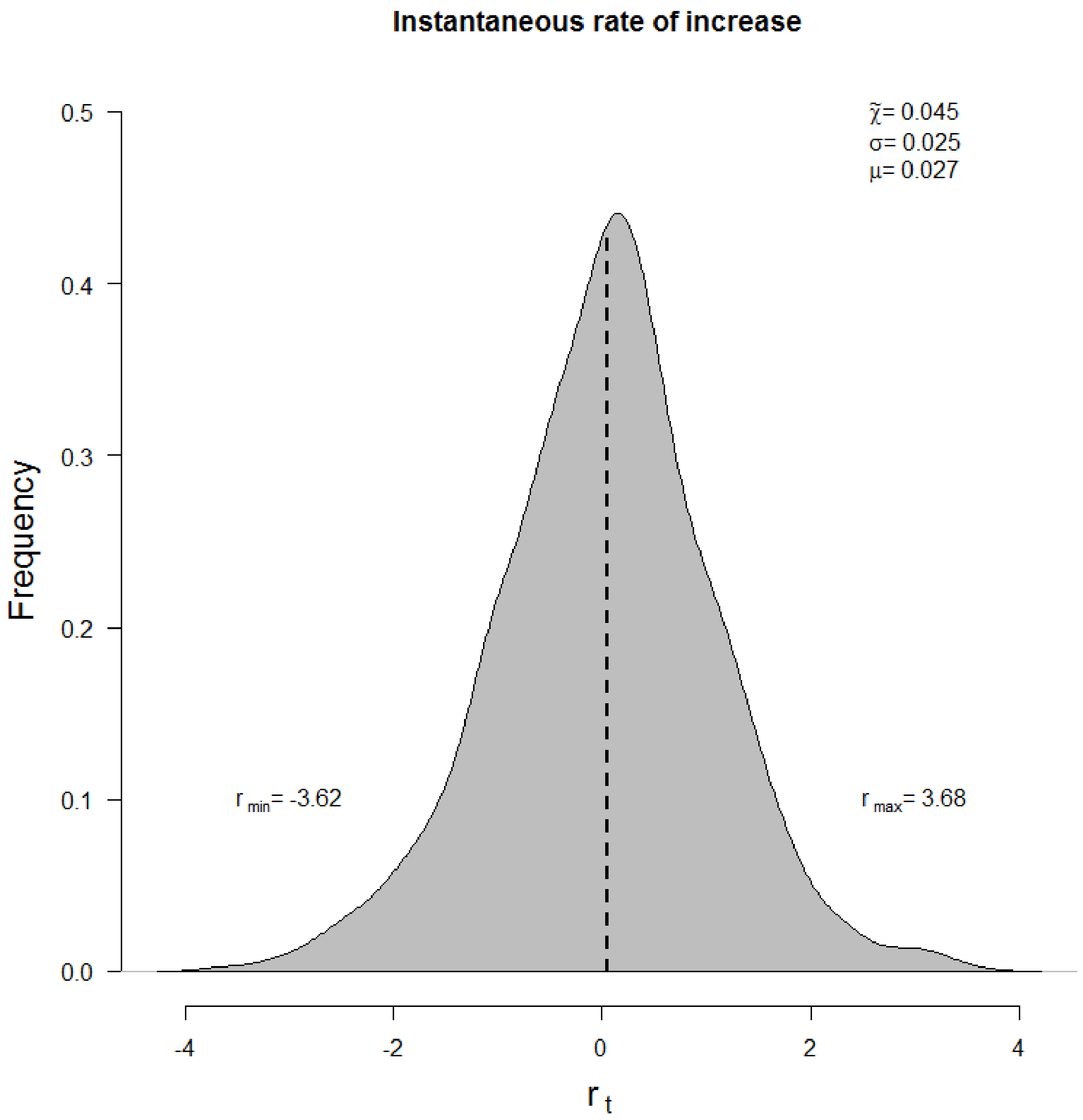

Figure 28 Density plot of instantaneous rate of increase frequencies from the transect groups in Hedmark between 2003 and 2014. Vertical dotted line depicts the median around which values were standardised. Upper right values refer to median, standard deviation and mean values. Minimum and maximum observed rate of increase are referred to as r_{min} and r_{max}.

The best performing model of spatially explicit, first order density dependent growth was the interaction between the red fox abundance and relative density of agricultural land in the landscape (Table A 2; Table A 3). The density dependent structure in the red fox population was asymmetric throughout the agricultural landscape indicating higher variability in abundance in areas with little agricultural land. Landscapes with more agriculture sustained a slightly higher equilibrium and increasingly stable abundances of red fox, as the equilibrium point (i.e. $r_t = 0$) increased along the agricultural gradient. (Figure 8).

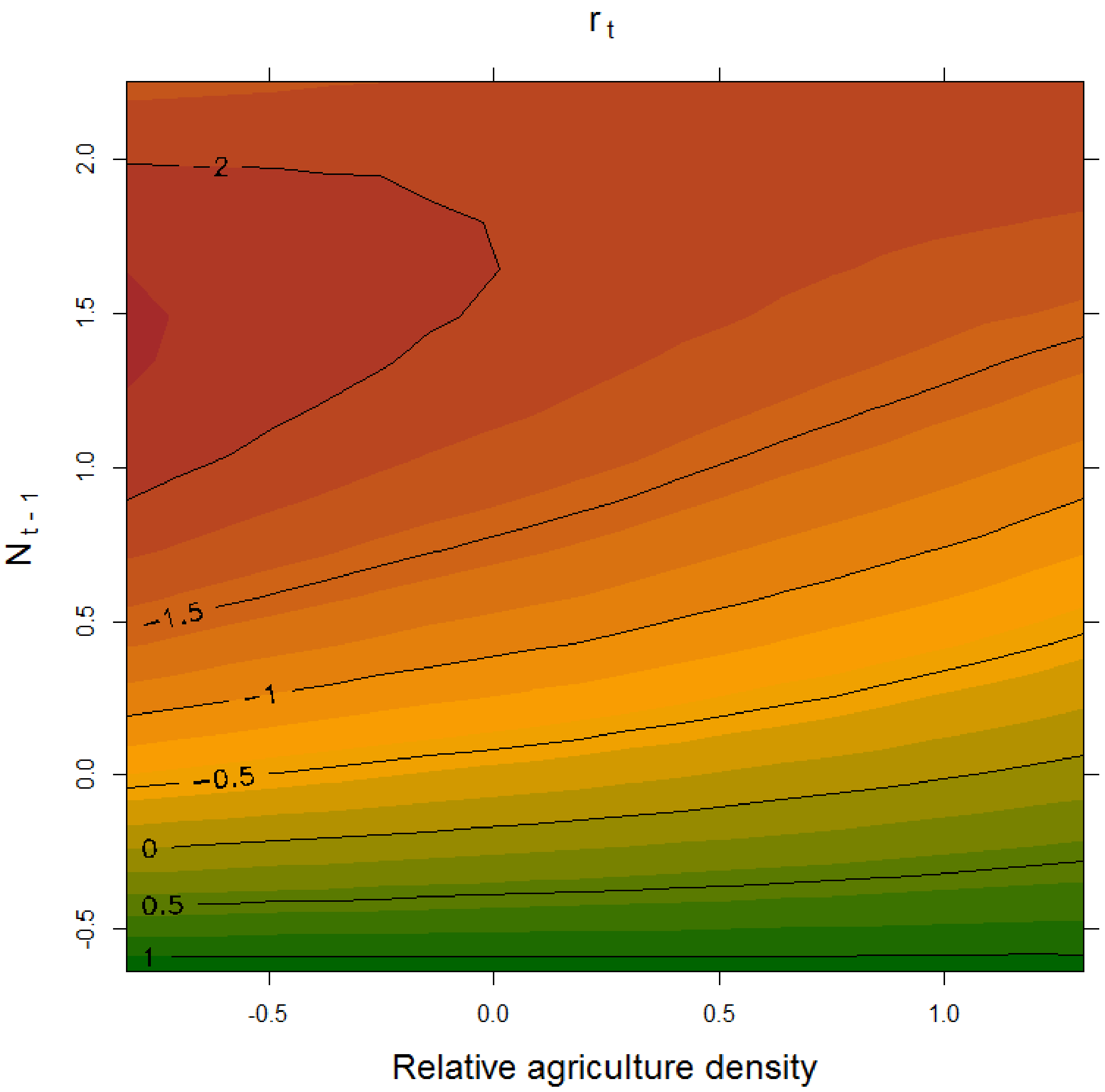

Figure 29 Model weighted predictions of the interaction between agricultural land and red fox abundance (N_{t-1}) on the instantaneous rate of increase in the red fox population. Red to green gradient depict negative to positive instantaneous rate of increase.

