

Gilbert Ludwig

Mechanisms of Population Declines
in Boreal Forest Grouse



Gilbert Ludwig

Mechanisms of Population Declines
in Boreal Forest Grouse

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA303
toukokuun 11. päivänä 2007 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
in the building Ambiotica, Auditorium YAA303, on May 11, 2007 at 12 o'clock noon.



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2007

Mechanisms of Population Declines in Boreal Forest Grouse

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 176

Gilbert Ludwig

Mechanisms of Population Declines
in Boreal Forest Grouse



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2007

Editors

Jari Haimi

Department of Biological and Environmental Science, University of Jyväskylä

Irene Ylönen, Marja-Leena Tynkkynen

Publishing Unit, University Library of Jyväskylä

Jyväskylä Studies in Biological and Environmental Science

Editorial Board

Jari Haimi, Timo Marjomäki, Varpu Marjomäki

Department of Biological and Environmental Science, University of Jyväskylä

Cover picture by Gilbert Ludwig

URN:ISBN:9789513928254

ISBN 978-951-39-2825-4 (PDF)

ISBN 978-951-39-2805-6 (nid.)

ISSN 1456-9701

Copyright © 2007, by University of Jyväskylä

Jyväskylä University Printing House, Jyväskylä 2007

ABSTRACT

Ludwig, Gilbert Xavier

Mechanisms of Population Declines in Boreal Forest Grouse

Jyväskylä: University of Jyväskylä, 2007, 48 p.

(Jyväskylä Studies in Biological and Environmental Science

ISSN 1456-9701; 176)

ISBN 978-951-39-2825-4 (PDF), 978-951-39-2805-6 (nid.)

Yhteenveto: Kanaintukantojen laskuun vaikuttavat tekijät

Diss.

Populations of Finnish forest grouse have been declining during several decades. Using large data sets on both the individual and the population level, I have studied possible mechanisms and processes underlying the long-term declines of forest grouse in Finland. The observed decline in population size of Finnish forest grouse is most likely mediated through long-term changes in breeding success. The likely mechanisms underlying the long-term decrease in breeding success and population size in grouse are interactions between human land-use (modern forestry and agriculture) and predators exacerbated by detrimental effects of asymmetric climate change. The prime factor in human land-use includes modern forestry practices such as clear-cutting and large-scale drainage as well as fragmentation due to agriculture. The ensemble of these factors is one reason of increased densities of mesopredators, but the process has strongly been facilitated by the absence of large carnivores over the last century. In addition to increased mesopredator densities itself, a number of human caused landscape features, e.g. fragmentation and large-scale drainage, additionally increase predation risk on grouse, and may act as an ecological trap. This process has further been exacerbated climate change: chicks are increasingly hatching too early, before the onset of optimal brood rearing conditions. In order to stop the long term decline, improving breeding success can be regarded as a key management target, including e.g. control of mesopredators. Results suggest that top-down effects due to recent increases in lynx populations may be more effective in controlling mesopredators than the current state of active control through hunting. Furthermore, breeding success could be locally improved through forest management that favours occurrence of bilberry and protection of pine bogs, restoration of bogs and mires where drainage is not economically profitable, as well as by integrating weather and climate change into the equation of hunting management.

Keywords: AIC, Breeding success, climate change, drainage, grouse, population declines, predation, timing of breeding, top carnivores

Gilbert X. Ludwig, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author's address Gilbert Ludwig
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
E-mail gilludw@bytl.jyu.fi

Supervisors Academy Professor Rauno Alatalo
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Docent Pekka Helle
Finnish Game and Fisheries Research Institute
Tutkijantie 2E
FI-90570 Oulu
Finland

Docent Heli Siitari
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Reviewers Professor Esa Ranta
Integrative Ecology Unit
Department of Biological and Environmental Sciences
P.O. Box 65 (Viikinkaari 1)
FI-00014 University of Helsinki
Finland

Research Professor Hannu Pöysä
Finnish Game and Fisheries Research Institute
Yliopistonkatu 6
FI-80100 Joensuu

Opponent Professor Bernt-Erik Sæther
Norwegian University of Science and Technology
Department of Biology
Realfagbygget NTNU
NO-7491 Trondheim
Norway

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

1.	INTRODUCTION	9
1.1	A short history of Finnish grouse.....	9
1.2	Short-term fluctuations and population declines	12
1.3	Finnish grouse populations: The modern threat.....	14
1.4	A question of birth and death.....	16
2	THE APPROACH	21
2.1	Looking for answers.....	21
2.2	Study species	22
2.3	Individuals, populations, and communities.....	22
2.4	Field study	23
2.5	Population data	24
2.6	Statistics.....	25
3	RESULTS AND DISCUSSION	28
3.1	Weather, climate change and the timing of breeding (I-IV).....	28
3.2	Large-scale drainage (I, II, IV).....	33
3.3	Predation (I, II, V)	34
3.4	Habitat (I, II)	35
4	CONCLUSIONS.....	36
	<i>Acknowledgements</i>	38
	YHTEENVETO (RÉSUMÉ IN FINNISH).....	40
	REFERENCES.....	42

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original articles, which are referred to in the text by their roman numerals. I have been involved in planning and execution of all studies and contributed to fieldwork (I, II). I have planned and performed all data analyses and have written all articles. Contributions in statistics were made by Kari Nissinen (IV).

- I Ludwig, G.X, Alatalo, R.V., Helle, P. and Siitari, H. Determinants of individual nesting success in black grouse under variable predation. Manuscript.
- II Ludwig, G.X, Alatalo, R.V., Helle, P. and Siitari, H. Individual and environmental determinants of early brood survival in boreal black grouse. Manuscript.
- III Ludwig, G.X., Alatalo, R.V., Helle, P., Lindén, H., Lindström, J. & Siitari, H. 2006. Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proceedings of the Royal Society B* 273, 2009–2016
- IV Ludwig, G.X, Alatalo, R.V., Helle, P. Nissinen, K. and Siitari, H. Large-scale drainage and breeding success in boreal forest grouse. Submitted manuscript.
- V Ludwig, G.X., Alatalo, R.V., Heikkinen, S., Kojola, I., Helle, P. & Siitari, H. Restoring the balance of power: Large carnivore comeback reshapes the boreal forest community. Manuscript.

1 INTRODUCTION

1.1 A short history of Finnish grouse

The central question of this thesis is *Why are grouse populations declining in the boreal forests of Finland?* During more than the past four decades, all species of forest grouse, the capercaillie (*Tetrao urogallus*), the black grouse (*T. tetrix*) and the hazel grouse (*Bonasa bonasia*) have been declining on a nationwide scale. As to justify the task endeavoured by this thesis, I shall present a brief historical overview by highlighting the relationship between man and grouse. That is, the human dimension of grouse.

It is no exaggeration to say that grouse have a special place in the heart of the Finnish culture and society. In as much as in other areas of the northern hemisphere, Finnish grouse have been sources of rural sayings and beliefs, myths and superstitious attitudes ever since the arrival of the first settlers. A humble certificate of the close relationship between grouse and Finns is beautifully incorporated in the word *Metsola*. *Metsola* stems from the word *Metso* (capercaillie), which again originates from the word *Metsä* (forest). Traditionally, *metsola* has been understood as being the *home of all forest animals* (Lindén 2002). The roots of this relationship stem, by no means, from the ancient need of hunting in order to survive, in order to exist. It is a *predator-prey* relationship.

Grouse are, and have always been, highly wanted game to humans. Of course, while the centuries have passed by, the meaning of grouse hunting has gradually changed. In pre-industrial Finland, grouse were a critically important source of food, highly valued because of its high protein content. As in many old boreal cultures, abundant grouse populations guaranteed the welfare and existence of local Finnish communities. With the rise of agriculture and the industrial revolution, the importance of grouse became increasingly an economical one. For instance, from 1867 to 1938, Finnish game exports amounted in average to almost 500 tons of game each year (Airaksinen 1946). While this includes also other game, such as hares or waterfowl, the vast

majority of the export has always been made up of grouse. In modern times, grouse hunting, although of increasingly recreational nature, is still an important component of rural communities, driven by ancient traditions. It is by no means the most popular form of hunting in Finland. Besides of being a means of game population management, it is still very much considered as a means of experiencing and enjoying the forest, or simply, being *one* with *metsola*.

Another prime reason underlying the special relationship between grouse and humans are the peculiar dynamics exhibited by grouse populations. Similarly to other vertebrate species from higher latitudes, such as e.g. voles or lemmings, population sizes of grouse undergo pronounced fluctuations in both time and space. That is, local populations fluctuate in time, going through troughs and peaks. Troughs (years when grouse abundance where at the lowest) have commonly been called *katovuosi* (year of failure). Such phenomena have been observed for many grouse species, both in the old and the new world, and have long been faced with shock and consternation (e.g. Hastings 1948): Where have all the grouse gone?

It is the nature of these dynamics which is also at the origin of the scientific interest in grouse. The first attempts to gain scientific insights on grouse population fluctuations probably comes from the British Isles, when the English Ministry of Agriculture in 1905 named a commission to investigate what causes the years of failure in red grouse (*Lagopus lagopus scoticus*) (Grouse committee 1911). In 1912, the results were popularized in a book appropriately named *Grouse in Health and in Disease* (Lesley & Shipley 1912). In northern Europe, the first attempts to explain grouse fluctuations appear in the 1920'ies and 30'ies, such as e.g. Dahl (1922, 1935) and Kloster (1936) in Norway and Bromée (1936) in Sweden. Descriptions on fluctuations in Finnish game populations can be traced back to e.g. Merikallio (1922), Palmgren (1930) and Välikangas (1936). Airaksinen (1941) and Siivonen (1943) were probably the first to discuss grouse fluctuations in particular. The first scientific attempt to describe and interpret grouse fluctuations, largely based on annual game exports from 1867 to 1938, was done by Airaksinen (1946), and his results were published in the first volume of *Suomen Riista*. The years to follow can well be regarded as a milestone in Finnish grouse science, as a result of which grouse research has remained a key element in Finnish game research until today. This includes the vast work of Lauri Siivonen, e.g. on principles of forest bird management (Siivonen 1951), the predictability of autumn population size and years of failure (Siivonen 1953a, 1958), the fluctuation in the timing of hatching of grouse chicks (Siivonen 1953b), and, of course, his studies on short term fluctuations in grouse (e.g. Siivonen 1948, 1952, 1957).

Under the leadership of Paavo Rajala (e.g. Rajala 1962, 1966, 1974), voluntary nationwide grouse brood censuses were introduced in 1964 (see methods), and the counts were replaced by the wildlife triangle monitoring scheme in 1989. The fruits of this inauguration are nationwide time-series now over 40 years long. Considering the spatial and temporal dimension of such data, it goes without saying that Finnish grouse populations are among the best

known in the world. The time-series have ever since been extensively used. First, the counts being performed in mid August, they were used as proxy of local breeding success and densities, upon which the hunting bag could be evaluated. With years accumulating, however, the series became increasingly valuable to the study of population dynamics, such as short-term fluctuations and long-term trends. Early key works based on these time-series include e.g. Rajala (1974) and the dissertation of Lindén (1981a). Experimental work on captive bred grouse was an important branch of grouse research especially in the 70'ies and 80'ies, an approach that was, and still is, very useful when studying behavioural and physiological aspects of grouse biology that would be impossible to study in the wild. Some key works, just to name a few, include Lindén (1981b, 1984), Hissa et al. (1982, 1983) and Marjakangas et al. (1984). With the continuous development of research tools like telemetry or geographical information analysis (GIS) a shift towards behavioural and habitat studies can be observed. Early telemetry studies were performed by e.g. Helle et al. (1990) and Marjakangas (1996). Habitat studies, especially the effects of fragmentation and forestry on habitat quality, were an important focus especially during the 90'ies, with long-term monitoring data and GIS techniques being of increasing importance. Key studies include e.g. Helle and Helle (1991), Helle and Nikula (1996), Helle et al. (1996) and the dissertation of Sami Kurki (Kurki 1997, 1999, Kurki and Lindén 1993, 1995, Kurki et al. 1997, 1998, 2000). Sexual selection and lekking behaviour, especially in the black grouse, has been a focus of interest for evolutionary ecologist during the past 20 years. The long-term studies on the evolution of black grouse initiated by Alatalo (e.g. Alatalo et al. 1991, 1992, Höglund & Alatalo 1995, Siitari et al. 2007) have been the driving force in this area of research.

The most peculiar feature of short-term fluctuations in grouse is its common regularity, as well as its spatial synchrony. Using the transect-census data, Lindström et al. (1995) demonstrated the fluctuations of the three forest grouse species to be cyclic, having mostly a period of 6-7 years. Older data sets based on bag statistics suggest that cyclic nature was present since at least the early 1900's (Lindström et al. 1995). The phenomenon of cyclicity seems also strongly connected to the large-scale synchrony. That is, nearby populations commonly fluctuate in synchrony, and the degree of synchrony declines with distance between the populations. Likewise, grouse populations of different species in the same area commonly fluctuate in synchrony as well (Ranta et al. 1995). Interestingly, both the cycles and the synchrony have apparently disappeared by the middle of the 1980's (Ranta et al. 2004). The reasons thereof, however, are still unclear. Chapter III of the thesis shortly discusses this and presents a possible mechanism, involving asymmetric climate change, to explain the phenomenon of cycle loss. Whatever its reasons, the loss of cycles is certainly very intriguing in biological terms. In terms of population management, however, it is not unproblematic. The loss of cycles also implies some loss of predictability, rendering decisions on local hunting bags more difficult.

