OULU 2014
A 620

ACTA
UNIVERSITATIS OULUENSIS

A
SCIENTIAE RERUM
NATURALIUM

Marja Isomursu

HOST–PARASITE INTERACTIONS OF BOREAL FOREST GROUSE AND THEIR INTESTINAL HELMINTH PARASITES

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE, DEPARTMENT OF BIOLOGY

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MARJA ISOMURSU

HOST–PARASITE INTERACTIONS OF BOREAL FOREST GROUSE AND THEIR INTESTINAL HELMINTH PARASITES

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Kuusamonsali (Auditorium YB210), Linnanmaa, on 8 February 2014, at 12 noon

UNIVERSITY OF OULU, OULU 2014

Acta Univ. Oul. A 620, 2014

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ISBN 978-952-62-0363-8 (Paperback)
ISBN 978-952-62-0364-5 (PDF)

ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online)

Cover Design
Raimo Ahonen

JUVENES PRINT
TAMPERE 2014

Isomursu, Marja, Host–parasite interactions of boreal forest grouse and their intestinal helminth parasites.
University of Oulu Graduate School; University of Oulu, Faculty of Science, Department of Biology
Acta Univ. Oul. A 620, 2014
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Abstract

Parasites are an inseparable part of the life of wild birds. They may cause morbidity, mortality or reduction in fecundity. Parasite distribution in hosts is typically not uniform and many host factors (e.g. age) may affect the pattern of distribution. Under certain conditions, parasites even have the potential to regulate the host population. The grouse species of Finnish forests — the capercaillie *Tetrao urogallus*, the black grouse *Lyrurus tetrix* and the hazel grouse *Tetrastes bonasia* — harbour several species of intestinal helminth parasites. The populations have fluctuated in cyclic manner but the mechanisms behind the cycles are largely unknown. I studied the interactions of forest grouse and their intestinal helminth parasites by using intestinal samples collected by hunters in five game management districts during eight years (1995–2002). The most common parasite species in the samples was the nematode *Ascaridia compar*. Also, three species of cestodes (*Skrjabinia cesticillus*, *Paroniella urogalli* and *Hymenolepis* sp.) were found. Large size, male gender and age over 1 year were connected with an increased probability and intensity of *A. compar* infection. Juvenile grouse were commonly infected with cestodes while in adults infections were quite rare. The influence of inbreeding on the susceptibility to parasite infections was studied in the capercaillie by analysing microsatellite heterozygosity. The less heterozygous birds were more likely to be infected with *A. compar* and were more intensely infected suggesting negative influence of inbreeding on parasite resistance. An indirect negative effect of parasites was found by comparing bags hunted with a trained dog or without a dog. Grouse infected by cestodes were significantly more common in the dog-assisted bag. Thus, cestode infection seemed to make grouse more vulnerable to canine predation. The interaction between grouse population dynamics and parasites was studied by analyzing the grouse densities obtained from annual wildlife counts and parasite indices. *A. compar* was most common and most abundant in the years of grouse population decline. The grouse population growth rate was negatively correlated with the annual mean abundance of *A. compar*. Relative survival but not breeding success decreased as the abundance of *A. compar* increased. The findings suggest that *A. compar* influences the dynamics of Finnish grouse even though regular cyclic dynamics are no longer evident.

Keywords: black grouse, capercaillie, distribution, hazel grouse, heterozygosity, intestinal parasites, population dynamics, predation, regulation

Isomursu, Marja, Metsäkanalintujen ja niiden suolistoloismatojen väliset vuorovaikutukset.
Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta, Biologian laitos
Acta Univ. Oul. A 620, 2014
Oulun yliopisto, PL 8000, 90014 Oulun yliopisto