Discussion

In this paper, we show that the spatiotemporal dynamics of red foxes are closely interrelated with human landscape modification and activities. Red fox abundance related positively to relative settlement density and the density of moose offal from hunting. Furthermore, we found that negative feedback processes of first order dynamics (i.e. direct density dependence) dominated the structure of temporal variation in abundance. An increase in abundance of one reduced the instantaneous rate of increase by 1.3, implying relatively strong density dependence. Overall, the equilibrium of abundance (i.e. $r_t = 0$) was relatively high and temporal variability was low in areas dominated by agriculture.

Positive relationships between fox abundances and human settlements have been observed earlier (e.g. Panek & Bresiński 2002). Human dominated landscapes are attractive to red foxes primarily via anthropogenic subsidies in the form of increased scavenging opportunities (Rosalino *et al.* 2010; Selås, Johnsen & Eide 2010). Elevation was nonetheless included in the second best model, but other predictors representing climate and productivity gradients (i.e. elevation and latitude) were generally not ranked high. This implies that potential effects of settlements differ from those of landscape productivity and climate, and furthermore, that strong relationships between red fox abundances and anthropogenic influence mask potential effects of natural productivity and climate gradients.

Although there was a positive relationship between offal and red fox abundance, the relationship was weak. This is surprising given the multitude of forage- and diet studies identifying entrails, carrion and carcass remains as important items in red fox diets (Halpin & Bissonette 1988; Jędrzejewski & Jędrzejewska 1992; Cagnacci, Lovari & Meriggi 2003; DeVault, Jr & Shivik 2003; Sidorovich, Sidorovich & Izotova 2006; Panzacchi *et al.* 2008b; Needham *et al.* 2014). The inclusion of the offal term however, greatly improved the relative model performance over settlements alone and offal thus explained a large proportion of the variance in red fox abundance not accounted for by settlements. This specific pattern may be caused by the fact that offal from hunting is mainly available in a temporally narrow pulse during late autumn (Gomo *et al.* 2017). Additionally, as highlighted in several dietary studies, there is temporal variability in the importance of large herbivore remnants and carcasses. In Poland, deer carcasses from kills from large carnivores or other winter mortality were important buffer-foods when voles were scarce (Jędrzejewski & Jędrzejewska 1992) whereas the importance of carcasses from semi-domesticated reindeer (*Rangifer tarandus tarandus*) was inversely related to lemming (*Lemmus lemmus*) abundance in northern Norway (Killengreen *et al.* 2011). As such, the degree of scavenging for carcasses probably interacts with varying accessibility to voles, either via their abundance or e.g. snow cover (Willebrand *et al.* 2017).

The impact of such alternative sources of foods to the red fox needs to be better understood, but they are probably improving body condition preceding winter and thus winter survival (Needham *et al.* 2014).

The observed range in the estimated instantaneous rate of increase was higher than in other reports (e.g. Hone 1999), and we propose two explanations for this pattern. Firstly, dispersal of highly mobile juvenile red foxes (Englund 1980b) as well as considerable flexibility in space-use within home ranges (i.e. LoCoH 90 vs. MCP 100) (Walton *et al.* 2017) are innate components of the monitored population and secondly, the fluctuating nature of the boreal forest ecosystem should yield high variation in birth and death rates (Lindström 1982). In systems with fluctuating resources (e.g. vole cycles in the boreal forest) these two mechanisms are entwined because red foxes may show an aggregative and/or a demographic responses to spatiotemporal variability in resource distribution (Henden *et al.* 2010; McKinnon *et al.* 2013). It is worth noting that we cannot separate the two responses (i.e. aggregative and demographic) because changes in track frequencies may be due to changes in both red fox density and activity.

Density dependence across the agricultural continuum was asymmetric. As red fox abundance increased, the strength of density dependence progressively relaxed with increasing relative coverage of agricultural land. This suggests that the variability in red fox abundance is inversely related to the presence of agriculture because variable population dynamics is associated with strong density dependent growth (Hanski 1990). Both resource availability and social regulation may be underlying factors explaining this pattern. Previously, variation in space use across a large-scale productivity gradient have been observed (Walton *et al.* 2017), but the degree of heterogeneity in space use at smaller scales is less known, although probably similar (Kurki *et al.* 1998). Social regulation due to territoriality, is one potential mechanism that may decrease with increasing territory size (Goszczyński 2002), which again is inversely related to red fox density (Trewhella, Harris & McAllister 1988).

In Scandinavia, predation pressure exerted on alternative prey by generalist predators (e.g. red foxes) varies in phase with the vole cycle, and this relationship is termed the alternative prey hypothesis (Hagen 1952; Angelstam, Lindström & Widén 1984; Panzacchi *et al.* 2008a). The fundamental principal is that large annual variation in the main prey, typically voles, generates predator-mediated fluctuations in alternative prey species, e.g. grouse. Due to prey switching, predation pressure on alternative prey increase during vole population declines. As vole populations increase, alternative prey is again relieved of predation pressure due to lower red fox abundance and prey switching. Provisioning red foxes with alternative foods may buffer fox population declines following the crash in the vole cycle and this may well be a mechanism causing the observed asymmetry in population regulation along the agricultural continuum. Elevated baseline populations of predators in the low phase of the prey-cycle may subsequently limit cyclic amplitude in the prey population (Krebs *et al.* 2014). Moreover, negative feedback processes from predation in a cyclic system may also dampen prey fluctuations (Erlinge, Göransson & Hansson 1983; Erlinge *et al.* 1991). Ultimately, trophic cascades driven by increased scavenger abundance, survival and fecundity are expected implications of providing anthropogenic food subsidies (Newsome *et al.* 2015). Such effects on other trophic levels may for example involve stabilization of prey-species by preventing sequential years of population growth (Hansson 1988).

Several factors may interact with habitat quality and successively modulate effects of habitat on red fox density and population dynamics in the landscape (Gorini *et al.* 2012). In spite of the potential for complex regulatory mechanisms, single-factor explanations governing red fox distribution and performance along the farmland continuum is of particular interest to conservation (e.g. Tryjanowski *et al.* 2011) and determinants of density dependent structure needs to be pursued in future research in general (Sibly & Hone 2002). For conservational purposes, it is important to distinguish between factors increasing the landscape's carrying capacity from factors that stabilize red fox population growth. Such factors are inherently different in the potential impact on alternative and incidental prey in a fluctuating environment. Reducing anthropogenic subsidization, particularly preceding and during winter may prove a successful conservation action for farmland or other species currently depressed by red fox predation.

References

Andersen, R., Fagerheim, W.I. & Solheim, J. (2009) *Hjorteviltforvaltning. Hvordan Forvalte Store Beitedyr. Tre Scenarier.* Trondheim - In Norwegian.

Andren, H. (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology*, **73**, 794–804.

Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*.

Andren, H. & Angelstam, P. (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology*, **69**, 544–547.

Angelstam, P. (1983) *Population Dynamics of Tetraonids Especially the Black Grouse* Tetrao Tetrix L. *in Boreal Forests*. Uppsala University, Uppsala, Sweden.

Angelstam, P. (1984) Sexual and seasonal differences in mortality of the black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scandinavica*, **15**, 123–134.

Angelstam, P. (2004) Habitat Thresholds and Effects of Forest Landscape Change on the Distribution and Abundance of Black Grouse and Capercaillie. *Ecological Bulletins*, 173–187.

Angelstam, P., Lindström, E. & Widén, P. (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, **62**, 199–208.

Angerbjörn, A. (1989) Mountain hare populations on islands: effects of predation by red fox. *Oecologia*, **81**, 335–340.

Arditit, R. & Ginzburg, L.R. (1989) Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology*, **139**, 311–326.

Baddeley, A., Rubak, E. & Turner, R. (2015) Spatial point patterns: methodology and applications with R.

Baines, D., Moss, R. & Dugan, D. (2004) Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology*, **41**, 59–71.