The pronounced short-term fluctuations have by no means been a focus of interest throughout the decades, be it as food for discussions among hunters or as a playground for theoretical population ecologists. However, while the processes underlying the regulation of grouse populations still presents open questions, the focus of both hunters and scientists is increasingly turning towards the long-term declines observed in forest grouse. As revealed by over 40 years of time-series data, grouse densities have declined by about 60 % on average (Helle et al. 2000, Lindén 2002). The declines have been rather consistent until the 90'ies, when declines in the capercaillie and hazel grouse seemed to slowly level off, but the decline continued in the black grouse (Lindén 2002). Only during the past few years there are signs that the decline of black grouse might be levelling off in some areas of Finland. Figure 1 presents time-series of black grouse densities from 1964-2006 for all Finnish game districts (Figure 2).

1.2 Short-term fluctuations and population declines

The processes underlying short-term fluctuations are commonly termed *regulatory* processes, meaning that the population is regulated about an equilibrium density (Varley et al. 1973, Smith 1980). If this equilibrium density is constant over time, the population is said to be *persistent* (Royama 1992). In the real world, however, such equilibrium densities are rare, as they are commonly subject to change, e.g. in response to environmental changes, leading to decreases or increases of the equilibrium density. In case of a decrease, the population is no longer in a state of persistence, but is still being regulated about the declining trend. Thus, while *persistence* implies *regulation*, *regulation* does not imply *persistence* (Royama 1992). It is therefore important to distinguish the ecological mechanisms determining short-term fluctuations (i.e. population regulation) from those that determine the mean level around which the population fluctuates (i.e. the long-term trends). In practice, however, this is easier said than done.

An inherent problem of population declines is that a decline may not be a decline. For instance, a declining population could be on a trajectory towards a new equilibrium (Royama 1992, Turchin 2003), or it may simply be a form of low frequency variation (such as e.g. in a positively autocorrelated environment) and may not be under more threat than before (Ranta et al 2006). For the human perception, however, this is weak consolation at best, because one may not have the time or means to find out. The first prerequisite is to show that there is a significant negative slope over some appropriate time interval. By the time this work had started, this has been shown to be the case for all three forest grouse species, in nearly all game districts (Lindén 2002). For capercaillie and hazel grouse, the declines are most pronounced from 1964-1989, but the declines started to level off in a number of districts thereafter. The decline of black grouse, on the other hand, consistently continued after 1989,

and it is only during the past few years that some signs of recovery become apparent in some of the districts. While in ecological terms time-series of 40+ years length are not actually very long, they are long enough, in respect to average period of short-term fluctuations, that a trend can be evaluated with a high degree of certainty.

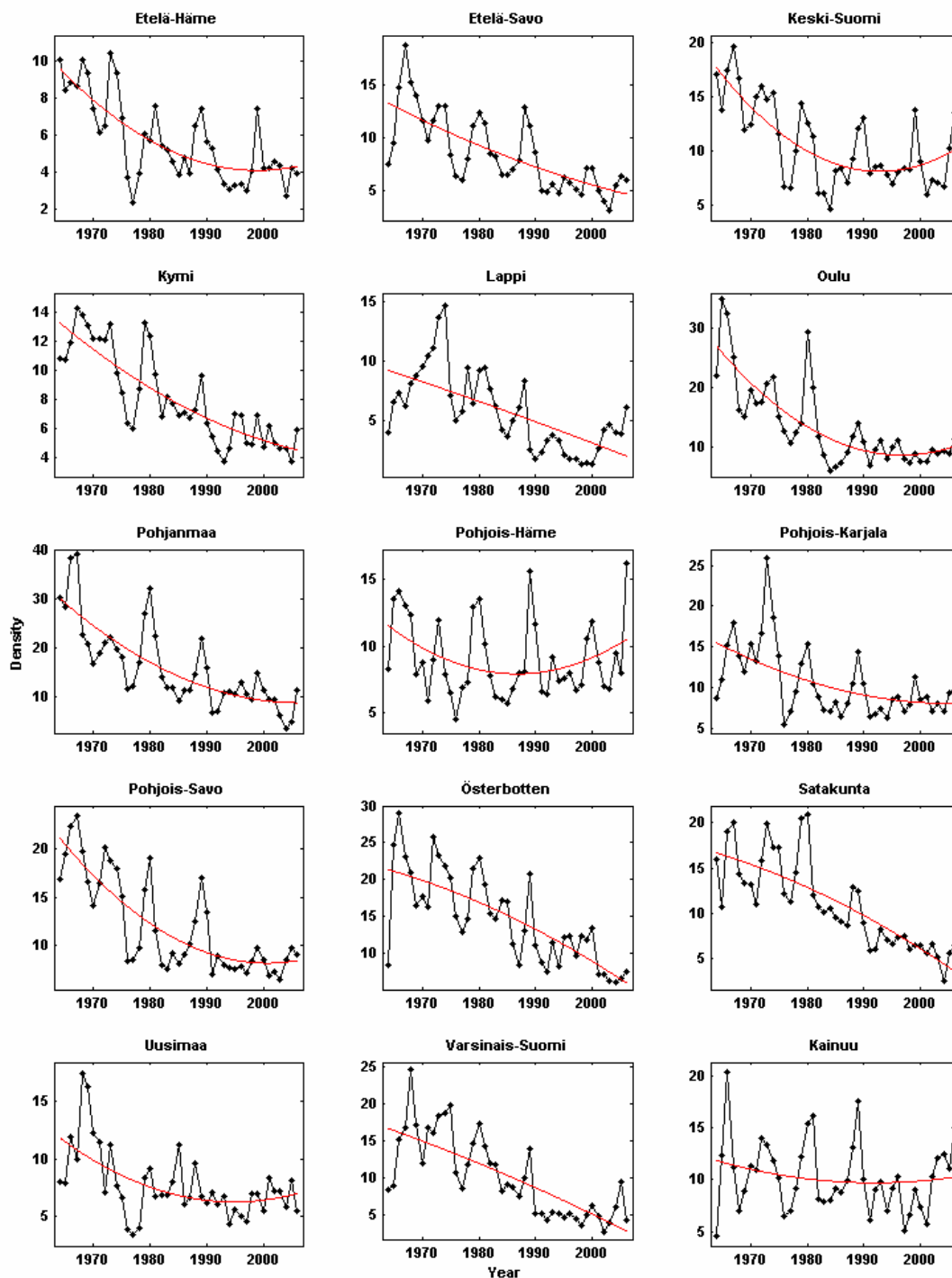


FIGURE 1 Time-series of black grouse densities from 1964-2006 in all Finnish game districts. The trends and changes therein are characterized by a second-order polynomial fit.

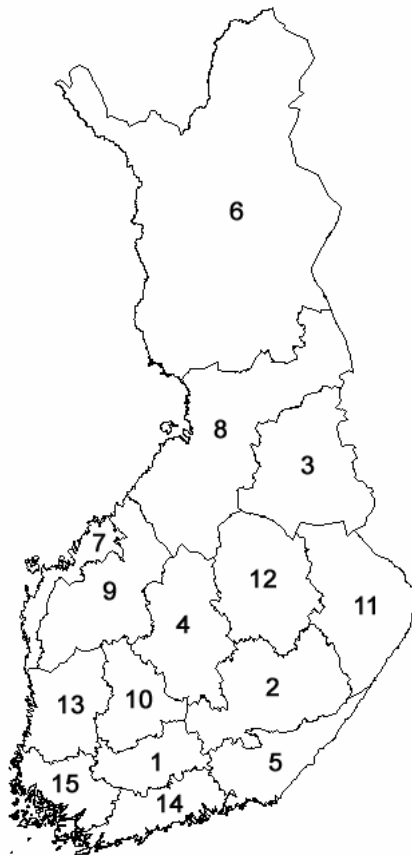


FIGURE 2 Finnish game districts (in alphabetic order): 1. Etelä-Häme, 2. Etelä-Savo, 3. Kainuu, 4. Keski-Suomi, 5. Kymi, 6. Lappi, 7. Österbotten, 8. Oulu, 9. Pohjanmaa, 10. Pohjois-Häme, 11. Pohjois Karjala, 12. Pohjois-Savo, 13. Satakunta, 14. Uusimaa, 15. Varsinais-Suomi

The second prerequisite is that the decrease can be interpreted. We need to be certain, or very confident at the least, that the observed trend is actually a reflection of e.g. some environmental change rather than just due to the stochastic dynamics the species exhibits (Ranta et al. 2006). In other words, we need a priori knowledge of the system under study to support the hypothesis that the putative decline is actually due to some unwanted change. A short summary of a priori knowledge and hypotheses are given below the next sub-header.

1.3 Finnish grouse populations: The modern threat

In grouse, predation is commonly the most important cause of non-hunting mortality (Willebrand 1988, Caizergues and Ellison 1997, Smith and Willebrand 1999). While grouse have evolved with and adapted to predators, temporally increasing predation pressure, e.g. as a result of increased abundance of small and medium sized predators (commonly called mesopredators), can hold population size of prey species below their carrying capacity and may cause

long-term population declines (Potts 1986, Marcström et al. 1988, Thirgood et al. 2000). In Finland and in Northern Europe in general, densities of small and medium sized predators, especially foxes (*Vulpes vulpes*) have markedly increased during the past 50 years (Lindström et al. 1994).

Two hypotheses are generally put forward to explain the observed increases in predator densities. First, intensified agricultural activities have increasingly fragmented the forest landscape, which has been shown to increase local densities of e.g. foxes (Andrén et al. 1985, Kurki & Lindén 1995, Huhta 1996, Kurki et al. 1998, 2000), or avian nest predators, such as corvids (Andrén 1992). Second, recent intensification of forest management, e.g. by clear cutting, have increased the proportion of young successional forest stages that are rich in grass dominated undergrowth (Esseen et al. 1992, Hansson 1992). Such habitats have been shown to attain very high densities of *Microtus*-voles, much higher than those of original forest rodent species (such as *Clethrionomys glareolus*) (Henttonen 1989). Since *Microtus* are the preferred prey of many generalist predators, such areas may sustain higher densities of their predators (Hansson & Henttonen 1988, Angelstam 1992, Kurki et al. 1998). However, it has also been argued that the disappearance of large carnivore populations, such as of wolves (*Canis lupus*) or lynx (*Lynx lynx*), may have enhanced, or facilitated, the increase in fox densities (Sæther 1999, Lindström 1999, Elmhagen and Rushton 2007, see also chapter V).

While foxes and mustelids are at least in theory capable of killing adult grouse, their main effects are most likely mediated through reductions in breeding success, either by destroying nests (chapter I) or by killing chicks (chapter II).

Modern forestry may be detrimental for grouse on other accounts, too. Human alteration of grouse habitat can influence both breeding success and adult survival through e.g. direct disturbance, changes in the spatial and temporal distribution of food or lack of cover (e.g. Miquet 1990, Kurki et al. 2000, Storch 2000). As an example, the coverage of bilberry (*Myrtillus myrtillus*) has significantly decreased during the past 50 years as a result of intensified forestry management (Reinikainen et al. 2000). Bilberry (e.g. buds) and its associated arthropod communities (especially lepidopteran larvae) are important food sources for both adults and chicks. Chapter II, among other things, evaluates the importance of *vaccinium* sp. (bilberry, lingon berry, bog bilberry) as an explanatory variable of early chick survival. Both chapters I (nest success) and II (early brood survival) investigate the role of predation and the extent to which variable predation interacts with both maternal and environmental variables in black grouse.

Also, large-scale drainage, as a means to increase timber productivity, is likely to have had a major impact on grouse populations. By the end of the 1980'ies, a total of almost 1.5 million km of ditches had been established, which comprises an area of over 5.8 million hectares of drained bogs and mires. The impact of these practices on regional landscapes and entire biocoenoses has certainly been tremendous, and, among other things, has increased both total forest surface and timber production (Hökkä et al. 2002). The potential effects of

drainage, however, on the viability of grouse populations, and animal populations in general, have received very little attention (Rajala and Lindén 1982, Helle and Ludwig 2003). Indirect effects of drainage are likely to be related to classical edge effects (Andrén 1992), by e.g. affecting abundance or movement patterns in both mammalian and avian predators. Indirect effects may also be related to alterations of arthropod communities and hence affect food availability for chicks. Newly hatched chicks may also drown in ditches. These questions are addressed in Chapters I, II and IV.

The effect of weather on grouse populations has long been a controversial one. While the role of weather has been questioned (Lindström 1996), field studies suggest weather to strongly affect e.g. early chick survival (Erikstad & Andersen 1983, Erikstad 1985, Storch 1994, Bousquet and Rotella 1998). Siivonen (1958) further suggested that spring conditions may affect the condition of the hen and subsequently her breeding success. This is based on the early vegetation theory and predicts that in warm springs more food is available for the hens, which favours weight gain during the pre egg laying stage. I will return to this question in results and discussion.