Tiivistelmä

Loiset kuuluvat erottamattomana osana luonnonvaraisten lintujen elämään. Ne voivat aiheuttaa sairautta, kuolleisuutta tai hedelmällisyyden alentumista. Tyypillisesti loiset ovat levinneet isäntäpopulaatioon epätasaisesti ja monet isännän ominaisuudet (esim. ikä) vaikuttavat levinneisyyteen. Tietyissä oloissa loiset voivat jopa säädellä isäntäpopulaatiotaan. Suomalaiset metsäkanalinnut — metso *Tetrao urogallus*, teeri *Lyrurus tetrix* ja pyy *Tetrastes bonasia* — ovat useiden suolistoloismatolajien isäntiä. Metsäkanapopulaatiot ovat vaihdelleet syklisesti, mutta syklejä aiheuttavat mekanismit ovat yhä tuntemattomia. Tutkin metsäkanalintujen ja niiden suolistoloisten välisiä vuorovaikutuksia käyttäen metsästäjien vuosina 1995–2002 viidestä eri riistanhoitopiiristä keräämiä suolistonäytteitä. Yleisin loislaji näytteissä oli kanalintusuolinkainen, *Ascaridia compar*. Myös kolme heisimatolajia (*Skrjabinia cesticillus*, *Paroniella urogalli* ja *Hymenolepis* sp.) todettiin. Suuri koko, koirassukupuoli ja yli yhden vuoden ikä olivat yhteydessä suurempaan kanalintusuolinkaistartunnan todennäköisyyteen ja voimakkuuteen. Nuorilla (alle 1 v.) linnuilla heisimadot olivat yleisiä, kun taas aikuisilla tartunnat olivat varsin harvinaisia. Sisäsiittoisuuden vaikutusta loistartuntaherkkyyteen tutkittiin metsolla mikrosatelliittiheterotsygotian perusteella. Vähemmän heterotsygoottiset metsot olivat todennäköisemmin ja voimakkaammin suolinkaisten infektoimia, mikä viittaa sisäsiittoisuuden negatiiviseen vaikutukseen loisten vastustuskykyyn. Loisten epäsuora haitallinen vaikutus havaittiin, kun verrattiin koiran kanssa ja ilman koiraa metsästettyä lintusaalista. Heisimadot olivat selvästi yleisempiä linnuilla, jotka oli metsästetty koiran kanssa kuin ilman koiraa metsästetyillä. Heisimatotartunta näytti siis altistavan metsäkanoja koiraeläinten saalistukselle. Metsäkanalintu- ja loispopulaatioiden välistä vuorovaikutusta tutkittiin analysoimalla vuosittaisia metsäkanatiheyksiä ja loisten runsautta. Kanalintusuolinkainen oli yleisimmillään ja runsaimmillaan metsäkanatiheyden laskuvuosina. Metsäkanapopulaation vuosittainen kasvuvauhti korreloi negatiivisesti kanalintusuolinkaisen vuosittaisen runsauden kanssa. Suhteellinen elossasäilyvyys laski kanalintusuolinkaisen runsauden lisääntyessä, mutta lisääntymistuloksen suhteen ei ollut samaa ilmiötä. Löydökset viittaavat siihen, että kanalintusuolinkaisella on vaikutusta suomalaisten metsäkanalintukantojen vaihteluihin, vaikka syklisiä kannanvaihteluja ei enää havaitakaan.

Asiasanat: heterotsygotia, kanalintusuolinkainen, levinneisyys, metso, metsäkanalintu, populaatiodynamiikka, pyy, saalistus, suolistoloiset, säätely, teeri

Acknowledgements

The most important people supporting the making of this thesis have been the main supervisors and co-authors Osmo Rätti and Pekka Helle. The grouse parasite project was originally their creation and the author was kindly and warmly welcomed to join the group when the wheels had already been rolling for a good while. Especially Osmo Rätti had a crucial role in planning and pushing the project forward. I humbly thank you both.

I also want to thank the following:

Professor Arja Kaitala for kindly supervising the thesis – especially the final stages – and for helping to improve the summary of the thesis.

Docent Sven Nikander for his invaluable expertise in identifying the parasite species.

Docent Jouni Aspi, Marko Mutanen and Anssi Vainikka for being the doctoral training follow-up group.

Co-authors Tuula Hollmén and Tuija Liukkonen for their important contribution in the articles.

Professors Jacob Höglund and Timo Soveri for reviewing this thesis.

Pekka Isomursu for linguistic guidance.

My employer, the Finnish Food Safety Authority Evira, and all my co-workers there for practical help and for their positive and supportive attitude towards the long PhD project.

The Education Fund for financial support during the final preparation of the thesis.

The personnel of the Finnish Game and Fisheries Research Institute (Jorma Korhonen, Ulriikka Ojanen and Paavo Kumpu) for pre-handling the intestinal samples.

I express my sincerest and warmest thanks to all the grouse hunters who took part in collecting the vast material, making this study possible.