Baines, D., Richardson, M. & Warren, P. (2017) The invertebrate diet of Black Grouse Tetrao tetrix chicks: a comparison between northern England and the Scottish Highlands. *Bird Study*, **64**, 117–124.

Baines, D., Aebischer, N.J. & Macleod, A. (2016) Increased mammalian predators and climate change predict declines in breeding success and density of capercaillie *Tetrao urogallus*, an old stand specialist, in fragmented Scottish forests. *Biodiversity and Conservation*, **25**, 2171–2186.

Bartoń, K. & Zalewski, A. (2007) Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography*, **16**, 281–289.

Benson, T., Brown, J. & Bednarz, J. (2010) Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology*, **79**, 225–234.

Berryman, A. & Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos*, **92**, 265–270.

Bogdziewicz, M. & Zwolak, R. (2013) Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review. *European Journal of Forest Research*, **133**, 1–11.

Brainerd, S.M., Helldin, J.O., Lindstrom, E.R., Rolstad, E., Rolstad, J. & Storch, I. (1995) Pine marten (Martes martes) selection of resting and denning sites in Scandinavian managed forests. *Annales Zoologici Fennici*, **32**, 151–157.

Brinchmann, A. (1926) Coccidiosen hos lirype. *Bergens Museums Årbok*, p. Bergen Museum, Bergen, Norway - In Norwegian.

Brittas, R. & Willebrand, T. (1991) Nesting habitats and egg predation in Swedish black grouse. *Ornis Scandinavica*, **22**, 261–263.

Brommer, J.E., Pietiäinen, H., Ahola, K., Karell, P., Karstinen, T. & Kolunen, H. (2010) The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. *Global Change Biology*, **16**, 577–586.

Burnham, K. & Anderson, D. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer.

Cagnacci, F., Lovari, S. & Meriggi, A. (2003) Carrion dependence and food habits of the red fox in an Alpine area. *Italian Journal of Zoology*, **70**, 31–38.

Caizergues, A. & Ellison, L.N. (2000) Age-specific reproductive performance of black grouse *Tetrao tetrix* females. *Bird Study*, **47**, 344–351.

Carricondo-Sanchez, D., Samelius, G., Willebrand, O. & Willebrand, T. (2016) Spatial and temporal variation in the distribution and abundance of red foxes in the tundra and taiga of northern Sweden. *Eur J Wildl Res*.

Cavallini, P. & Lovari, S. (1991) Environmental factors influencing the use of habitat in the red fox, Vulpes vulpes. *Journal of Zoology*, **223**, 323–339.

Christiansen, E. (1979) Skog- og jordbruk, smågnagere og rev. *Tidsskrift for skogbruk*, **87**, 115–119.

Coates, P.S., Connelly, J.W. & Delehanty, D.J. (2008) Predators of greater sage-grouse nests identified by video monitoring. *Journal of Field Ornithology*, **79**, 421–428.

Coates, P.S. & Delehanty, D.J. (2010) Nest predation of greater sage-grouse in relation to microhabitat factors and predators. *Journal of Wildlife Management*, **74**, 240–248.

Conover, M. (2007) *Predator-Prey Dynamics: The Role of Olfaction*. CRC Press, Boca Raton, FL.

Cornulier, T., Yoccoz, N.G., Bretagnolle, V., Brommer, J.E., Butet, A., Ecke, F., Elston, D.A., Framstad, E., Henttonen, H., Hornfeldt, B., Huitu, O., Imholt, C., Ims, R.A., Jacob, J., Jedrzejewska, B., Millon, A., Petty, S.J., Pietiainen, H., Tkadlec, E., Zub, K. & Lambin, X. (2013) Europe-wide dampening of population cycles in eystone herbivores. *Science*, **340**, 63–66.

Dahl, K. (1924) Norges Jeger og Fiskerforbunds Tidsskrift - In Norwegian. *Norges Jeger og Fiskerforbunds Tidsskrift - In Norwegian*, pp. 169–189.

Danell, K. & Hörnfeldt, B. (1987) Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. *Oecologia*, **73**, 533–536.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, Or, the Preservation of Favoured Races in the Struggle for Life*. J. Murray, London, UK.

DeVault, T., Jr, O.R. & Shivik, J. (2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems.

Oikos, **102**, 225–234.

Dinsmore, S.J., White, G.C. & Knopf, F.L. (2002) Advanced techniques for modeing avian nest survival. *Ecology*, **83**, 3476–3488.

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.

Elmhagen, B., Kindberg, J., Hellström, P. & Angerbjörn, A. (2015) A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio*, **44**, 39–50.

Englund, J. (1980a) Population dynamics of the red fox (Vulpes vulpes L., 1758) in Sweden. *The Red Fox*.

Englund, J. (1980b) Yearly variations of recovery and dispersal rates of fox cubs tagged in Swedish coniferous forests. *Biogeographica*.

Erikstad, K. & Spidsø, T. (1982) The influence of weather on food intake, insect prey selection and feeding behaviour in willow grouse chicks in northern Norway. *Ornis Scandinavica*.

Erlinge, S., Goransson, G., Hogstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylven, M. (1983) Can vertebrate predators regulate their prey? *The American Naturalist*, **123**, 125–133.

Erlinge, S., Goransson, G., Hogstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylven, M. (1988) More Thoughts on Vertebrate Predator Regulation of Prey. *The American Naturalist*, **132**, 148–154.

Erlinge, S., Göransson, G. & Hansson, L. (1983) Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos*, **40**, 36–52.

Erlinge, S., Agrell, J., Nelson, J. & Sandell, M. (1991) Why are some microtine populations cyclic while others are not? *Acta Theriologica*.

Errington, P. (1946) Predation and vertebrate populations. *The Quarterly Review of Biology*.

ESRI INC. (2011) ArcGIS.

Etterson, M.A., Greenberg, R. & Hollenhorst, T. (2014) Landscape and regional context differentially affect nest parasitism and nest predation for wood thrush in central Virginia, USA. *The Condor*, **116**, 205–214.

Etterson, M., Nagy, L., Robinson, T. & Johnson, D. (2007) Partitioning risk among different causes of nest failure. *The Auk*.

Fletcher, Q.E., Boutin, S., Lane, J.E., Lamontagne, J.M., Mcadam, A.G., Krebs, C.J. & Humphries, M.M. (2010) The functional response of a hoarding seed predator to mast seeding. *Ecology*, **91**, 2673–2683.

Flint, P.L. & Grand, J.B. (1997) Survival of Spectacled Eider Adult Females and Ducklings during Brood Rearing. *The Journal of Wildlife Management*, **61**, 217–221.

Foley, J.A. (2005) Global Consequences of Land Use. *Science*, **309**, 570–574.

Formosof, A.N. (1933) The Crop of Cedar Nuts, Invasions Into Europe of the Siberian Nutcracker (Nucifraga caryocatactes macrorhynchus Brehm) and Fluctuations in Numbers of the Squirrel (Sciurus vulgaris L.). *The Journal of Animal Ecology*, **2**, 70.

Frafjord, K., Becker, D. & Angerbjörn, A. (1989) Interactions between arctic and red foxes in Scandinavia—predation and aggression. *Arctic*.

Gelman, A. & Su, Y.-S. (2016) Data Analysis Using Regression and Multilevel/Hierarchical Models - R package version 1.9-3.

Gomo, G., Mattisson, J., Hagen, B.R., Moa, P.F. & Willebrand, T. (2017) Scavenging on a pulsed resource: quality matters for corvids but density for mammals. *BMC Ecology*, **17**, 22.

González, A. de & Cox, D. (2007) Interpretation of interaction: A review. *The Annals of Applied Statistics*, **1**, 371–385.

Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M. & Nilsen, E.B. (2012) Habitat heterogeneity and mammalian predator-prey interactions: Predator-prey interactions in a spatial world. *Mammal Review*, **42**, 55–77.

Goszczyński, J. (2002) Home ranges in red fox: territoriality diminishes with increasing area. *Acta Theriologica*.

Graf, R.F., Bollmann, K., Suter, W. & Bugmann, H. (2005) The importance of spatial scale in habitat models: Capercaillie in the Swiss Alps. *Landscape Ecology*, **20**, 703–717.