Assuming the effect of weather exists, its role may increase in importance if weather patterns change over time, e.g. as a result of global warming. Climatic conditions influence biological processes (Sæther 1997) and changes in long-term climatic trends are demonstrably affecting living systems (Parmesan & Yohe 2003). In non-migratory birds, for instance, a mismatch may occur when patterns of regional climatic change differ between the egg-laying and hatching season, i.e. when climate change is seasonally asymmetric. Consequently, the synchrony between offspring requirements and maximum food availability and/or optimal weather conditions may become disrupted. Chapter III investigates the effect of weather and climate change on early chick survival, as well as its possible long-term consequences on population size and dynamics. The effect of weather on early chick survival is also investigated in chapter II, and to some extent in chapters I and IV. Considering the arguments above, it seems safe to assume that the long-term declines of grouse populations are real, at least for human perception, and that there is a need to identify the mechanisms by which the declines are brought about.

1.4 A question of birth and death

Ignoring immigration and emigration, population renewal can be reduced down to two major processes: birth and death (Ranta et al. 2006). That is, the change in population size from one year to another can be simply characterized as the amount of births minus the amount of deaths. As simple as this insight may be, the mechanisms determining annual birth and death rates are far from trivial. The processes of birth and death in Finnish grouse are best viewed in the context of the annual censuses, which have been performed on a nationwide scale since 1964 (see methods). In mid August, when the counts are normally

performed, the number of observed birds in a given area will depend on a) the number of birds present one year before (I hereby ignore the possibility of delayed density-dependence), b) the proportion of the birds present one year before that have died during the entire period and c) the amount of hatched chicks that survived the period from hatching until the day of the count. That is, annual mortality can be partitioned into two parts: mortality of adult and yearling birds from one count to another (consequently referred to as *adult persistence*) and mortality of chicks that have hatched during the year of count. The annual birth rate, on the other hand, is a result of the rate of *nesting success*, which, in combination with the chick survival rate, will determine the annual breeding success. That is, in the context of grouse censuses, annual breeding success is here defined the number of chicks produced and alive at the count, relative to the number of adult birds. Because juveniles and adults are counted separately, such an index can be easily computed by taking the residuals of the simple linear regression of juvenile vs. adult densities. This index, called *reproductive output* (Lindström et al. 1997), is used in Chapters III and IV.

It is safe to assume that fluctuations in both breeding success and adult persistence are important in determining annual population size. The issue of which is more important, however, has been somewhat controversial. Rajala (1974) concluded that annual fluctuations in black grouse and capercaillie are largely dependent on adult persistence, not breeding success. Similar conclusions were made for Finnish forest grouse (Kauhala & Helle 2002), Norwegian black grouse (Spidsö et al. 1997) and black grouse in the French Alps (Caizergues & Ellison 1997).

Kauhala & Helle (2002) showed that adult persistence was a more important determinant of the population growth rate than is breeding success. They concluded that processes affecting breeding success, such as increases in predator densities, would be of minor importance when determining long-term trends in grouse populations. This argument, however, may reflect the consequences on short-term fluctuations rather than on long-term trends. As mentioned earlier, the processes driving these two population dynamical features (short-term fluctuations and long-term trends), although likely to be related, need not be one and the same.

When studying mechanisms of population declines, what should be our focus, breeding success or adult persistence? The obvious answer is, of course, both. Unfortunately this would be beyond the scope of this thesis. I have therefore decided to focus on one aspect, breeding success. As mentioned above, fluctuations in annual breeding success are commonly viewed as a less important predictor of future population size than adult survival. I argue that this may be true for short-term fluctuations, but that such insight cannot necessarily be extrapolated to long-term trends.

First, density-dependence in breeding success and adult survival may have different lags. When grouse fluctuations were clearly cyclic, peak and troughs had the following characteristics. A peak year was characterized by an increase in population size (as compared to the previous year), but a decrease in breeding success. The opposite is true during troughs: Population size has

decreased as compared to the previous year, although breeding success has already turned into the increasing phase. That is, while density-dependence in adult year-to-year survival may be direct, it may be delayed for breeding success, or vice versa. Indeed, delayed density-dependence is a precondition for the occurrence of cycles (Royama 1992). In other words, comparing breeding success in year $t+1$ to adult survival from year t to $t+1$ as a predictor of population size in year $t+1$ is like comparing apples to oranges.

Second, whatever demographic element is the key to declines, one would suspect that demographic element itself to be in a state of decline. Figure 3 shows time series of reproductive output of black grouse for all game districts from 1964-2006, and figure 4 shows the same for adult persistence. We find that while reproductive output has been largely declining throughout the country, adult persistence has not. It needs to be said that the change in the monitoring scheme in 1989 (from line transects to wildlife triangles, see methods) may affect the quadratic fit. However, looking at the trends within each monitoring period, we find that the conclusion is still valid. Also, a high degree of similarity between the methods was found when both were done simultaneously in 1988 (Lindén et al. 1989). Adult persistence has consistently either remained stable or has increased. Reproductive output has consistently decreased during the line transect period, but has started to recover in a number of districts during the wildlife triangle period. Similar trends can be observed for population size (Fig. 1). While the shift from one monitoring system to another may be problematic, proportional changes within a given monitoring scheme are likely to reflect real changes. On the basis of these observations I therefore justify my choice of using breeding success as the primary demographic element to investigate mechanisms of population declines.

It is clear, however, that processes affecting adult survival must not be neglected. Among these, hunting and predation by goshawk (Tornberg 2000) need special attention. The issue of hunting is particularly important, because through hunting management adult survival can be actively influenced. Key questions also include the extent to which hunting mortality is compensatory, the effect of selective trophy hunting (Coltman et al. 2003), which may occur when e.g. hunting black grouse from the autumn lek.

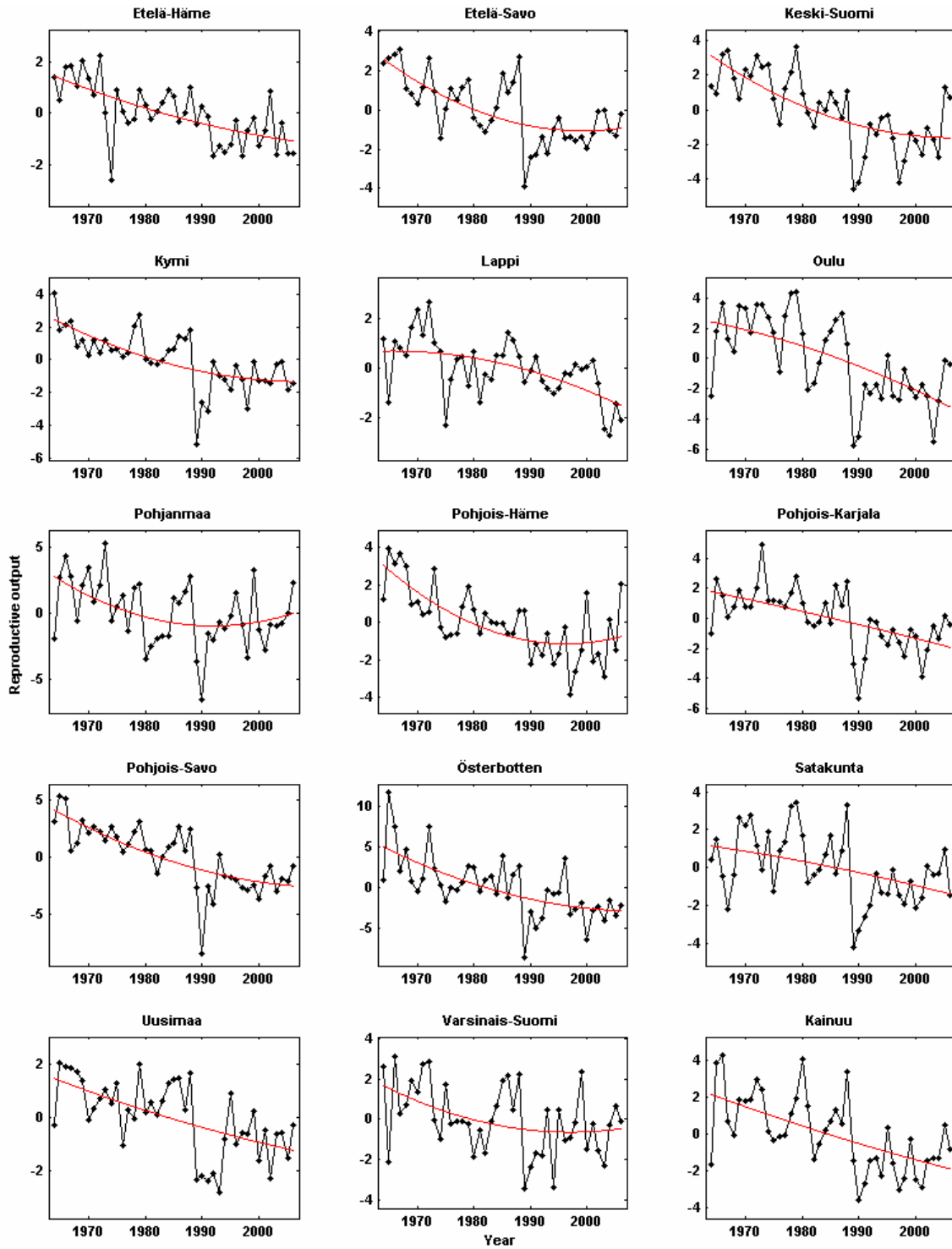


FIGURE 3 Time-series of black grouse reproductive output from 1964-2006 in all Finnish game districts. Reproductive output is defined as the residuals of the district-wise regression of juvenile vs. adult density. The trends and changes therein are characterized by a second-order polynomial fit.

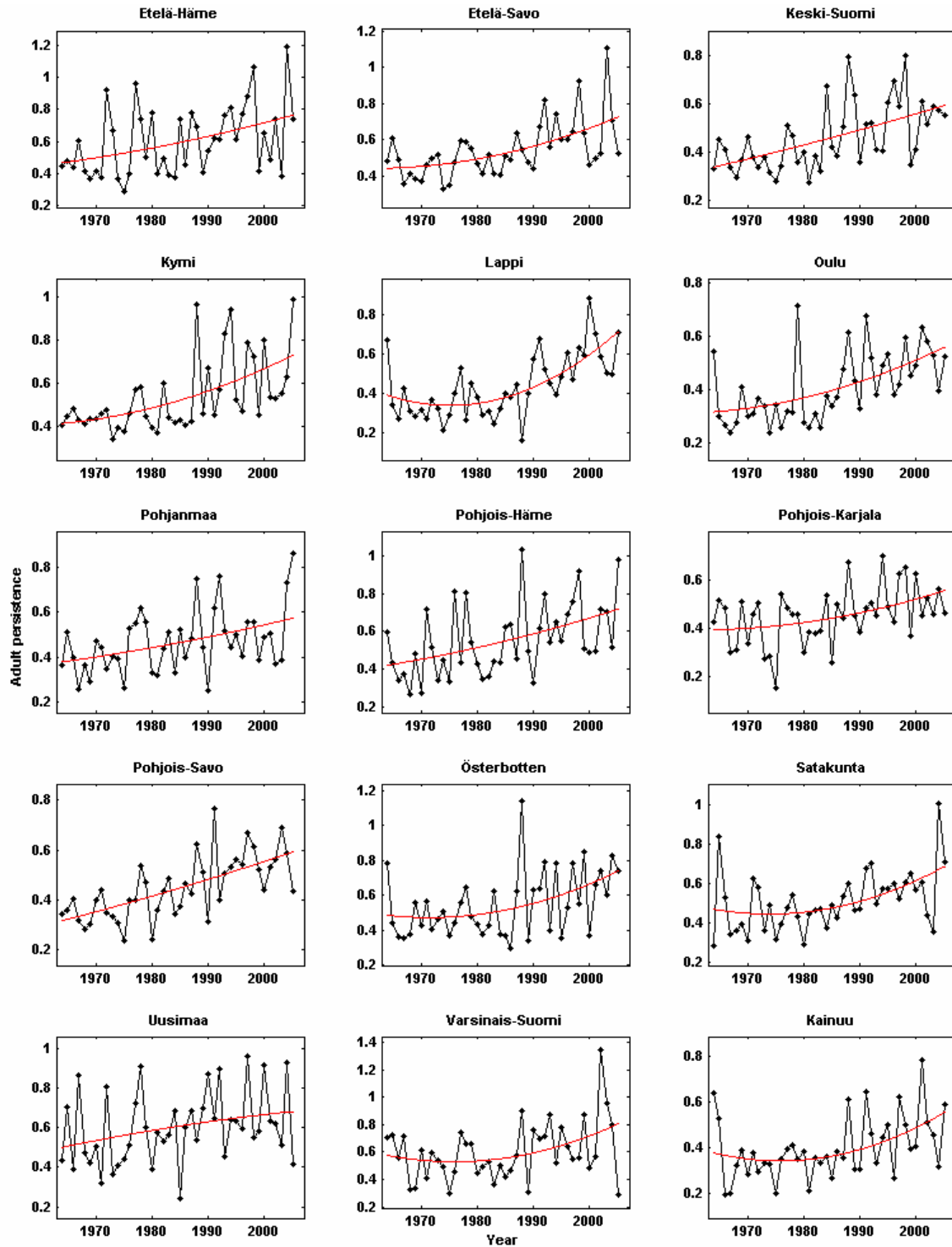


FIGURE 4 Time-series of adult persistence in black grouse from 1964-2006 in all Finnish game districts. Adult persistence is a measure of year-to-year survival and is defined as $S_t = A_{t+1}/N_t$, where A = adult density, N = total density and t = year. The trends and changes therein are characterized by a second-order polynomial fit.

2 THE APPROACH

2.1 Looking for answers

The original task of this thesis was to gain novel knowledge on the processes and mechanisms that underlie the observed long-term declines of grouse. As in scientific research in general this is best done by integrating current knowledge with new, carefully planned studies. That is, we are looking for new answers without ignoring old ones.

While it has been shown that both density-dependent and density-independent processes account for population regulation (Royama 1992, Turchin 2003, Ranta et al. 2006), declines are more commonly driven by exogenous (i.e. density-independent) forces (Royama 1992, Turchin 2003). For that reason I have mainly focused on exogenous processes. The main questions addressed by chapters I-V include:

- How do properties of the nesting and brood rearing environment affect nesting success and early brood survival, and how do they interact with the quality of individual birds and/or fluctuating predator densities (I-II)?
- Does the advancing phenology of spring affect the timing of mating and hatching, and what are the consequences thereof on long-term breeding success? Moreover, are the observed patterns possibly linked to the loss of cyclicity (III)?
- How and to what extent has large-scale drainage affected the long-term breeding success of grouse (IV)?
- Is the recovery of large carnivores (e.g. lynx) capable of eliciting recoveries of grouse populations, e.g. by controlling medium-sized predators that prey upon grouse (V)?

In the next sections, I shortly introduce the study species and briefly elaborate the general approach that I have chosen to address the questions above.

2.2 Study species

There are five grouse (Order Galliformes, Family Tetraonidae) species occurring in Finland, two lekking and three non-lekking species (Johnsgaard 1983). The lekking species are black grouse and the capercaillie. Non lekking monogamous species include the hazel grouse, willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*L. mutus*). In this study we only deal with the three true forest grouse species, the black grouse, the capercaillie and the hazel grouse. The reason thereof is that the data available for willow and rock ptarmigan is too sparse to adequately address the questions asked. Furthermore, this thesis focuses in particular on the black grouse. Both studies on individual (chapter I and II) and all studies on the population level (chapters III-V) include the black grouse. Capercaillie and hazel grouse are additionally dealt with in chapter IV-V.

While each species does have its distinct ecology, such as habitat preferences, there are also substantial similarities in their ecologies. For instance, all three species are non-migratory and ground-nesting birds inhabiting similar areas, and hence share common conditions, such as e.g. local predator densities and weather conditions. The argument that there might be regulatory processes common to all three species is best demonstrated by the decadal long synchrony between population fluctuations of the three species in any given area (Ranta et al. 1995). For more thorough descriptions of the study species and their main ecological features see e.g. Johnsgaard (1983), Hudson and Rands (1988) or Madge et al. (2002).

2.3 Individuals, populations, and communities

In order to study processes underlying changes in population size, we may use three general approaches: Analysis of observational data, mathematical modelling or experimentation (Turchin 2003).

Mathematical modelling has been a common tool in Finnish grouse research during the past decades (e.g. Lindström 1994, 1996a, 1996b, Lindström et al. 1996, Ranta et al. 1995), but it has largely been used in the context of short-term fluctuations, such as cycles and large-scale synchrony. As a matter of fact, the mathematical modeling of declining but strongly density-dependent populations can be problematic. For instance, models that successfully mimic some cyclic but stationary process often fail to retain the observed dynamics if they are forced to decline. Such an approach, of course, would be extremely useful, and further efforts are needed to develop appropriate techniques (see e.g. Royama 1992:85-88).

Manipulative experimentation, on the other hand, is often considered as *the* way to address ecological phenomena. For instance Krebs (1995) argued that progress in revealing the mechanisms underlying population fluctuations may only be achieved by careful experimentation. I find this view too simplistic.

First, true experimentation to address population level questions in species like grouse are commonly very expensive and overly laborious, or their ethics may be questioned, such as e.g. predator removal (Marcström et al. 1988, Kauhala et al. 2000). Secondly, this is not an either or question. Ideally, different approaches may be used synergistically.

Statistical analysis of observational data can further be divided into two groups: observational data from individual animals (such as individual behaviour, e.g. in a field study) and from populations (e.g. time series from monitoring programs).

One important rationale of this work has been to take advantage of observations on both the individual and the population level. Although the subjects of population ecology and animal behaviour have largely developed independently (Sutherland 1996), they are very much related to each other. Populations are made up of individuals, and population level processes are ultimately brought about by processes on the individual level. The problem is, linking individual behaviour to population dynamics is often a very difficult endeavour. The usefulness of using both approaches can nevertheless be diverse. For instance, in chapter III, we take advantage of a large amount of observations on individual copulations to evaluate the impact of climate change on the timing of breeding and subsequently on early chick survival on the population level. Furthermore, both individual and population level approaches may reveal different hypotheses. Eventually, a hypothesis revealed on one level can then be tested on the other level. An example thereof is provided by chapter IV. While an effect of drainage on breeding success could be demonstrated, the mechanisms remained unclear. This question was then addressed on the individual level, and we gained further insight into possible mechanisms (I, II).

Finally, it needs to be mentioned that populations are commonly not isolated but interact with other populations, e.g. by through interference competition (Begon et al. 2006) or predator-prey relationships (Taylor 1984). That is, changes in a population of one species may elicit changes in populations of other species, ultimately affecting community structure. Investigating the possible effects of increasing lynx densities on fox, and subsequently on grouse populations, chapter V makes a step in this direction.

2.4 Field study

Chapters I and II are field studies and are entirely on the individual level. Chapter III includes both individual and population data. All three chapters are about black grouse only.

The field studies I and II are telemetry studies and deal with nesting success and early brood survival. They address the question on how individual (or maternal) and environmental conditions interact with each other and/or with fluctuating predator densities to determine nesting success and early

brood survival. Although non-manipulative, this can be viewed as a natural experiment, where the different levels of both individual and exogenous forces (weather, habitat quality, predator densities) are naturally fluctuating. In addition to monitoring nests and broods, the environment of both nest and brood sites are accurately described. Details on capture, monitoring and variables used are presented in the methods of chapters I and II.

In chapter III we use observational data on individual matings. This data has accumulated during a long-term study on black grouse lekking behaviour initiated 1987 by Rauno Alatalo (Alatalo et al. 1991, 1992, Siitari et al. 2007). The data was used to identify the proximate causes of timing of breeding and hatching. This in turn allowed us to model the timing of both breeding and hatching for the entire period for which population data is available (see below). Finally, we used this information to evaluate the effect of weather on early chick survival as well as the potential effects of climate change on long-term breeding success. The paper also evaluates the possible cause-effect relationship between climate change and loss of cyclicity.

2.5 Population data

Population data has been used for studies III-V. The data is based on nationwide annual counts of individual grouse and were kindly provided by the Finnish Game and Fisheries Research Institute. The monitoring period can be divided into two parts. Between 1964 and 1988, grouse brood counts were performed annually by hunters and other volunteers in mid August on transect lines. Average route length varied between 30 and 50 km, and the annual total lengths of investigated routes ranged from 20'000 to 30'000 km. On each route 3 persons cover a band of 60 m width. All observations of individual grouse that are observed within the band are used to calculate transect specific indices (individuals/km²). Since juveniles and adults are counted separately, densities can be evaluated for both. The transect-lines were initially situated in what local hunters perceived as good brood habitat and did not change over the years. It has been argued, however, that because of habitat deterioration, the localities of the transect-lines have become more random. Further details can be found from Rajala (1974) or Lindén (2002). In 1989, the wildlife triangle scheme was introduced. This monitoring scheme replaced the transect-line counts of grouse, but the concept was expanded in order to include other game species as well. The dimension of triangles is 3 x 4 km, and they are somewhat more randomly distributed than the line-transects used to be in the early years. Otherwise, the sampling method for grouse is the same. Snow track counts are performed in mid winter and include the majority of mammalian game. Old tracks are marked on a first inspection, and new tracks are counted the following day. Chapter V uses track data for fox and lynx, and the track index is defined as the number of tracks per 10km and 24h. The summer counts are continued to be performed in mid August and concern mainly grouse, although signs of some

other species are registered as well. Further details on the wildlife triangle method are provided by Lindén et al. (1996). Today, the spatial and temporal extent of the combined series, 43 years of grouse counts covering an entire country of 330 000 km², is unprecedented. Just to give an example, during the wildlife triangle period alone, almost 200'000 grouse have been counted individually, and the number is manifold for the line-transect period!

Chapter III uses black grouse data from both periods (1964-2003) for the district of Central Finland in order to evaluate the potential effects of seasonally asymmetric climate change. Chapter IV uses line-transect data of most districts from 1965-1988. The data is used in conjunction with district specific drainage indices to evaluate the effect of large-scale drainage on the breeding success of black grouse, capercaillie and hazel grouse. Finally, chapter V uses wildlife triangle data to investigate the effect of recovering lynx populations onto fox populations, and the possible cascading effect upon grouse populations.

2.6 Statistics

“*What model to use?*” is probably *the* critical question in making valid inference from data in biological processes. It is not uncommon that biologist collect data on 50, 100 or more variables, hoping that some statistical method will sort the wheat from the chaff. There is of course nothing wrong with collecting lots of variables, but the simultaneous analysis of large numbers of variables, such as in multivariate methods, may bear a number of dangers, such as uncovering spurious results (Flack and Chang 1987, Miller 1990). One inherent problem of increasing numbers of variables (and hence increasing number of parameters to be estimated) is that while the model bias decreases (towards a better coefficient of determination), the model variance increases exponentially (Burnham and Anderson 2002). That is, in such “over-fitted” models, the precision of the estimators is poor.

Chapters I and II deal with individual and environmental effects on nesting success and early brood survival. The analytical challenge there was to find relevant variables that best explain a binary outcome (nest success/destruction and brood survival/death). A common approach to analyze this type of data and questions is the use of logistic regression (Menard 1995). This is a general omnibus approach for the estimation of model parameters, given an appropriate model. The difficulty is to find the appropriate model, or models, yielding the most parsimonious trade-off between bias and variance. Burnham and Anderson (2002) advocate the use of information-theory, a concept that is based on *a priori* knowledge of the biological process under study. That is, rather than using a shot-gun strategy followed by *ad hoc* hypothesis, one should formulate a set of biologically meaningful *a priori* hypotheses. The selection of the best model, or models, is then commonly carried out by means of an information criterion. The criterion most commonly used for such situations is the Akaike information criterion

(AIC), as well as the AIC adjusted for small sample sizes (AIC_c) (Burnham & Anderson 2002). The criterion is calculated on the basis of the residuals and the number of the parameters to be estimated (that is, it punishes for excessive numbers of explanatory variables). For a given set of candidate models, we may then select the best model, or models, according to the AIC. The AIC works on smaller-is-better basis and the best model is commonly set to zero. In other words, among the candidate set, this is the model that best approaches the *true* model, which is of course unknown. For all other candidate models, the difference (Δ_i) in respect to the best model is calculated. I also calculate Akaike weights (w_i) which represent the relative weight, or importance, of a model as opposed to others. Models with a $\Delta_i < 2$ are normally considered as alternative models. There are, however, situations where this approach may be too conservative. The AIC procedure was initially developed for processes with negligible noise and sampling error (Burnham & Anderson 2002). Applying the most conservative AIC based model selection procedure to field data that inherently includes noise and sampling error may therefore bear the risk of rejecting potentially important hypotheses. For such situations, Burnham and Anderson propose a confidence set of for the best model. This set simply includes all models whose weights, from highest to lowest sum up to just ≥ 0.95 . In practice this means that models with Δ_i of up to 4-7 are included in the set of alternative best models.

Variability induced by study site and year was accounted for by introducing the categorical control variables year and site in all of the models. In this way, site and year dependent variation was effectively standardized across all candidate models, and the differences between candidate models largely reflect differences in the predictive ability of the explanatory variables. In each of the model I restricted the number of main effects (in addition to year and site) to a maximum of two explanatory variables. In addition to reasons mentioned above, I did so because large numbers of predictor variables with respect to n response variables result in data too thin to accurately estimate parameters (Hosmer and Lemeshow 1989), compromising thereby comparison of different effects. I finally estimated relative weights of variables being present in at least one alternative model as well as the direction and strength of the effect by averaging the odds ratios (Burnham and Anderson 2002) across the models where the variable is present. Given the data at hand, this is probably the most efficient way of identifying the variables that matter. Furthermore, it gives also insight into the relative importance of each variable and the differences in the relative importance of different levels (e.g. variables on the maternal or environmental level, and predation). Likewise, I have used AIC for model selection in chapter IV, in order to discern between four competing *a priori* hypotheses.

Statistics in chapter three are very simple and consist of different steps. First, I identify the variable and the time period that are critical in determining the timing of the mating and the hatching peak by using cross-correlation and shifting windows. The regression that I obtained (based on individual data) was then used to estimate the hatching peaks back to 1964. This is very critical, since

now we may estimate the conditions the majority of chicks have had from 1964 onwards. Again, I used cross-correlation and shifting windows of different lengths in order to identify a possible critical post-hatch period and the extent to which environmental conditions during that period affect the breeding success. We then set up a hypothesis that the observed result may have caused the loss of cyclicity in grouse populations and test this hypothesis with computer simulations.