Güthlin, D., Storch, I. & Küchenhoff, H. (2013) Landscape variables associated with relative abundance of generalist mesopredators. *Landscape Ecology*, **28**, 1687–1696.

Hagen, Y. (1952) *Rovfuglene Og Viltpleien*, 1st ed. Gyldendal, Oslo, Norway (in Norwegian).

Halpin, M. & Bissonette, J. (1988) Influence of snow depth on prey availability and habitat use by red fox. *Canadian Journal of Zoology*, **66**, 587–592.

Hanski, I. (1990) Density Dependence, Regulation and Variability in Animal Populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **330**, 141–150.

Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *The Journal of Animal Ecology*, **60**, 353–367.

Hansson, L. (1988) The domestic cat as a possible modifier of vole dynamics. *Mammalia*, **52**, 159–164.

Hansson, L. (1992) Landscape ecology of boreal forests. *Trends in ecology & evolution*, **7**, 299–302.

Hansson, L. & Henttonen, H. (1988) Rodent dynamics as community processes. *Trends in ecology & evolution*, **3**, 195–200.

Hedwall, P. & Brunet, J. (2013) Changes in the abundance of keystone forest floor species in response to changes of forest structure. *Journal of vegetation Science*, **24**, 296–306.

Heiberg, G. (1995) *Essays Og Artikler*. Grøndahl og Dreyer, Oslo, Norway.

Helldin, J.-O. (1999) Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography*, **22**, 324–336.

Helldin, J.O. (2000a) Population trends and harvest management of pine marten *Martes martes* in Scandinavia. *Wildlife Biology*, **6**, 111–120.

Helldin, J.O. (2000b) Seasonal diet of pine marten Martes martes in southern boreal Sweden. *Acta Theriologica*, **45**, 409–420.

Helle, P. & Ikonen, K. (2015) Wildlife monitoring in Finland - on-line information to game administration, hunters and wider public, http://www.metla.fi/life/lifedata/pdf/Helle_IBFRA_2015.pdf

Henden, J., Ims, R. & Yoccoz, N. (2009) Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. *Journal of Animal Ecology*.

Henden, J., Ims, R., Yoccoz, N. & Hellström, P. (2010) Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. *Oikos*.

Henden, J., Stien, A. & Bårdsen, B. (2014) Community-wide mesocarnivore response to partial ungulate migration. *Journal of Applied Ecology*, **51**.

Henttonen, H. (1989) Does an increase in the rodent and predator densities, resulting from modern forestry, contribute to the long-term decline in Finnish tetraonids? *Suomen Riista*, **35**, 83–90.

Herman-Brunson, K.M., Jensen, K.C., Kaczor, N.W., Swanson, C.C., Rumble, M.A. & Klaver, R.W. (2009) Nesting ecology of greater sage-grouse Centrocercus urophasianus at the eastern edge of their historic distribution. *Wildlife Biology*, **15**, 395–404.

Hersteinsson, P. & MacDonald, D.W. (1992) Interspecific Competition and the Geographical Distribution of Red and Arctic Foxes Vulpes Vulpes and Alopex lagopus. *Oikos*, **64**, 505–515.

Hijmans, R.J. (2016) raster: Geographic Data Analysis and Modeling.

Hjeljord, O. (2015) *INA Fagrapport 30: Ryper Før Og Nå*. Fakultet for miljøvitenskap og teknologi Institutt for naturforvaltning, Ås, Norway - In Norwegian.

Holling, C. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385–398.

Hone, J. (1999) On rate of increase(r): patterns of variation in Australian mammals and the implications for wildlife management. *Journal of Applied Ecology*.

Hornfeldt, B. & Carlsson, B. (1990) Effects of cyclic food supply on breeding performance in Tengmalm's owl (Aegolius funereus). *Canadian Journal of Zoology*, **68**, 522–530.

Hudson, P.J. (1992) *Grouse in Space and Time : The Population Biology of a Managed Gamebird*. Game Conservancy Ltd.

Huhta, E., Helle, P., Nivala, V. & Nikula, A. (2017) The effect of human-modified landscape structure on forest grouse broods in two landscape types. *Ecosphere*, **8**, e01950.

Höglund, N. (1953) Vem tar tjäderns egg? *Svensk Jakt - In Swedish*, **91**, 416–420.

Höglund, N. (1960) Studies of the winter diet of pine marten *(Martes m. martes)* in County Jämtland. *Viltrevy (Swedish Wildlife)*, **1**, 319–337.

Hörnfeldt, B. (1978) Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia*, **32**, 141–152.

Hörnfeldt, B., Hipkiss, T. & Eklund, U. (2005) Fading out of vole and predator cycles? *Proceedings of the Royal Society*, **272**, 2045–2049.

Ims, R., Henden, J. & Killengreen, S. (2008) Collapsing population cycles. *Trends in Ecology & Evolution*, **23**, 79–86.

IUCN. (2016) IUCN, http://www.iucnredlist.org

Jahren, T., Storaas, T., Willebrand, T., Fossland Moa, P. & Hagen, B.-R. (2016) Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years. *Animal Biology*, **66**, 363–400.

Johnson, D.H. (2007) Methods for estimating nest success: An historical tour. *Studies in Avian Biology*, **34**, 1–12.

Josefsson, T., Gunnarson, B., Liedgren, L., Bergman, I. & Östlund, L. (2010) Historical human influence on forest composition and structure in boreal Fennoscandia. *Canadian Journal of Forest Research*, **40**, 872–884.

de Jounge, J. (1981) *Predation of the Pine Marten* (Martes Martes) *in Relation to Habitat Selection and Food Abundance during Winter in Central Sweden*.

Jędrzejewski, W. & Jędrzejewska, B. (1992) Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Biatowieza National Park, Poland. *Ecography*, **15**, 212–220.

Kauhala, K., Helle, P. & Helle, E. (2000) Predator Control and the Density and Reproductive Success of Grouse Populations in Finland. *Ecography*, **23**, 161–168.

Kelly, C. & Price, T.D. (2005) Correcting for Regression to the Mean in Behavior and Ecology. *The American Naturalist*, **166**, 700–707.

Kidd, N.A.C. & Lewis, G.B. (1987) Can Vertebrate Predators Regulate Their Prey? A Reply. *The American Naturalist*, **130**, 448.

Killengreen, S.T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N.G. & Ims, R.A. (2011) The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. *Journal of Animal Ecology*, **80**, 1049–1060.

Kjellén, N. & Roos, G. (2000) Population trends in Swedish raptors demonstrated by migration counts at Falsterbo, Sweden 1942–97. *Bird Study*, **47**, 195–211.

Klaus, S. (1985) Predation among capercaillie in a reserve in Thuringia. *Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. World Pheasant Association, Reading, UK.

Kolstad, M., Wegge, P. & Bø, T. (1985) *The Habitat Ecology of Black Grouse (*Tetrao Tetrix L.*) during Spring and Summer in East Norway*. Direktoratet for Vilt og Ferskvannsfisk, Trondheim, Norway (in Norwegian).

Korpela, K. (2014) *Biological Interactions in the Boreal Ecosystem Under Climate Change - Are the Vole and Predator Cycles Disappearing?* University of Jyväskylä.

Krebs, C.J., Bryant, J., Kielland, K., O'Donoghue, M., Doyle, F., Carriere, S., DiFolco, D., Berg, N., Boonstra, R., Boutin, S., Kenney, A.J., Reid, D.G., Bodony, K., Putera, J., Timm, H.K., Burke, T., Maier, J.A.K. & Golden, H. (2014) What factors determine cyclic amplitude in the snowshoe hare (*Lepus americanus*) cycle? *Canadian Journal of Zoology*, **92**, 1039–1048.

Krott, P. & Lampio, T. (1983) Naadan esiintymisesta Suomessa 1900-luvulla. (In Finnish with English summary: occurrence of the pine marten *(Martes martes)* in Finland in the 1900s). *Suomen riista*, **30**, 60–63.

Kurki, S., Nikula, a, Helle, P. & Linden, H. (1998) Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology*, **67**, 874–886.

Kämmerle, J.-L., Coppes, J., Ciuti, S., Suchant, R. & Storch, I. (2017) Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. *Ecosphere*, **8**, e01934.

Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford, Uk.

Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen press, London, UK.

Lakka, J. & Kouki, J. (2009) Patterns of field layer invertebrates in successional stages of managed boreal forest: Implications for the declining Capercaillie Tetrao urogallus L. population. *Forest Ecology and Management*, **257**, 600–607.

Lande, U., Herfindal, I., Willebrand, T., Fossland Moa, P. & Storaas, T. (2014) Landscape characteristics explain large-scale variation in demographic traits in forest grouse. *Landscape Ecology*, **29**, 127–139.

Lehikoinen, A., Ranta, E. & Pietiäinen, H. (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia*, **165**, 349–355.

Leopold, A. (1933) *Game Management*. Charles Scribner's Sons, New York.

Leopold, A. (1937) Pheasant Nesting Study. *The Wilson Bulletin*, **49**, 91–95.

Leopold, A. (1949) *A Sand County Almanac - and Sketches Here and There*. Oxford University Press.

Lesley, A.. & Shipley, A.E. (1912) *Grouse in Health and in Disease*. Smith, Elder & Company, London, UK.

Lindén, H. (1981) Estimation of juvenile mortality in capercaillie, Tetrao urogallus and the black grouse, Tetrao tetrix from indirect evidence. *Finnish Game Research*, **39**, 35–51.

Lindén, H. (1988) Latitudinal gradients in predator-prey interactions, cyclicity and synchronism in voles and small game populations in Finland. *Oikos*, **52**, 341–349.

Lindén, H. & Helle, P. (2003) The rise and fall of Black Grouse populations in Finland since 1860s. *Proceedings of the European Conference Black Grouse – Endangered Species of Europe* (eds P. Málková & P. Procházka), pp. 113–114. Journal of Ornithology, Prague, Czech Republic.

Lindstrom, E.R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., Lemnell, P.A., Martinsson, B., Skold, K. & Swenson, J.E. (1994) Disease reveals the predators: Sarcoptic mange, red fox predation, and prey populations. *Ecology*, **75**, 1042–1049.

Lindström, E. (1982) *Population Ecology of the Red Fox (Vulpes Vulpes L.) in Relation to Food Supply*. University of Stockholm.

Lindström, E. & Brainerd, S. (1995) Pine marten—red fox interactions: a case of intraguild predation? *Annales Zoologici Fennici*, **32**, 123–130.

Lindström, J., Ranta, E., Lindén, M. & Lindén, H. (1997) Reproductive Output, Population Structure and Cyclic Dynamics in Capercaillie, Black Grouse and Hazel Grouse. *Journal of Avian Biology*, **28**, 1–8.

Lindström, E., Angelstam, P., Widén, P. & Andrén, H. (1987) Do predators synchronize vole and grouse fluctuations? An experiment. *Oikos*, **48**, 121–124.

Linnell, J.D.C., Broseth, H., Odden, J. & Nilsen, E.B. (2010) Sustainably harvesting a large carnivore? Development of eurasian lynx populations in Norway during 160 years of shifting policy. *Environmental Management*, **45**, 1142–1154.

Linnell, J.D.C., Fiske, P., Odden, J., Brøseth, H., Herfindal, I. & Andersen, R. (2007) An evaluation of structured snow-track surveys to monitor Eurasian lynx Lynx lynx populations. *Wildlife Biology*, **13**, 456–466.

Linnell, J.D.C., Odden, J., Pedersen, V. & Andersen, R. (1998) Records of intra-guild predation by Eurasian lynx, *Lynx lynx*. *Canadian Field Naturalist*, **112**, 707–708.

Linnell, J.D.C., Swenson, J.E. & Anderson, R. (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, **4**, 345–349.

Livezey, B.C. (1980) Effects of selected observer-related factors on fates of duck nests. *Wildlife Society Bulletin*, **8**, 123–128.

Loison, A. & Langvatn, R. (1998) Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia*, **116**, 489–500.

Lovel, T. (ed). (1979) Woodland Grouse Symposium., p. 180pp. WPA, Inverness, Scotland.

Ludwig, G. (2007) *Mechanisms of Population Declines in Boreal Forest Grouse*. University of Jyväskylä.

Ludwig, G., Alatalo, R. V, Helle, P. & Siitari, H. (2010) Individual and environmental determinants of daily black grouse nest survival rates at variable predator densities. *Annales Zoologici Fennici*, **47**, 387–397.

Magnússon, K., Brynjarsdóttir, J. & Nielsen, O. (2004) *Population Cycles in Rock Ptarmigan* Lagopus Muta*: Modelling and Parameter Estimation*. University of Iceland, Division of Applied Mathematics and Computer Science / Icelandic Institute of Natural History, Reykjavik, Iceland.

Major, R. & Kendal, C. (1996) The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*, **138**, 298–307.

Marcström, V. (1960) Studies on the Physiological and Ecological Background to the Reproduction of the Capercaillie, Tetrao Urogallus Lin.(Reprinted from Viltrevy.)[A Thesis. With.

Marcström, V., Keith, L.B., Engren, E. & Cary, J.R. (1989) Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Canadian Journal of Zoology*, **67**, 658–668.

Marcström, V., Kenward, R. & Engren, E. (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *The Journal of Animal Ecology*, **57**, 859–872.

Marjakangas, A. & Törmälä, L. (1997) Female age and breeding performance in a cyclic population of black grouse *Tetrao tetrix*. *Wildlife Biology*, **3**, 195–203.

Martin, T. (1993) Nest predation and nest sites. *BioScience*, **43**, 523–532.

Mayfield, H.F. (1975) Suggestions for calculating nest success. *The Wilson Bulletin*, **87**, 456–466.

McElreath, R. (2016) *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. CRC-Press.

McKinney, M. (2002) Urbanization, biodiversity, and conservation the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population. *BioScience*, **52**, 883–890.

McKinnon, L., Berteaux, D., Gauthier, G. & Bêty, J. (2013) Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos*, **122**, 1042–1048.

McKinnon, L., Smith, P. a, Nol, E., Martin, J.L., Doyle, F.I., Abraham, K.F., Gilchrist, H.G., Morrison, R.I.G. & Bêty, J. (2010) Lower predation risk for migratory birds at high latitudes. *Science*, **327**, 326–327.

Messmer, T.A., Brunson, M.W., Reiter, D. & Hewitt, D.G. (1999) United States Public Attitudes regarding Predators and Their Management to Enhance Avian Recruitment. *Wildlife Society Bulletin*, **27**, 75–85.

Miljødirektoratet & Naturdata. (2016) Hjorteviltregisteret, www.hjorteviltregisteret.no

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Csanyi, S. & Stenseth, N.C. (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology*, **43**, 721–734.

Moen, A. (1999) *Vegetation* (ed A. Lillethun). National Mapping Authority, Hønefoss, Norway.

Montgomerie, R.D. & Weatherhead, P.J. (1988) Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology*, **63**, 167.

Moore, R.P. & Robinson, W.D. (2014) Artificial bird nests ,external validity, and bias in ecological field studies. *Ecology*, **85**, 1562–1567.

Moran, P.A.P. (1950) Notes on Continuous Stochastic Phenomena. *Biometrika*, **37**, 17–23.

Moreno-Opo, R., Afonso, I., Jiménez, J., Fernández-Olalla, M., Canut, J., García-Ferré, D., Piqué, J., García, F., Roig, J., Muñoz-Igualada, J., González, L.M. & López-Bao, J.V. (2015) Is it necessary managing carnivores to reverse the decline of endangered prey species? Insights from a removal experiment of mesocarnivores to benefit demographic parameters of the pyrenean capercaillie. *PLoS ONE*, **10**, 1–17.

Moss, R. (1986) Rain, breeding success and distribution of capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* in Scotland. *Ibis*, **128**, 65–72.

Moss, R., Storch, I. & Müller, M. (2010) Trends in grouse research. *Wildlife Biology*, **16**, 1–11.

Myrberget, S. (ed). (1977) Foredrag fra Nordisk Skogsfuglsymposium 1976. *Nordisk Skogsfuglsymposium 1976*, p. 94. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway - In Norwegian.

Myrberget, S. & Hagen, Y. (1974) Reproduksjon hos lirype og skogsfugl i Setesdalen 1919-1934. *Sterna - In Norwegian*, **13**, 23–33.

Mörner, T. (1992) Sarcoptic mange in Swedish wildlife. *Revue Scientifique et Technique (International Office of Epizootics)*, **11**, 1115–1121.