In chapters IV and V I have used linearized mixed models (SPSS 14) in order to model population data on a nationwide scale. Linear mixed models expand the general linear model so that the data are permitted to exhibit correlated and non-constant variability (both of which definitely occur in grouse populations!). The mixed linear model, therefore, provides the flexibility of modeling not only the means of the data but their variances as well. The advantage of this type of approach is that we can model large data sets (e.g. nationwide monitoring data) simultaneously by the taking advantage of their ability to deal with different hierarchical levels (e.g. districts (IV) or sub-plots (V)). Further details on the methods can be found in the corresponding chapters.

3 RESULTS AND DISCUSSION

Detailed descriptions of results as well as tables and figures can be found in the respective chapters. In the next three sections I shall highlight the most important results, with an emphasis on weather and climate change.

3.1 Weather, climate change and the timing of breeding (I-IV)

The timing of breeding, weather and climate change are the main issues of chapter III, but effects of weather (temperature and/or rain) are also dealt with in chapters I, II and IV.

The timing breeding, here defined as the timing of the hatching peak was very strongly dependent on the mean maximum daily temperature in spring. In chapter III, we used observation data on individual matings from 1987 to 2003 (691 matings) and found a very strong correlation ($r = -0.91$) between the mean maximum daily temperature of the last three weeks of April and the timing of the hatching peak. The period of importance changes (but only slightly) when adding the years 2004-2006 to the data (total $N = 1249$ copulations). We find that the period yielding the strongest correlation ($r = -0.93$), starts a little earlier (last week of March) but ends at the same time. The contour plot in figure 5 shows correlations between mean copulation peaks and mean maximum daily temperatures of periods differing in length and starting date. As can be seen from the dark blue diagonal area, any period starting from mid March onwards and lasting until end of April/beginning of May predicts the hatching peak very well. The reason why maximum daily temperature performed better than mean or minimum daily temperature is probably due to the fact that in April, night temperatures may be still well below zero, but day temperatures may reach already 20°C. From own observations we have experienced that a series of warm and sunny days in April may significantly speed up lekking activity, even if the nights are still on the freezing side.

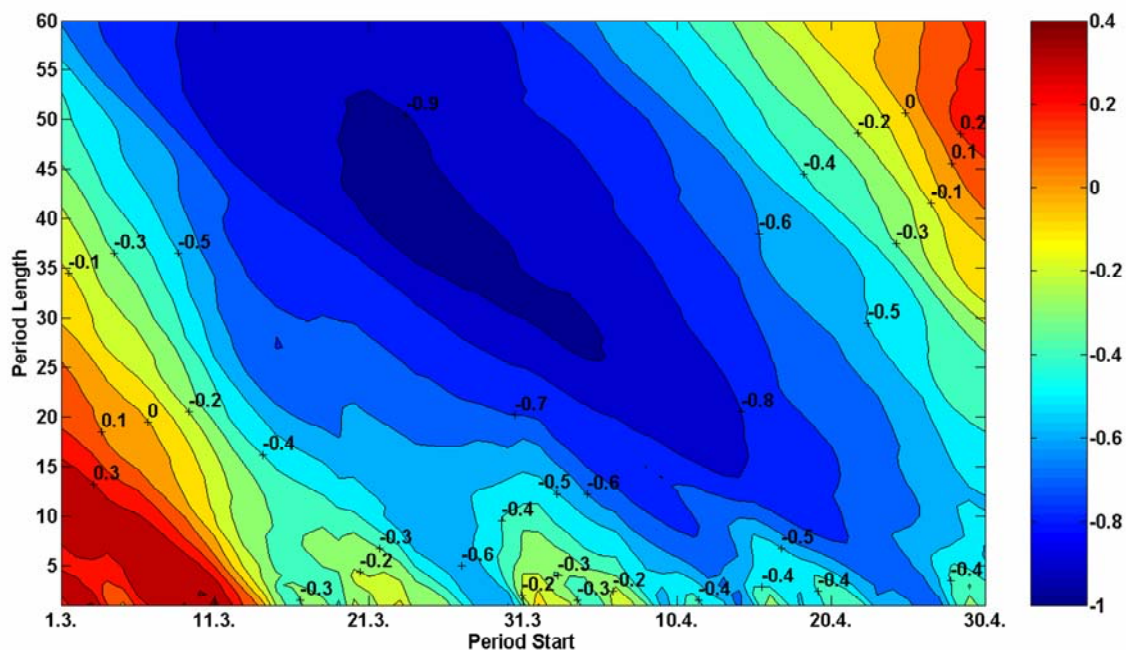


FIGURE 5 Correlations between mean copulation peaks and mean maximum daily temperatures of periods differing in length and starting date. Data consists of individual lek observations ($N = 1249$) from 1987-2006.

No matter which period we choose from the dark blue diagonal area, looking at long-term meteorological data we find a significant increase in temperature, suggesting an advancement of spring (e.g. Fig. 1c in III), and I show that as a consequence the timing of both the mating and the hatching peak have advanced as well. While such a scenario seems common in a large number of bird species (Crick and Sparks 1999), the current situation turns out to be problematic for the grouse. While spring has warmed up and hence has advanced, early summer (the time of hatching and early brood rearing) has not, in other words climate change is seasonally asymmetric. There is therefore an increasing risk to hatch too early, before the arrival of optimal conditions (weather conditions and/or food availability). Cross-correlations of reproductive output with mean maximum daily temperatures of post-hatching periods varying in length showed a strong positive effect of temperature during the first then days after hatching (Fig. 2a-c in III). Because the post-hatch periods have advanced, they have, on average, cooled down, and the negative effect of cold post-hatch conditions has become stronger and more frequent in time. Consequently asymmetric climate change has increasingly affected the breeding success of black grouse. The effect is likely to be mediated through thermoregulation problems (Hissa et al. 1983) and/or food availability. Interestingly, mean maximum daily temperatures yielded again better results than minimum or mean daily temperatures. This suggests that even relatively short periods of e.g. direct sunshine may warm up the environment to the extent allowing the chicks to forage rather than being warmed up by their mother, and possibly for insects to emerge.

Using equation 2.2. in chapter III, we then show that an increase in both strength and frequency of an exogenous driver (here the mismatch caused by asymmetric climate change) may account for the loss of cyclicality in grouse populations (Figure 4 in III). Based on data from central Finland only, these results cannot necessarily be extrapolated to the rest of the country. However, while spring temperatures have risen, early summer temperatures remained rather stable or even cooled down everywhere in Finland (Figure 6a, b), but the advancement of spring is more pronounced in the south. Hence the extent of asymmetry changes with latitude (Figure 6c). If asymmetric climate change is involved in the loss of cyclicality, we may argue that this loss should be more pronounced in the south than in the north. Further research is needed to assess the validity of this hypothesis.

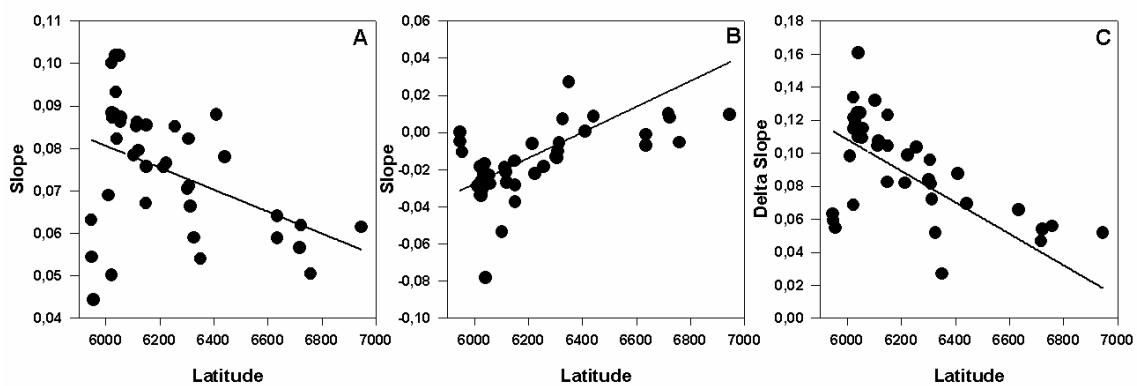


FIGURE 6 Relationships between latitude and temperature trends 1964-2004 in April (A) and June (B). Positive slopes indicate warming up and negative slopes cooling down. The difference between the slopes (delta slope, C) is a measure of climate change asymmetry. Data were obtained from the Finnish Meteorological institute (contract n. dno 1/410/03) and include 38 weather stations. Latitudes are according to Finnish KKJ coordinate grid.

While it is well known that climate change is an ubiquitous and omnipresent feature of our planet's natural history, recent climate change is said to occur at unprecedented speed and to be largely human induced (IPCC 2007). Using weather data from Central Finland, I extrapolated the results on calculated hatching dates (III) back to 1884. The time-series thereof are shown in figure 7a. As the smoothing-spline indicates, spring warming, and hence the advance of hatching has fluctuated greatly in this 122 year period, but the recent advance, starting in the beginning of the 1970'ies, has been very consistent, the hatching peaks on average being nowadays earlier than ever during this period. While grouse, as much as any other organism, may adapt to novel conditions, the rapidity of the advance may jeopardize the evolutionary response. This is indeed the case. I checked for an evolutionary response in the timing of the lekking peak (rather than in the timing of hatching, as in chapter III), including copulation data from 1987-2006. Stepwise regression of observed mean copulation dates on both April temperatures and year showed no significant effect of year ($P = 0.13$) and its partial slope was negative ($\beta = -0.15$). An evolutionary response would imply a positive and significant slope. Figure 7b

shows the residuals plotted against time. It may therefore be argued that the speed of current climate change may be too fast for grouse to adapt yet.

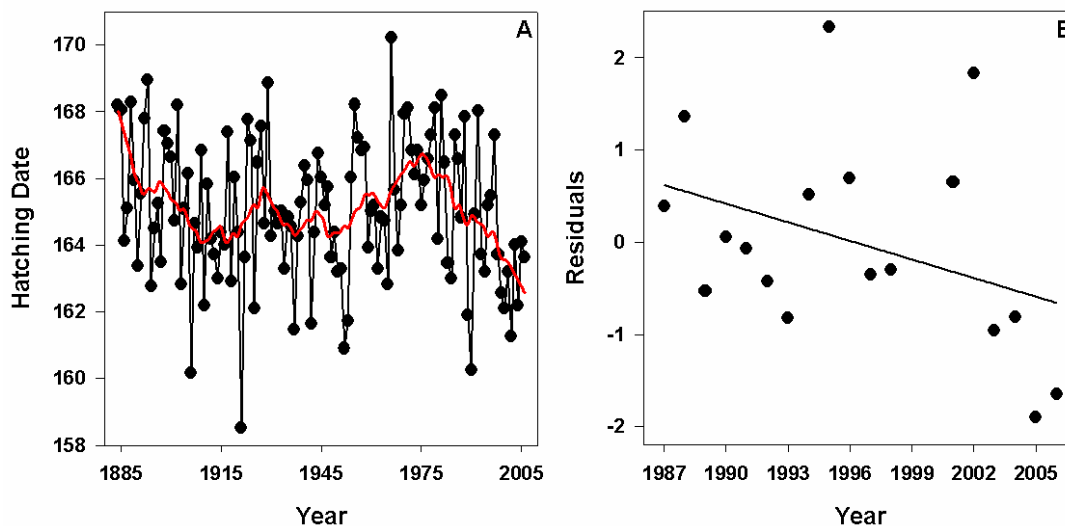


FIGURE 7 A) Calculated mean hatching dates for central Finland from 1884 to 2006. Temporal changes in periodic trends are represented by a smoothing spline. B) Lack of evolutionary response in the timing of the copulation peak. See text for details.

Finally, it is worth contrasting our results to the early vegetation theory first presented by Siivonen (1958). As mentioned before, the theory predicts a good year in terms of breeding success if pre egg laying conditions are warm (i.e. an early and warm spring). Indeed he found that the difference between good and bad years was best explained by the difference in mean spring (April) temperature (Siivonen 1958). Furthermore, comparing good to bad years he found no difference in e.g. June temperatures. This is probably due to the following. We have shown in chapter III how important it is to correctly identify the length of the critical post hatch period *and* the timing of the hatching peak (which differs from year to year). Ignoring this fact may therefore lead to erroneous conclusions. However, we still have a problem, as our results are still the other way round. While according to Siivonen an early spring predicts a good year, our hypothesis would predict the opposite. So either one of us is wrong, or something has changed. The latter is probably the correct answer. Using the calculated mean hatching dates from figure 7a I plotted these against annual game exports (in kilograms) from central and southern Finland during the period 1884 to 1938 (Airaksinen 1946) (figure 8a). This statistics includes other game too, but the clear majority thereof is made up by grouse. The annual statistic will therefore mainly be influenced by the annual catch, which is assumed to be a function of population size or productivity. Although mean grouse body mass may affect the statistic as well, I believe that this statistic reflects population peaks and troughs rather well. In figure 8b, on the other hand, I plot the hatching dates against black grouse population density in

central Finland for the period 1964-2006. Although the regression fits are not very good, we find that the direction of the relationship has clearly changed. It is therefore possible that due to asymmetric climate change, the negative effects of early and cold post hatch conditions outweigh the positive effects of early (warm) spring on hen condition. Indeed, while hen weight was the most important determinant of nest success (I), maternal effects were generally rather weak in comparison to environmental effects (I,II).