Naturresursinstitutet. (2017) Luke, http://stat.luke.fi/sv/tilasto/4481

Needham, R., Odden, M., Lundstadsveen, S. & Wegge, P. (2014) Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. *Acta theriologica*.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. & Dickman, C.R. (2015) The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, **24**, 1–11.

Newton, I. (1998) *Population Limitation in Birds*. Academic Press, New York.

Novoa, C., Desmet, J.-F., Brenot, J.-F., Muffat-Joly, B., Arvin-Bérod, M., Resseguier, J. & Tran, B. (2011) Demographic traits of two alpine populations of Rock Ptarmigan. *Ecology conservation and management of grouse* (eds B. Sandercock, K. Martin, & G. Segelbacher), pp. 267–280. University of California Press, Los Angeles, United States.

Nur, N. (1984) The Consequences of Brood Size for Breeding Blue Tits I. Adult Survival, Weight Change and the Cost of Reproduction. *The Journal of Animal Ecology*, **53**, 479–496.

O'Donoghue, M., Boutin, S., Krebs, C. & Zuleta, G. (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208.

Odden, J., Linnell, J.D.C. & Andersen, R. (2006) Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research*, **52**, 237–244.

Ordiz, A., Milleret, C., Kindberg, J., Månsson, J., Wabakken, P., Swenson, J.E. & Sand, H. (2015) Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere*, **6**, art284.

Panek, M. & Bresiński, W. (2002) Red foxVulpes vulpes density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. *Acta Theriologica*.

Panzacchi, M., Linnell, J.D.C., Melis, C., Odden, M., Odden, J., Gorini, L. & Andersen, R. (2010) Effect of land-use on small mammal abundance and diversity in a forest-farmland mosaic landscape in south-eastern Norway. *Forest Ecology and Management*, **259**, 1536–1545.

Panzacchi, M., Linnell, J.D.C., Odden, J., Odden, M. & Andersen, R. (2008a) When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. *Canadian Journal of Zoology*, **86**, 116–126.

Panzacchi, M., Linnell, J.D.C., Odden, M., Odden, J. & Andersen, R. (2009) Habitat and roe deer fawn vulnerability to red fox predation. *Journal of Animal Ecology*, **78**, 1124–1133.

Panzacchi, M., Linnell, J.D.C., Serrao, G., Eie, S., Odden, M., Odden, J. & Andersen, R. (2008b) Evaluation of the importance of roe deer fawns in the spring-summer diet of red foxes in southeastern Norway. *Ecological Research*, **23**, 889–896.

Pasanen-Mortensen, M., Pyykönen, M. & Elmhagen, B. (2013) Where lynx prevail, foxes will fail – limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography*, **22**, 868–877.

Pebesma, E. (2004) Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, **30**, 683–691.

Pianka, E.R. (1974) Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*, **71**, 2141–5.

Picozzi, N. (1975) Crow predation on marked nests. *The Journal of Wildlife Management*, **39**, 151–155.

Picozzi, N., Moss, R. & Kortland, K. (1999) Diet and survival of capercaillie Tetrao urogallus chicks in Scotland. *Wildlife Biology*.

Prugh, L.R., Stoner, C.J., Clinton, W.E., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The Rise of the Mesopredator. *BioScience*, **59**, 779–791.

Pulliainen, E. (1980) Food and feeding habits of the pine marten in Finnish Forest Lapland forest in winter. *Proceedings of the Worldwide Furbearer Conference*, p. Frostburg, Md.

Pulliainen, E. (1981) A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish Forest Lapland over 13 winters. *Annales Zoologici Fennici*.

Pöysä, H., Jalava, K. & Paasivaara, A. (2016) Generalist predator, cyclic voles and cavity nests: testing the alternative prey hypothesis. *Oecologia*, **182**, 1083–1093.

R Core Team. (2016) R: A Language and Environment for Statistical Computing.

Rajala, P. (1974) The Structure and Reproduction of Finnish Populations of Capercaillie, Tetrao Urogallus, and Black Grouse, Lyrurus Tetrix, on the Basis of Late Summer Census Data from 1963-66. *Finnish Game Research*, 1–51.

Ranta, E., Helle, P. & Lindén, H. (2004) Forty years of grouse monitoring in Finland. *Suomen Riista*.

Ranta, E., Lindstrom, J. & Linden, H. (1995) Synchrony in tetraonid population dynamics. *Journal of Animal Ecology*.

Redpath, S. & Thirgood, S. (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology*, **68**, 879–892.

Richardsen, K. (2012) *Den Store Rovviltkrigen - En Undersøkelse Av Lov Om Udrydding Af Rovdyr Og Om Freding Af Andet Vildt (1845)*. University of Tromsø (In Norwegian).

Richardson, T.W., Gardali, T. & Jenkins, S.H. (2009) Review and meta-analysis of camera effects on avian nest success. *Journal of Wildlife Management*, **73**, 287–293.

Rosalino, L., Sousa, M., Pedroso, N. & Basto, M. (2010) The influence of food resources on red fox local distribution in a mountain area of the western Mediterranean. *Vie et milieu*.

Sandercock, B.K., Martin, K. & Hannon, S.J. (2005) Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. *Oecologia*, **146**, 13–24.

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

Seiskari, P. (1962) On the winter ecology of the capercaillie, *Tetrao urogallus*, and the black grouse, *Lyrurus tetrix*, in Finland. *Papers on Game Research*, **22**, 1–119.

Selås, V., Johnsen, B. & Eide, N. (2010) Arctic fox Vulpes lagopus den use in relation to altitude and human infrastructure. *Wildlife Biology*.

Selås, V., Sonerud, G.A., Framstad, E., Kalas, J.A., Kobro, S., Pedersen, H.B., Spidso, T.K. & Wiig, O. (2011) Climate change in Norway: warm summers limit grouse reproduction. *Population Ecology*, **53**, 361–371.

Selås, V. & Vik, J.O. (2006) Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897-1976. *Journal of Zoology*, **269**, 299–308.

Semenow Tjan Shanskiy, O.I. (1979) *Ecology of Tetraonids* (ed T. from R. by A.A.C. for S. Translations). U.S. Department of Agriculture and National Science Foundation, Whashington D.C., USA.

Sibly, R. & Hone, J. (2002) Population growth rate and its determinants: an overview. *of the Royal Society B: Biological …*.

Sidorovich, V., Sidorovich, A. & Izotova, I. (2006) Variations in the diet and population density of the red fox Vulpes vulpes in the mixed woodlands of northern Belarus. *Mammalian Biology-Zeitschrift*, **71**, 74–89.

Siivonen, L. (1953) On the destruction of gallinaceous birds. *Suomen Riista*, **8**, 46–48.

Siivonen, L. (1957) The problem of the short-term fluctuations in numbers of tetraonids in Europe.

Papers on Game Research, **19**, 1–44.

Silverman, B.W. (1986) *Density Estimation for Statistics and Data Analysis*. Chapman and Hall.

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

Sirkiä, S., Nikula, A., Helle, P., Lindén, H., Norrdahl, K., Suorsa, P. & Valkeajärvi, P. (2011) Contemporary mature forest cover does not explain the persistence of Capercaillie (Tetrao urogallus) lekking areas in Finland. *Ornis Fennica*, **88**, 208–216.

Skara, A.B. & Steinset, T.A. (2016) Statistics Norway, https://www.ssb.no/jord-skog-jakt-og-fiskeri/statistikker/elgjakt

Small, R., Marcström, V. & Willebrand, T. (1993) Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography*, **16**, 360–364.

Smedshaug, C., Selås, V., Lund, S. & Sonerud, G. (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biology*, **5**, 157–166.

Smith, C.C. & Reichman, O.J. (1984) The Evolution of Food Caching by Birds and Mammals. *Annual Review of Ecology and Systematics*, **15**, 329–351.

Solomon, M.E. (1949) The Natural Control of Animal Populations. *The Journal of Animal Ecology*, **18**, 1.

Solvang, H., Pedersen, H.C., Storaas, T. & Hagen, B.R. (2009) *Rapport for Skogsfugltaksering 2005-2008*. Høgskolen i Hedmark, Elverum, Norway (in Norwegian).

Spence, J. (2001) The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology & Evolution*, **16**, 591–593.

Spidsø, T., Wegge, P. & Storaas, T. (1984) Renesting in capercaillie in southern Norway. *The Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. York, UK.