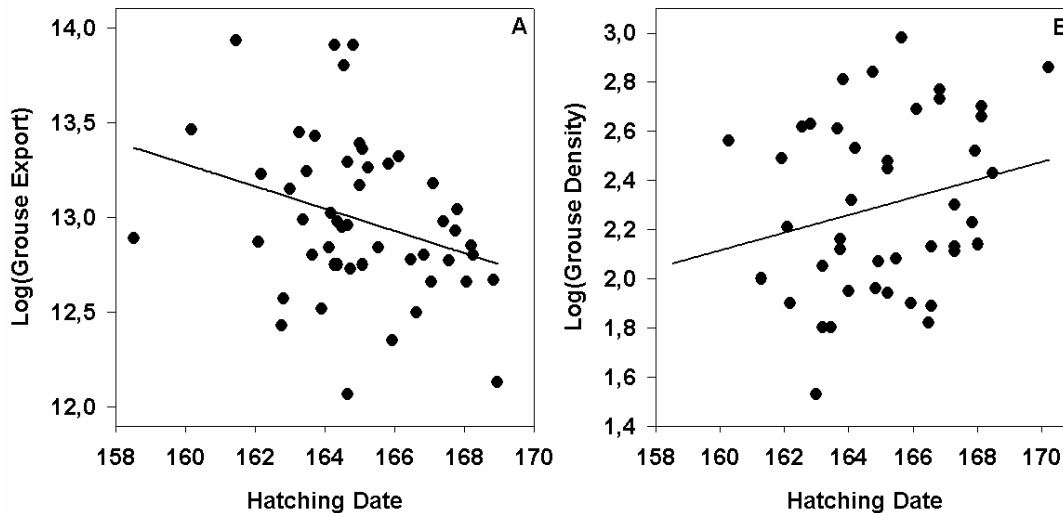


FIGURE 8 Something has changed. Plots of hatching dates against two proxies of population productivity, (A) grouse exports from 1884-1939 (lacks the years 1916-1919), and (B) black grouse density in Central Finland 1964-2006.

Our conclusions on the effect of weather during approximately the first ten days after hatching were also confirmed in our field study investigating early brood survival (II). Both temperature and rain were the two most important determinants of early survival. Our results support the existence of a threshold temperature, below which the probability of early brood loss is clearly higher. A similar threshold temperature has also been suggested for alpine black grouse in Switzerland (Zbinden and Salvioni 2004). Rain on the other hand, while seemingly being even more important than temperature, affected chick survival mostly at low temperatures. Neither temperature nor rain during the incubation stage had any effect on nesting success. This result is somewhat in contrast with those in chapter IV. There we found a negative and significant effect of local precipitation in May (the egg laying and part of the incubation period) on the reproductive output of all three grouse species. The effect, however, seemed strongest in conjunction with the additive effect of drainage.

3.2 Large-scale drainage (I, II, IV)

The possible impact of large-scale on grouse populations has received very little attention (Rajala and Lindén 1982, Helle and Ludwig 2003). This is despite the fact that drainage activities from the 1950'ies until the end of the 1980'ies have been profound and dramatic. By 1988, a total of almost 1.5 million km of ditches had been established, which comprises an area of over 5.8 million hectares of drained bogs and mires. While the establishment of new ditches has virtually stopped ever since, old ditches are commonly re-excavated every 15-20 years (Heikurainen 1980) The network of existing ditches, and the effects thereof on grouse populations is therefore likely to persist.

The reproductive output of all grouse species from 1965 to 1988 was negatively affected by large-scale drainage, but only in the southern and central part of Finland, where drainage intensity is highest (IV). AIC based model selection however revealed the combined additive effects of drainage and May precipitation to be by far the better model as compared to either effect alone.

While a negative effect of drainage seems uncontested, the interpretation of the actual mechanisms is not as straightforward. Possible bottom-up effects are likely to include changes in the vegetation structure (Rajala and Lindén 1982) and subsequently in the structure of arthropod communities, which may affect food abundance and availability for chicks during early life. For instance, grouse chicks have a high demand of easily digestible and nutritious insect food during early life (Rajala 1959; Moss and Hanssen 1980, Wegge et al. 2005). Changes in arthropod communities that affect food availability for chicks may therefore impair the high protein demand of chicks during early development. Study II however, revealed a somewhat positive effect of drainage, possibly because in our study area drained areas had a higher coverage of *vaccinium sp.* *Vaccinium*-species, especially bilberry (*V. myrtillus*) are commonly associated with occurrence of lepidopteran larvae, known to be important food for chicks (Wegge et al. 2005).

Top down effects, on the other hand, are supported by results chapter I, where predation on nests was significantly higher in drained areas, but only in years when predator densities were high. Similarly to fragmentation by e.g. agriculture or clear-cutting, increased mammalian and avian predation due to edge-effects (Andrén 1992) may be one explanation. Furthermore, when becoming fledglings, grouse chicks will cross ditches with a short burst of flight. This may render them more conspicuous and hence more vulnerable to predation by e.g. goshawk or corvids.

Drowning in ditches may be another potential threat that is common to all three grouse species. Dead chicks are occasionally found from ditches by e.g. hunters that monitor local nesting success after hatching. The clear additive effects of both precipitation and drainage supports to some extent supports the drowning hypothesis.

3.3 Predation (I, II, V)

The depredation of nests is by no means the single most important cause of nest loss in grouse. Indeed, declines in grouse breeding success are commonly associated with increased rates of nest depredation (Marcström et al. 1988, Baines 1991, Caizergues & Ellison 1997, Kurki et al. 1997;1998, Kauhala & Helle 2002). Furthermore, predation may be an important component of early grouse chick survival (e.g. Kastdalen & Wegge 1991, Braun et al. 1993, Larson et al. 2001, Park et al. 2002, Manzer 2004).

The field studies covered a period of 4 years (3 years in II) and the years were characterized by clear differences in local predator densities. The results largely support the importance of mammalian predation, especially on nesting success, and to some extent on early brood survival. However, while the effect of both nest and brood predation seems evident, a number of questions remain open. First, the role of avian predators, such as corvids (Andrén 1992), in nest predation could not be clarified to our satisfaction. Second, in order to predict the effect of possibly declining predator densities (e.g. fox) on grouse densities, one would need more qualitative and quantitative information on type and strength of the functional response in the predator-prey relationship. The question of the functional relationship becomes particularly important considering the scenario presented in V.

Chapter V is an important contribution. It shows that the problem of grouse declines is not merely a population problem but also a question of community functioning. During much of the past century, the loss of large carnivores has strongly facilitated the increase of medium-sized carnivores, such as foxes (Sæther 1999, Elmhagen and Rushton 2007), a process commonly called mesopredator release (Soulé 1988, Crooks and Soulé 1999). According to our results, the recent recovery of a large carnivore, the Eurasian Lynx, is likely to have reversed this process, which consequently is favouring the recovery of grouse populations, especially black grouse and capercaillie. Interestingly, the single most important cause of lynx recovery relates to changes in management policies implemented by the European Union. This demonstrates that political decisions indeed may play a key role in large-scale biological conservation.

However, the extent to which grouse breeding success and ultimately population size will recover will probably depend on both absolute fox densities and the type of functional relationship between predator and prey. For generalist predators, a sigmoid (Type III) response is generally assumed (Taylor 1984, Turchin 2003). With such a response, an increase in prey density occurs only if the per capita death rate due to predation drops below the per capita growth rate of the prey (Turchin 2003). Now for any given per capita death rate due to predation, the total number of birds killed increases with numbers of predators. In other words, whether a given decline in predators will elicit an increase in the prey population will be influenced by the initial predator density. For instance, grouse recoveries in north-eastern Finland are

more pronounced than in the south, despite that the southern fox population has decreased to a similar extent than north-eastern one. However, despite a similar trend, southern fox densities are still 2-3 times higher than in the north-east. It can therefore be argued that in southern grouse, the current overall death rate due to predation is still commonly above the growth rate, while in the north-east it has already shifted below the critical threshold.

3.4 Habitat (I, II)

While in-depth analyses on habitat selection were out of the scope of this thesis, a number of key habitat variables emerged in I and II. Both nest and brood sites were found in a rather wide array of habitat types, ranging from clear cuts to mature economical forest stands. The effects of habitat variables on the nesting success seemed dependent on the perceived predation pressure. An interaction between predator index and the visibility of the nest indicated that low visibility of the nest increased the chance of nesting success when mammalian predators are abundant. What provides the cover, however, did not seem to matter, as long as it provided cover. Similarly, nests in drained areas were more preyed upon when mammalian predators were abundant.

The most critical habitat variable influencing early brood loss was the cover of *vaccinium* sp. *Vaccinium* sp., especially bilberry (*V. myrtillus*) is commonly associated with the abundance of lepidopteran larvae, known to be an important food for chicks (Wegge et al. 2005). The long-term decline in the coverage of bilberry (Reinikainen et al. 2000) is therefore another forestry management related process which may have affected long-term breeding success in grouse. However, further investigations are needed to evaluate the effects of habitat structure on the availability of insect food for the chicks.

4 CONCLUSIONS

Finnish grouse populations have been declining for at least the past four decades, in average by about 60 %. While some signs of local recoveries have become apparent in capercaillie and hazel grouse during the nineties, black grouse densities have continued to decline. During the recent years, however, signs of recovery of all three species have become more apparent.

Why are grouse populations declining? Be it a human weakness or strength, researchers, conservationists, wildlife managers or policy makers have the common tendency to simplify their answers, often by polarizing a single cause or process. Well, the most certain conclusion of this thesis is that there is no such simple solution. As I have elaborated earlier, population declines are thought to be driven by exogenous processes, such as environmental changes. These may act by e.g. reducing long-term breeding success and adult survival or by reducing carrying capacities by e.g. habitat deterioration or destruction, or by any combination thereof. The observed decline in population size of Finnish forest grouse is most likely mediated through long-term changes in breeding success. This conclusion comes from the simple observation that grouse breeding success has significantly decreased in time, while adult survival has not. This does not, however, question the importance of adult survival in population regulation about an equilibrium level. The likely mechanisms underlying the long-term decrease in breeding success and population size in black grouse are interactions between human land-use (modern forestry and agriculture) and predators exacerbated by detrimental effects of asymmetric climate change. The prime factor in human land-use include modern forestry practices such as clear-cutting and large-scale drainage and fragmentation due to agriculture. The ensemble of these factors is one reason of increased densities of medium sized predators, but the process has strongly been facilitated by the absence of large carnivores during the past century. Increased densities of mesopredators by itself may be capable in decreasing breeding success. However, a number of human caused landscape features, e.g. fragmentation and large-scale drainage, may additionally increase predation risk, and may act

as an ecological trap. This ongoing process has further been exacerbated by climate change.

Weather commonly acts through *random hits*, but the process of asymmetric climate change causes these to become stronger and more frequent. But of course, there is little we can do about the effect of weather, as no management practice can possibly improve weather conditions. The key lies in evaluating the local conditions experienced by chicks in their early life, and use this information as a management tool. That is, in order to avoid excess mortality in early and/or cold years, hunting in the subsequent season should be reduced, or hunting should not occur at all.

In order to stop the long term decline, improving breeding success can be regarded as a key management target. This includes control of medium sized predators, both actively (hunting) and by letting large predators such as lynxes to recover. However, considering the effect of lynxes upon fox populations, top down control by large carnivores seems a far more efficient way than the current state of active control through hunting. Furthermore, breeding success could be locally improved through forest management that favours occurrence of bilberry and protection of pine bogs, restoration of bogs and mires where drainage is not economically profitable, as well as by integrating weather and climate change into the equation of hunting management.

Acknowledgements

First of all, I would like to express my gratitude to my supervisors Rauno Alatalo, Pekka Helle and Heli Siitari. During this journey, you gave me everything I could have possibly wished for. You gave me the opportunity and responsibility to work on this project. You gave me all the freedom to work my way, yet I always had the security of your guidance. Whenever I needed help, you were there. Thank you very much, for all your help, for your time, and most importantly, for your friendship! It has been my great pleasure to work with you. It has been a privilege.

I would like to thank my fellow co-authors Harto Lindén, Jan Lindström, Kari Nissinen, Ilpo Kojola and Samuli Heikkinen, for all their input and help they have been giving. Thanks to Harto Lindén, for his warm hospitality whenever I visited Helsinki, and for giving me the opportunity to present our results at the famous *Riistapäivät*. I also want to thank to Jan Lindström for the kind hospitality when I visited Glasgow. I very much enjoyed that stay! Also, I will always remember the great days in the North Pennines, thanks to the enjoyable hospitality given by David Baines and Phil Warren!

Those PhD years would have been much less enjoyable, and much less fun, without the fellow group members Christophe Lebigre, Marjo Pihlaja and Miina Kovanen. Thank you for being there, for cheering me up, for all the discussions, and especially, for all the fun! Special thanks goes to my room mate Christophe. Sitting right next to me, he was consistently exposed to the cyclic nature of my moods, always withstanding them with *grandeur*! Thank you for listening!