Statistics Norway. (1934) *Pelsdyrtellingen I Norge*. H Aschehoug & Co. - In Norwegian, Oslo, Norway - In Norwegian.

Statistics Norway. (2016) Statistics Norway, https://www.ssb.no/statistikkbanken/selectvarval/Define.asp?subjectcode=&ProductId=&MainTable=Smaavilt2&nvl=&PLanguage=0&nyTmpVar=true&CMSSubjectArea=jord-skog-jakt-og-fiskeri&KortNavnWeb=srjakt&StatVariant=&checked=true

Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, Uk.

Stigler, S.M. (1997) Regression towards the mean, historically considered. *Statistical methods in medical research*, **6**, 103–14.

Storch, I. (1993) Habitat selection by capercaillie in summer and autumn: Is bilberry important? *Oecologia*, **95**, 257–265.

Storch, I. (1994) Habitat and survival of capercaillie Tetrao urogallus nests and broods in the Bavarian Alps. *Biological Conservation*, **70**, 237–243.

Storch, I. (2002) On spatial resolution in habitat models: Can small-scale forest structure explain capercaillie numbers? *Conservation Ecology*.

Storch, I. (2007) *Grouse: Status Survey and Conservation Action Plan 2006-2010* (ed I. Storch). WPA, IUCN and Fordingbridge, UK, Gland, Switzerland.

Storch, I. (2015) Conservation status and threats to grouse worldwide: an update. *Oral presentation - International Grouse Symposium*, p. Reykjavik, Iceland.

Storch, I., Lindström, E. & de Jounge, J. (1990) Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriologica*, **35**, 311–320.

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

Storaas, T., Kastdalen, L. & Wegge, P. (1999) Detection of forest grouse by mammalian predators: A possible explanation for high brood losses in fragmented landscapes. *Wildlife Biology*, **5**, 187–192.

Storaas, T. & Wegge, P. (1984) High nest losses in capercaillie and black grouse in Norway. *The Third International Grouse Symposium* (eds T.W.I. Lovel & P.J. Hudson), p. 282. York, UK.

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

Storaas, T., Wegge, P. & Kastdalen, L. (2000) Weight-related renesting in capercaillie *Tetrao urogallus*. *Wildlife Biology*, **6**, 299–303.

Stubsjøen, T., Sæther, B.-E., Solberg, E.J., Heim, M. & Rolandsen, C.M. (2000) Moose (*Alces alces*) survival in three populations in northern Norway. *Canadian Journal of Zoology*, **78**, 1822–1830.

Summers, R.W., Green, R.E., Proctor, R., Dugan, D., Lambie, D., Moncrieff, R., Moss, R. & Baines, D. (2004) An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *Journal of Applied Ecology*, **41**, 513–525.

Summers, R.W., Willi, J. & Selvidge, J. (2009) Capercaillie *Tetrao urogallus* nest loss and attendance at Abernethy Forest, Scotland. *Wildlife Biology*, **15**, 319–327.

Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology*, **73**, 167–178.

Sundell, J., O'hara, R., Helle, P., Hellstedt, P. & Henttonen, H. (2013) Numerical response of small mustelids to vole abundance: delayed or not? *Oikos*.

Swenson, J. & Angelstam, P. (1993) Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Canadian Journal of Zoology*, **71**, 1303–1310.

Søilen, E. (1995) *Sportsmenn I Veideland - Norges Jeger- Og Fiskerforbund*. StikkaTrykk, Billingstad, Norway (In Norwegian).

The Norwegian Mapping Authority. (2017) The Norwegian Mapping Authority, http://kartverket.no/en/

Thompson, I.D., Davidson, I.J., O'Donnell, S. & Brazeau, F. (1989) Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Canadian Journal of Zoology*, **67**, 1816–1823.

Thorson, J., Skaug, H., Kristensen, K. & Shelton, A. (2015) The importance of spatial models for estimating the strength of density dependence. *Ecology*.

Tjernberg, M. (1981) Diet of the golden eagle *Aquila chrysaetos* during the breeding season in Sweden. *Ecography*, **4**, 12–19.

Tonteri, T., Salemaa, M., Rautio, P., Hallikainen, V., Korpela, L. & Merilä, P. (2016) Forest management regulates temporal change in the cover of boreal plant species. *Forest Ecology and Management*, **381**, 115–124.

Tornberg, R. (2001) Pattern of goshawk *Accipiter gentilis* predation on four forest grouse species in northern Finland. *Wildlife Biology*, **7**, 245–256.

Tovmo, M., Mattisson, J., Kleven, O. & Brøseth, H. (2016) *Overvaking Av Kongeørn I Noreg 2015. Resultat Frå 12 Intensivt Overvaka Område*, NINA Rappo. Trondheim - In Norwegian.

Trewhella, W., Harris, S. & McAllister, F. (1988) Dispersal distance, home-range size and population density in the red fox (Vulpes vulpes): a quantitative analysis. *Journal of Applied Ecology*.

Tryjanowski, P., Hartel, T., Báldi, A. & Szymański, P. (2011) Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. *Acta Ornithologica*.

Turchin, P. (2003) *Complex Population Dynamics : A Theoretical/empirical Synthesis*. Princeton University Press.

Vanha-Majamaa, I. & Jalonen, J. (2001) Green Tree Retention in Fennoscandian Forestry. *Scandinavian Journal of Forest Research*, **16**, 79–90.

Vickery, P., Hunter Jr., M. & Wells, J. (1992) Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos*, **63**, 281–288.

Viltdata. (2017) Viltdata, https://rapport.viltdata.se/statistik/

Vos, A. (1995) Population dynamics of the red fox (Vulpes vulpes) after the disappearance of rabies in county Garmisch-Partenkirchen, Germany, 1987—1992. *Annales Zoologici Fennici*, **32**, 93–97.

Vuorisalo, T., Talvitie, K., Kauhala, K., Bläuer, A. & Lahtinen, R. (2014) Urban red foxes (Vulpes vulpes L.) in Finland: A historical perspective. *Landscape and Urban Planning*, **124**, 109–117.

Walther, G., Post, E., Convey, P., Menzel, A. & Parmesan, C. (2002) Ecological responses to recent climate change. *Nature*.

Walton, Z., Samelius, G., Odden, M. & Willebrand, T. (2017) Variation in home range size of red foxes Vulpes vulpes along a gradient of productivity and human landscape alteration. *PLoS ONE*, **12**.

Watanabe, S. (2010) Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, **11**, 3571–3594.

Wegge, P. (1985) *The Sociobiology, Reproduction, and Habitat of Capercaillie Tetrao Urogallus L. in Southern Norway*. University of Montana.

Wegge, P. & Grasaas, T. (1977) Bestandsstudier av storfugl på Sørlandet. *Viltrapport 5* (ed S. Myrberget), pp. 22–39. Direktoratet for vilt og ferskvannsfisk - In Norwegian, Trondheim, Norway - In Norwegian.

Wegge, P. & Kastdalen, L. (2007) Pattern and causes of natural mortality of capercaille, *Tetrao urogallus*, chicks in a fragmented boreal forest. *Annales Zoologici Fennici*, **44**, 141–151.

Wegge, P. & Kastdalen, L. (2008) Habitat and diet of young grouse broods: resource partitioning between Capercaillie *(Tetrao urogallus)* and Black Grouse *(Tetrao tetrix)* in boreal forests.

Journal of Ornithology, **149**, 237–244.

Wegge, P. & Rolstad, J. (2011) Clearcutting forestry and Eurasian boreal forest grouse: Long-term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix* reveals unexpected effects on their population performances. *Forest Ecology and Management*, **261**, 1520–1529.

Wegge, P. & Storaas, T. (1990) Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway. *Oecologia*, **82**, 527–530.

Willebrand, T. (1992) Breeding and age in female black grouse Tetrao tetrix. *Ornis Scandinavica*, **23**, 29–32.

Willebrand, T. & Marcström, V. (1988) On the danger of using dummy nests to study predation. *Auk*, **105**, 378–379.

Willebrand, T., Willebrand, S., Jahren, T. & Marcström, V. (2017) Snow tracking reveals different foraging patterns of red foxes and pine martens. *Mammal Research*, **In print**, 1–10.

Wood, S.N. (2006) *Generalized Additive Models : An Introduction with R*. Chapman & Hall/CRC.