This thesis involved a substantial amount of fieldwork, and there is no way this could have been achieved without the endurance of the many people that have been actively helping: Panu Halme, Matti Halonen, Elli Haukivuori, Heikki Helle, Jenny Hämäläinen, Laura Häsä, Asko Ijäs, Tuomo Jurmu, Janne Kilpimaa, Miina Kovanen, Christophe Lebigre, John Loehr, Ulla-Stiina Mahlamäki, Eeli Mykkänen, Reea Mäkinen, Ossi Nokelainen, Laura Okkonen, Tuomo Pihlaja, Elina Rantanen, Raimo Saunanen and Ilona Yliniemi. Panu and Heikki were a major help when I started my fieldwork in 2003, and Heikki introduced me to the hidden secrets of telemetry. Laura and Ulla-Stiina did the incredible work of monitoring the habitat properties of hundreds and hundreds of brood and nest sites, thereby withstanding the often intolerable exposure to zillions of moskitos, blackflies and mooseflies. Laura, Miina and Tuomo J. did a major part of the brood monitoring from 2004 onwards. Heikki, John, Panu, Raimo, Tuomo J. and Tuomo P. were all involved in the exhaustive predator counts. To all of you I want to say: *Kiitos, nostan hattua!* I am also grateful for all the landowners, local hunters and game societies in Petäjävesi, Keuruu, Multia, Jämsänkoski, Jämsä and Jyväskylän maalaiskunta to allow the radio tagging of the female grouse. Indeed, you have been very cooperative. Moreover, thousands of hunters and other volunteers have been annually involved in the grouse counts ever since 1964, and since 1989 additionally in the snow track counts all over the country. This assiduous endeavor is unique worldwide and

deserves high respect. Without the *sisu* of these people we would not be where we are now. I am greatly indebted and very thankful to all the people doing this hard work.

I am very thankful to the precious work and comments provided by Esa Ranta and Hannu Pöysä, who critically reviewed and pre-examined the thesis. I also want to thank to Veijo Kaitala, whose support during difficult times made me stay in science. Many people have been giving valuable comments to manuscripts, including the members of the *round table* (nowadays *journal club*), Christophe Lebigre, Marjo Pihlaja as well as a number of anonymous referees. I am very thankful to them. Special thanks goes to Maxine Iversen for the help with the language in some of the manuscripts. Many other people from our section have helped me in one way or another: Johanna Mappes, Mikko Mönkkönen, Jari Haimi, Hannu Ylönen, our technical staff Juha Ahonen, Tarmo Halinen and Hannu Kautto, and of course the computer rescuers Harri Kovanen and Samuli Koskimaa. Thanks to you all.

I am grateful to all friends that have been supporting me during the years. Discussions and kickboxing with Kristian Meissner were essential to keep my mind fresh. Thanks also to John Loehr for shared outdoor activities and discussions. I particularly want to express my dearest gratitude to my mother Elvira. Thank you for all your support, for all the courage and love you have been giving to me and my family, and for always having faith in me.

Finally, nothing would make sense without my family. My beloved wife Riitta and our two wonderful children Iina Annika and Leif Ilari have been my oasis throughout my studies and my work! Thank you so much for all your love, your invaluable support and your great patience.

This thesis was funded by the Maj and Tor Nessling Foundation and the Finnish Centre of Excellence in Evolutionary Research.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Kanalintukantojen laskuun vaikuttavat tekijät

Suomen metsäkanalintukannat ovat vähentyneet merkittävästi ainakin viimeisen 40 vuoden ajan. Pesiin ja poikasiin kohdistuvaa saalistusta on yleisesti pidetty tärkeimpänä syynä kanalintukantojen laskuun. Hakkuiden ja nuorten metsien osuuden lisääntymisen on katsottu lisänneen myyräkantoja ja niitä syöviä generalistipetoja, lisäten näin myös kanalintujen pesiin ja poikasiin kohdistuvaa saalistusta. Toisaalta ei ole tiedossa, miten voimakkaasti suurpetojen vähentyminen on voinut edesauttaa generalistipetojen, kuten ketun, runsastumista. Samoin ei tiedetä, miten vuosikymmeniä jatkunut soiden ojitus on vaikuttanut metsäkanalintuihin. Väitöskirjani tavoitteena oli vastata kysymykseen *Miksi metsäkanalinnut ovat vähentyneet talousmetsissä* ja selvittää laskuun vaikuttavia tekijöitä. Vastatakseni tähän kysymykseen yhdistin laajat yksilötason tutkimukset läntisen Keski-Suomen teerillä ja Riista- ja kalatalouden tutkimuslaitoksen ohjauksessa kerättävän jo yli 40 vuoden pituisen aineiston metsäkanalintulaskennoista.

Eräs tärkeimmistä johtopäätöksistäni on, että vuosikymmenten aikana laskenut poikastuotto on keskeisessä roolissa kanalintukantojen laskussa. Tämä on todennäköistä, koska ainakaan teerellä vuotuinen aikuiskuolleisuus ei ole lainkaan lisääntynyt. Hengissä säilyminen on päinvastoin osittain jopa parantunut.

Pedot ja niiden lisääntyminen ovat edelleenkin tärkeänä osasyynä poikastuoton laskuun. Uudet tulokset pesien seurannasta viittaavat siihen, että soiden ojitus on lisännyt saalistusriskiä ainakin teerenpesillä. Populaatio- ja ojitusaikeisiin perustuva tutkimukseni osoittaa lisäksi, että ojitus on vaikuttanut haitallisesti metson, teeren ja pyyn vuotuisen poikastuottoon Etelä- ja Keski-Suomessa, muttei Pohjois-Suomessa. Todennäköisempinä syinä voidaan pitää reunavaikutuksen kautta lisääntynyttä saalistusta, eri aika- ja paikkaskaaloilla tapahtuneita muutoksia kenttäkerroksen kasvillisuudessa ja hyönteisyhteisöissä, sekä poikasten hukkumista ojiin.

Suurpetojen, erityisesti ilveksen, voimakas lisääntyminen on aikasarja-analyysien mukaan vähentänyt ainakin alueellisesti kettutiheyksiä, mikä heijastuu jo nyt positiivisesti metsäkanalintuihin. Tämä viittaa vahvasti siihen, että suurpetojen vähentyminen 1900-luvulla edesauttoi generalistipetojen lisääntymistä. Kyseinen tapahtumasarja on erittäin merkittävä, ja saattaa ulottua muihinkin eläinryhmiin. Ilves kilpailee ketun kanssa ravinnosta, ja siksi ilves vähentää tehokkaasti kettuja. Ketun vähentyminen voi lisätä sen saalislajien yksilömääriä, kuten metsäkanalintuja, vaikka ne itsekin ovat ilveksen saaliskohteita.

Yleisesti on esitetty, että alkukesän sääoloilla voi olla suuri vaikutus vuotuisiin kanalintujen kannanvaihteluihin. Tämän tekijän totesin erittäin merkittäväksi, mutta yllättäen niin, että myös itse tekijä on muuttunut pitkällä aikavälillä. Selityksenä on ilmastonmuutos, joka on vaikuttanut eri tavoin pesinänajoituksen määräävään huhtikuun lämpötilaan ja poikasten kuoriutumishetken sääoloihin. Lämmenneet huhtikuut ovat aikaistaneet pesintää (aineistoa

läntisen Keski-Suomen teeristä 1987 lähtien), mutta kesäkuussa kuoriutumisaikojen lämpötila ei ole muuttunut, ja poikaset kuoriutuvat nykyään yhä useammin epäedullisissa oloissa. Monilla lintulajeilla on muuallakin todettu, että ilmaston muuttuminen on aiheuttanut pesinnän poikkeamisen suotuisimmasta ajankohdasta. Aiemmin ei kuitenkaan ole osoitettu, että tämä nk. "mismatching"-ilmiö voi todella johtaa populaatioiden koon pienenemiseen. Lisäksi esitän mallin, joka selittää 1980-luvulla havaitun syklisyyden häviämisen metsäkanalintupopulaatioista.

Poikastuoton turvaaminen on mitä todennäköisimmin paras keino hillitä kanalintukantojen alamäkeä. Tulokseni viittaavat siihen, että toipuva ilveskanta on tehokas keino pitämään kettutiheydet alhaisina, joskin esimerkiksi eteläisessä Suomessa kettutiheydet ovat vieläkin liian suuria. Poikastuottoa voitaisiin parantaa myös sellaisella metsähoidolla, joka suosisi mustikan elpymistä tai lisääntymistä. Myös rämeiden suojelulla ja ojitettujen mutta taloudellisesti merkityksettömien soiden ennallistamisella voitaisiin parantaa poikastuottoa. Lisäksi kannattaisi hyödyntää paikallista tietoa kuoriutumisen jälkeisistä sääoloista, varsinkin aikaisina vuosina. Vuoden aikaisuus ja alkukesän kylmyys ja sateisuus olisi hyvä ottaa huomioon, kun päätetään syksyisistä metsästyskiintiöistä.

REFERENCES

- Airaksinen, K. 1941. Riistakannan suuruuden vaihtelusta. *Metsästys ja Kalastus* 30 (in Finnish).
- Airaksinen, K. 1946. Kanalintujen runsaudenvaihtelusta Suomessa (Fluctuations in numbers of Gallin in Finland). *Suomen Riista* 1, 75-92 (in Finnish).
- Alatalo, R., Höglund, J. & Lundberg, L. 1991. Lekking in the black grouse - a test of male viability. *Nature* 352, 155-156.
- Alatalo, R., Höglund, J., Lundberg, L. & Sutherland, J. 1992. Evolution of black grouse leks - female preferences benefit males in larger leks. *Behavioral Ecology* 3, 53-59.
- Andrén, H. (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73, 794-804.
- Andrén, H., Lindström, E. & Widen, P. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. *Holarctic Ecology* 8, 285-298.
- Angelstam, P. (1992) Conservation of communities - the importance of edges, surroundings and landscape mosaic structure. In Hansson (ed.): *Ecological principles of nature conservation*. Elsevier Applied Science, London, UK.
- Baines, D. 1991. Factors contributing to local and regional variation in black grouse breeding in northern Britain. *Ornis Scandinavica* 22, 264-270.
- Begon, M., Townsend, C.R. & Harper, J.L. 2006. *Ecology: from individuals to Ecosystems*. Blackwell publishing, Oxford.
- Bousquet, K.R. & Rotella, J.J. 1998. Reproductive success of sharp-tailed grouse in Montana. *Prairie Naturalist* 30, 63-70.
- Braun, C.E., Martin, K. & Robb, L.A. 1993. White-tailed ptarmigan. In Poole, A. & Gill, F. (eds.): *The Birds of North America*, No. 68, 1-24. Philadelphia: The Academy of Natural Sciences & Washington: The American Ornithologists' Union.
- Bromeé, F. 1936. Växlingar i Västerbottens viltbestånd med särskild hänsyn till skågsfågeln. Västerbottens läns jaktvårdsförenings Årsbok 1936.
- Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer Verlag.
- Caizergues, A. & Ellison, L.N. 1997. Survival of black grouse (*Tetrao tetrix*) in the French Alps. *Wildlife Biology* 3, 177-186.
- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426, 655-658.
- Dahl, K. 1922. Ti aars iagttagelser over skogsfugl og ryper. *Norsk Jaeg. Og Fisk. For. Tidsskr.* 51.
- Dahl, K. 1935. Priodiske variasjoner i småviltbestanden. VI. Nordiske Jaegerkongress 1935, Oslo.

- Crick, H.Q.P. & Sparks, T.H. 1999. Climate change related to egg-laying trends. *Nature* 399, 423-424.
- Crooks, K.R. & Soulé, M.E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400, 563.
- Elmhagen, B. & Rushton, S.P. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters*, 10, 197-206.
- Erikstad K.E. 1985. Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. *Ornis Scandinavica* 16, 181-90.
- Erikstad K.E. & Andersen, R. 1983. The effect of weather on food intake, insect prey selection and feeding time in different sized willow grouse broods. *Ornis Scandinavica* 14, 249-252.
- Esseen P.A., Ehnström, B., Ericson, L. & Sjöberg, K. 1992. Boreal forests - the focal habitats of Fennoscandia. - In Hansson, L. (ed): *Ecological principles of nature conservation*. Elsevier Applied Science.
- Flack, V.F. & Chang, P.C. 1987. Frequency of selecting noise variables in subset regression analysis: a simulations study. *The American Statistician* 41, 84-86.
- Grouse committee 1911. *The final report of 1911*. London.
- 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.
- Hastings, J. 1948. The mystery of the ten year cycle. *Hunting and Fishing in Canada* 9.
- Heikurainen, L. 1980. Drainage condition and tree stand in peatlands drained 20 years ago. *Acta Forestalia Fennica* 167, (In Finnish with English summary).
- Helle, P. and Helle, T. 1991. How do changes in forest structure explain recent changes in Finnish grouse populations. *Suomen Riista* 37, 56-66 (in Finnish with English summary).
- Helle, P. and Nikula, A. 1996. Usage of geographic information systems (GIS) in analyses of wildlife triangle data. *Finnish Game Research* 49, 26-36.
- Helle, P. & Ludwig, G. 2003. Onko ojituksella vaikutusta metsäkanalintujen määrään? In Jortikka, Sinikka, Varmola, Martti & Tapaninen, Sirkka (eds.): *Soilla ja kankailla - metsien hoitoa ja kasvatusta Pohjois-Suomessa*. Metsäntutkimuslaitoksen tiedonantoja 903, 33-40 (in Finnish).
- Helle P., Jokimäki, J. & Lindén, H. 1990. Habitat selection of the male capercaillie in Northern Finland - a study based on telemetry. *Suomen Riista* 36, 72-81 (in Finnish with English summary).
- Helle, P., Lindén, H. & Wikman, M. (2002) Metsäkanalintujen viimeaikaisista runsaudenmuutoksista Suomessa. *The Yearbook of the Linnut Magazine* 2002, 9 (In Finnish).