Zwickel, F.C. & Bendell, J.F. (1967) Early mortality and the regulation of numbers in blue grouse. *Canadian Journal of Zoology*, **45**.

Östlund, L., Zackrisson, O. & Axelsson, A. (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, **27**, 1198–1206.

Åhlen, P.-A., Willebrand, T., Sjöberg, K. & Hörnell-Willebrand, M. (2013) Survival of female capercaillie Tetrao urogallus in northern Sweden. *Wildlife Biology*, **19**, 368–373.

Appendix

Model components

We modelled red fox abundance likelihoods with Gamma-Poisson (i.e. negative binomial) error distributions, whilst we modelled density dependent growth likelihoods with gaussian (i.e. Normal) error distributions.

Abundance models:

$$Y_i \sim GammaPoisson\left(\mu_i, C_i\right)$$

Growth models:

$$Y_i \sim Normal(\mu_i, \sigma)$$

We fitted municipality and year as group-level effects for the linear predictors for abundance and growth models respectively. Offset for abundance models was the log of transect length (km) and log of days since last snowfall. For abundance models, spatial autocorrelation was accounted for at the municipality level whilst in growth models, spatial autocorrelation was accounted for between transect groups.

Abundance models:

$$\log\left(\mu_i\right) = \log(length_i) + \log(days_i) + a_{MUNICIPALITY_i} + \gamma_{MUNICIPALITY_i} + \beta x_i$$

Growth models:

$$\mu_i = \alpha_{YEAR_i} + \gamma_{TRANSGROUP_i} + \beta x_i$$

The prior distribution for the spatial autocorrelation component was formalized by a Gaussian process distribution (i.e. multivariate normal) of a *K*-dimensional (22 dimensions for municipalities and 255 dimensions for transect groups) matrix of zero means in order for the distribution to express the deviance from the expected mean intercept α in the linear predictor.

$$\gamma \sim MVNormal((0,\dots,0)K)$$

The covariance matrix *K* describing covariance between the i_{th} and j_{th} group-level factor was defined as the product of the maximum covariance between any two group-levels η^2, the exponential covariance decline rate ρ^2 and squared distance *D* between the i_{th} and j_{th} group-level factor. The last term, $\delta_{ij}\sigma^2$ (i.e. jitter term) provides additional covariance for multiple observations from the same group-level factors and was fixed to 0.01.

$$K_{ij} = \eta^2\, exp(-\rho^2 D_{ij}^2) + \delta_{ij}\sigma^2$$

Prior distributions of hyper- and model parameters were weakly informed (i.e. flat priors). Model parameters for fixed effects β were normally distributed and set to μ = 0 and σ = 10 for all beta coefficient priors. The grand mean intercept parameter α was set to μ = 0 and σ = 1. Scale parameter C was formalized as a half-Cauchy distribution with *location* of zero and *scale* of 2 (i.e. relatively wide) whilst standard deviation σ, maximum covariance η^2 and covariance decline rate ρ^2 were half-cauchy distributions with *location* of zero and *scale* of 1.

$$\beta \sim Normal(0,10)$$
$$\alpha \sim Normal(0,1)$$
$$C \sim HalfCauchy(0,2)$$
$$\sigma \sim HalfCauchy(0,1)$$
$$\rho^2 \sim HalfCauchy(0,1)$$
$$\eta^2 \sim HalfCauchy(0,1)$$

Table A 4 Bayesian mixed effect regression models for red fox abundance ranked according to widely applicable information criterion (WAIC). ΔWAIC is change in WAIC relative to the highest ranking model. K is number of parameters in the model. Weight is Akaike model weight. The constant model is highlighted in bold.

Model	**WAIC**	**K**	**ΔWAIC**	**weight**
Settlements+Offal	24327.7	38.8	0	0.82
Elevation+Settlements	24331.3	40.3	3.7	0.13
Settlements*Offal	24334.6	41.2	6.9	0.03
Settlements*Elevation	24336.3	42.5	8.6	0.01
Latitude+Settlements	24337.7	39.3	10.1	0.01
Settlements	24338.2	38.8	10.5	0
Latitude*Settlements	24342.3	40.9	14.7	0
Elevation+Agriculture	24447.8	45.0	120.2	0
Elevation*Agriculture	24452.5	47.0	124.8	0
Agriculture+Offal	24457.6	42.9	129.9	0
Agriculture*Offal	24467.6	46.8	139.9	0
Latitude+Agriculture	24476.4	44.6	148.7	0
Agriculture	24477.6	43.9	149.9	0
Latitude*Agriculture	24482.3	46.1	154.6	0
Elevation	24555.4	47.5	227.7	0
Offal	24622.2	46.5	294.5	0
Latitude+Offal	24624.6	48.3	296.9	0
Latitude*Offal	24630.1	50.8	302.5	0
Latitude	24640.1	48.1	312.4	0
Constant	24643.4	46.8	315.8	0

Table A 5 Bayesian mixed effect regression models for red fox density dependence ranked according to widely applicable information criterion (WAIC). ΔWAIC is change in WAIC relative to the highest ranking model. K is number of parameters in the model. Weight is Akaike model weight. The constant model is highlighted in bold.

Model	WAIC	K	ΔWAIC	weight
Agriculture*Density^2	4119.1	156.3	0	0.62
Settlements*Density^2	4121.8	151.9	2.6	0.17
Agriculture*Density^2+Offal	4122.6	156.9	3.5	0.11
Settlements*Density^2+Offal	4122.8	152.9	3.6	0.10
Density^2	4151.9	167.1	32.7	0
Offal*Density^2	4159.1	170.0	39.9	0
Elevation*Density^2	4159.6	168.7	40.4	0
Elevation*Density^2+Offal	4161.6	169.3	42.4	0
Latitude*Density^2+Offal	4161.8	169.8	42.6	0
Latitude*Density^2	4162.0	170.2	42.8	0
Constant	5074.7	30.4	955.6	0

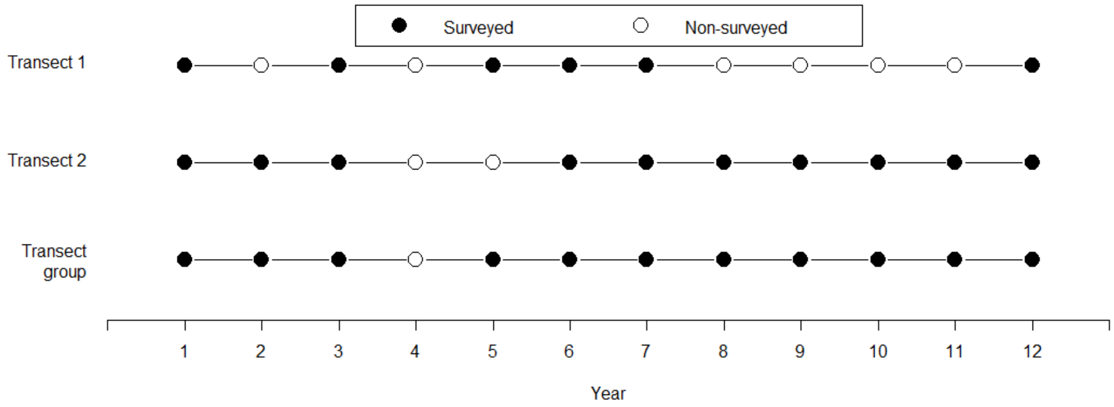

Figure A 4 Schematic representation of transect grouping prior to analysis of spatial variability. In this particular example, the first four years of the transect group are excluded because of only three years of consecutive monitoring after grouping.

Table A 6 Parameter estimates for the best performing models explaining red fox abundance (top) and population growth (bottom). Credible intervals are given at the 95 % level.

	α	**β1**	**β2**	**β3**	**β4**	**B5**
	Intercept	**Settlement**	**Offal**			
Abundance	-0.79	0.47	0.12			
95% CI	-0.88 -0.7	0.03 0.41	-0.02 0.27			

	Intercept	**Agri**	**Abundance**	**Abundance²**	**Agri:Abundance**	**Agri:Abundance²**
Growth	-0.11	0.42	-1.93	0.56	0.5	-0.33
95% CI	-0.26 0.04	0.3 0.53	-2.07 -1.8	0.48 0.66	0.28 0.72	-0.51 -0.16