- Helle, P., Nikula, A., Kumpu, P. & Kurki, S. 1996. Located observations in wildlife triangle scheme: use of geographic information systems. *Suomen Riista* 42, 52-66 (in Finnish with English summary).
- 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. (in Finnish with English summary).
- Hissa, R., Rintamäki, H., Saarela, S., Marjakangas, A., Hohtola, E. & Lindén, H. 1982. Energetics and development of temperature regulation in gallinaceous birds. *Suomen Riista* 29, 29-39 (in Finnish with English summary).
- Hissa, R., Saarela, S., Rintamäki, H., Lindén, H. & Hohtola, E. 1983. Energetics and development of temperature regulation in capercaillie *Tetrao urogallus*. *Physiological Zoology* 56, 141-151.
- Höglund, J. & Alatalo, R. 1995. *Leks*. Princeton University Press.
- Hökkä, H., Kaunisto, S., Korhonen, K.T., Päivänen, J., Reinikainen, A. & Tomppo, E. (2002) *Suomen Suometset 1951-1994. Metsätieteen aikakausikirja* 2B, 201-357. (in Finnish with English summary).
- Hosmer, D.W. & Lemeshow, S. 1989. *Applied logistic regression*. John Wiley & Sons.
- Hudson, P.J. & Rands, M.R.W. (eds.) 1988. *Ecology and Management of Gamebirds*. BSP. Oxford.
- Huhta E. 1996. Effects of forest fragmentation on reproductive success of birds in boreal forests. PhD thesis. University of Jyväskylä.
- IPCC 2007. *Climate Change 2007. Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Summary for Policymakers*, 10th Session of Working Group I of the IPCC, Paris, February 2007.
- Johnsgaard, P.A. (1983) *The grouse of the world*. Croom Helm, London & Canberra.
- Kastdalen, L. & Wegge, P. 1991. Chick mortality in capercaillie grouse. Internal report, Institut for Biologi og Naturforvaltning, noroges Landbruks-hogskole.
- Kauhala, K. & Helle P. 2002. The impact of predator abundance on grouse populations in Finland - a study based on wildlife monitoring counts. *Ornis Fennica* 79, 14-25.
- Kauhala, K., Helle, P. & Helle, E. 2000. Predator control and the density and reproductive success of grouse populations in Finland. *Ecography* 23, 161-168.
- Kloster, R. 1936. Bergens Jaeger- og Fisker-Foenings rypeundersökelse 1921-1927. Et resumé VI. Nordiske Jaegerkongress 1935, Oslo.
- Krebs, C.J. 1995. Two paradigms of population regulation. *Wildlife Research* 22, 1-10.
- Kurki, S. 1997. Spatial variation in the breeding success of forest grouse: the role of predation in fragmented boreal forest landscapes. PhD thesis, University of Turku.

- Kurki, S. 1999. Effects of fragmentation on breeding success of grouse. Suomen Riista 45, 16-24 (in Finnish with English summary).
- Kurki, S. & Lindén, H. 1993. The effect of forest area on grouse densities obtained in wildlife triangle censuses. Suomen Riista 39, 61-73 (in Finnish with English summary).
- 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. Abundance of red fox and pine marten in relation to the composition of boreal forest landscapes. Journal of Animal Ecology 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.
- Larson, M.A., Clark, M.E. & Winterstein, S.R. 2001. Survival of ruffed grouse chicks in northern Michigan. Journal of Wildlife Management 65, 880-886.
- Lesley, A.S. & Shipley, A.E. 1912. *Grouse in health and in disease*. London.
- Lindén, H. 1981a. Changes in Finnish tetraonid populations and some factors influencing mortality. Finnish Game Research 39, 3-11.
- Lindén, H. 1981b. Growth rates and early energy requirements of captive juvenile capercaillie, *Tetrao urogallus*. Finnish Game Research 39, 53-67.
- Lindén, H. 1984. Annual patterns in the ecological energetics of the capercaillie, *Tetrao urogallus*, in captivity. Finnish Game Research. 42, 19-27.
- Lindén, H. (ed.) 2002. Metsäkanalintutkimuksia. Riista- ja Kalatalouden tutkimuslaitos, Metsästäjien Keskusjärjestö. Gummerus oy.
- Lindén, H., Wikman, M. & Helle, E. 1989. Tetraonid populations in Finland in 1988: A comparison between the route censuses and the wildlife triangles. Suomen Riista 35, 36-42 (in Finnish with English Summary).
- Lindén, H., Helle, E., Helle, P. & Wikman, M. 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. Finnish Game Research 49, 4-11.
- Lindström, E.R. 1989. The role of medium-sized carnivores in the Nordic boreal forest. Finnish Game Research, 46, 53-63.
- Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J.E. 1994. Disease reveals the predator – Sarcoptic mange, red fox predation, and prey populations. Ecology 75, 1042-1049.
- Lindström, J. 1994. Tetraonid population studies – state of the art. Annales Zoologici Fennici 31, 347-364.
- Lindström, J. 1996a. Weather and grouse population dynamics. Wildlife Biology 2, 93-99.

- Lindström 1996b. Modelling grouse population dynamics. PhD thesis, University of Helsinki.
- Lindström, J., Ranta, E., Kaitala, V. & Lindén, H. 1995. The clockwork of Finnish tetraonid population dynamics. *Oikos* 74, 185-194.
- Lindström, J., Ranta, E. & Lindén, H. 1996. Large-scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland. *Oikos* 76, 221-227.
- 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.
- Madge, S. & McGowan, P.J.K 2002. *Pheasants, partridges and grouse*. Christopher Helm Publishers.
- Marcström, V., Kenward, R.E. & Engren, E. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. *Journal of Animal Ecology* 57, 859-872.
- Manzer, D. 2004. Sharp-tailed grouse breeding success, survival, and site selection in relation habitat measured at multiple scales. PhD thesis, University of Alberta.
- Marjakangas, A. 1996. Nest losses in a boreal black grouse population. *Suomen Riista* 42, 25-31 (in Finnish with English summary).
- Marjakangas, A., Rintamäki, H. & Hissa, R. 1984. Thermal responses in the capercaillie and the black grouse roosting in snow. *Physiological Zoology* 57, 99-104.
- Menard, S. 1995. *Applied logistic regression analysis*. Sage, Thousand Oaks.
- Merikallio, E. 1922. Oulangan seudun ja Kaakkois-Kuolajärven linnusto. *Acta Societas Fauna et Flora Fennica* 48.
- Miller, A.J. 1990. *Subset selection in regression*. Chapman and Hall, London.
- Miquet, A. 1990. Mortality in black grouse *Tetrao tetrix* due to elevated cables. *Biological Conservation* 54, 349-355.
- Moss, R., & Hanssen, I. 1980. Grouse nutrition. *Nutrition Abstracts and Reviews* B 50, 555-567.
- Palmgren, P. 1930. Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands mit besonderer Berücksichtigung Ålands. *Acta Zoologica Fennica* 7.
- Park, K.J., Booth, F., Newborn, D. & Hudson, P.J. 2002. Breeding losses of red grouse in Glen Esk (NE Scotland): comparative studies, 30 years on. *Annales Zoologici Fennici* 39, 21-28.
- Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.
- Potts, G.R. 1986. *The partridge. Pesticides, predation and conservation*. Collins.
- Rajala, P. 1959. On the food habits of capercaillie juveniles. *Suomen Riista* 13, 143-155 (in Finnish).
- Rajala, P. 1962. On the estimation of brood density of the tetraonids. *Suomen Riista* 15, 175-180 (in Finnish with English summary).

- Rajala, P. 1963. The number of tetraonid birds and their occurrence in various habitat types in the Oulu district according to compass line census, 1966. *Suomen Riista* 19, 130-144 (in Finnish with English summary).
- Rajala, P. 1974. Finnish tetraonid populations in August 1972 compared with the period 1963-1971 according to route census. *Suomen Riista* 25, 56-63 (in Finnish with English Summary).
- Rajala, P. & Lindén, H. 1982. Effect of drainage and fertilization of pine swamps on the abundance of some game animals. *Suomen Riista* 29, 93-97 (in Finnish with English summary).
- Ranta, E., Lindström J. and Lindén H. 1995. Synchrony in tetraonid population dynamics. *Journal of Animal Ecology* 64, 767-776.
- Ranta, E., Helle, P. & Lindén, H. 2004. Forty years of grouse monitoring in Finland. *Suomen Riista* 50, 128-136 (in Finnish with English summary).
- Ranta, E., Lundberg, P. & Kaitala, V. 2006. *Ecology of Populations*. Cambridge University Press.
- Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.) 2000. Changes in the frequency and abundance of forest and mire plants in Finland since 1950. Tammi, Helsinki (in Finnish with English Summary).
- Royama, T. 1992 *Analytical Population Dynamics*. Chapman & Hall, London, UK
- Sæther, B.-E. 1997 Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution* 12, 143-149.
- Sæther, B.E. 1999. Top dogs maintain diversity. *Nature* 400, 510-511.
- Siitari, H., Alatalo, R.V., Halme, P., Buchanan, K. L. & Kilpimaa, J. 2007: Color signals in the Black Grouse (*Tetrao tetrix*): signal properties and their condition dependency. *American Naturalist* 169, 81-92.
- Siivonen, L. 1943. Muutama näkökohtia riistan runsauden jaksottaisesta vaihtelusta. *Ibid.* 32.
- Siivonen, L. 1948. Structure of short-cyclic fluctuations in numbers of mammals and birds in the northern parts of the northern hemisphere. *Papers on Game Research* 1, 1-166.
- Siivonen, L. 1951. Metsälintujen voimaperäinen hoito on aloitettava viipymättä. *Suomen Riista* 6, 32-45.
- Siivonen, L. 1952. On the reflection of short-term fluctuations in numbers in the reproduction of tetraonids. *Papers on Game Research* 9, 1-43.
- Siivonen, L. 1953a. Can the abundance of tetraonids in fall be forecast? *Suomen Riista* 8, 42-45 (in Finnish with English summary).
- Siivonen, L. 1953b. Variation in the hatching time of the eggs of gallinaceous birds. *Suomen Riista* 8, 147-150 (in Finnish with English summary).
- Siivonen, L. 1957. The problem of short-term fluctuations in numbers of tetraonids in Europe. *Papers on Game Research* 19, 1-44.
- Siivonen, L. 1958. Metsälintukatojen perussyistä ja saatujen tulosten soveltavuusmahdollisuuksista. *Suomen Riista* 12, 43-54 (in Finnish).
- Smith, R.L. 1980. *Ecology and Field Biology*. Harper & Row, NY.

- Smith, A. & Willebrand, T. 1999. Mortality causes and survival rates of hunted and unhunted willow grouse. *Journal of Wildlife Management* 63, 722-730.
- Soulé, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M. and Hill, S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2, 75-92.
- Spidsö T.K., Hjeljord, O. & Dokk, J.G. 1997. Seasonal mortality of black grouse during a year with little snow. *Wildlife Biology* 3, 205-209.
- Storch, I. 1994. Habitat and survival of capercaillie *Tetrao urogallus* nests and broods in the Bavarian Alps. *Biological Conservation* 70, 237-243.
- Storch, I. 2000. Conservation status and threats to grouse worldwide: an overview. *Wildlife Biology* 6, 195-204.
- Sutherland, W.J. 1996. *From individual behaviour to population ecology*. Oxford University Press.
- Taylor, R.J. 1984. *Predation*. Chapman and Hall. New York.
- Thirgood, S., Redpath, S.M., Rothery & Aebischer, N.J. 2000. Raptor predation and population limitation in red grouse. *Journal of Animal Ecology* 69, 504-516.
- Tornberg, R. 2000. Effect of changing landscape structure on the predator-prey interaction between goshawk and grouse. PhD thesis, University of Oulu.
- Turchin, P. 2003. *Complex Population Dynamics*. Princeton University Press
- Varley, G.C., Gradwell, G.R. & Hassell, M.P. 1973. *Insect Population Ecology*. University of California Press, California.
- Wegge P., Olstad T., Gregersen H., Hjeljord O. & Sivkov A.V. 2005. Capercaillie broods in pristine boreal forest in northwestern Russia: the importance of insects and cover in habitat selection. *Canadian Journal of Zoology* 83, 1547-1555.
- Välikangas, I. 1937. Qualitative und quantitative Untersuchungen über die Vogelfauna der isolierten Insel Suursaari im Finnischen Meerbusen. I. Die Landvogelfauna. *Ann. Acad. Scient. Fenn. Ser. A. XLV*, No 5.
- Willebrand, T. 1988. Demography and ecology of a black grouse (*Tetrao tetrix*) population. PhD thesis, University of Uppsala..
- Zbinden N. & Salvioni M. 2004. Bedeutung der Temperatur in der frühen Aufzuchtzeit für den Fortpflanzungserfolg des Birkhuhns *Tetrao tetrix* auf verschiedenen Höhestufen im Tessin, Südschweiz. *Der Ornithologische Beobachter* 101, 307-318.