List of original articles

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I Isomursu M, Rätti O, Helle P & Hollmén T (2006) Sex and age influence intestinal parasite burden in three boreal grouse species. J Avian Biol 37: 516–522.

II Isomursu M, Rätti O, Liukkonen T & Helle P (2012) Susceptibility to intestinal parasites and juvenile survival are correlated with multilocus microsatellite heterozygosity in the Capercaillie (*Tetrao urogallus*). Ornis Fenn 89: 109–119.

III Isomursu M, Rätti O, Helle P & Hollmén T (2008) Parasitized grouse are more vulnerable to predation as revealed by a dog-assisted hunting study. Ann Zool Fenn 45: 496–502.

IV Isomursu M, Rätti O & Helle P (2013) Intestinal parasites as potential factors in the dynamics of fluctuating forest grouse populations in Finland. Manuscript.

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1 Introduction

The forest grouse are widely distributed and common game birds that have long been the object of active ecological research in Finland. The forest grouse population consists of three species, the capercaillie *Tetrao urogallus*, the black grouse *Lyrurus tetrix* and the hazel grouse *Tetrastes bonasia*. The species inhabit forest environment but they have differences e.g. in the breeding systems and body size. Since the early days of game biology, grouse have been known to harbour several parasite species, intestinal helminths being the most conspicuous ones. However, parasitological ecology of Finnish forest grouse has not received much attention since the pioneering work in the 1950's and 1960's even though parasites may have a variety of impacts on their hosts on individual and population level.

A prominent feature of the Finnish forest grouse that has intrigued ecologists has been the nature of population cycles. The forest grouse population peaks occurred every 6–7 years followed by equally regular crashes (Lindén 1989, Lindström *et al.* 1995). The pattern was similar in all three species with marked synchrony (Lindström *et al.* 1996). Despite the elaborate analyses of grouse cycles the driving factors behind them are still under debate. The dynamics changed to irregular fluctuations after a notable population decline starting from the 1960's and continuing to the early 1990's bringing more complexity to the issue (Ranta *et al.* 2004). By affecting directly or indirectly the mortality and reproduction of their hosts parasites can modify the host population dynamics. To assess the importance of parasites in grouse population dynamics the basics of the host-parasite interactions need to be examined. I set out to study the occurrence and distribution of intestinal parasites in relation to host factors. I also examine a possible indirect effect of parasites by comparing the hunting mortality of parasitized and non-parasitized grouse. Eventually, I come back to the fundamental question of grouse population fluctuations: is parasitic regulation possible in the Finnish forest grouse population?

1.1 Background of grouse parasite research

Diseases of game birds were regarded important in the early days of Finnish game biology and published reports are available since the 1920's (see literature in Lampio 1946). The forest grouse have always been highly valued game species. During the first decades of the 20th century — in addition to the amount of game consumed in Finland — the export statistics underline the economic importance of hunting. At its best, the foreign trade amounted to 500 000 kg annually, of which a large part consisted of capercaillie and other tetraonid birds (Airaksinen 1946). More than one third of all hunters participate in grouse hunting annually. Not surprisingly, the diseases and parasites of grouse have raised questions and concerns among the hunting public. Parasites and diseases were also the focus of international game research before the 1960's (Moss *et al.* 2010).

The population peaks and crashes of grouse and some mammals were recognised early by Finnish biologists (Siivonen 1948, Siivonen 1954). The possible connection between diseases and parasites and grouse population dynamics was also suggested early (Nansen in Anon. 1914, Lampio 1946). The proportion of diseased and parasitized grouse seemed to be highest when the population sizes of the capercaillie, the black grouse and the hazel grouse were at their lowest (Lampio 1946).

The ascarid nematode of grouse *Ascaridia compar*, received special attention from researchers in the 1950's and 60's. Muroma and Helminen (1956) collected faecal samples from grouse hunters and found that ascarids occurred all over the country in capercaillie and black grouse. Raitis and Helminen (1969) performed a more comprehensive study on *A. compar* using faecal and also some intestinal samples reporting parasite prevalences and observations on temporal and geographical occurrence of *A. compar* as well as some notions on the associations between host factors and *A. compar* infection.

A new era for the ecology of parasites was launched when the fundamental papers by Anderson and May (1978) and May and Anderson (1978) were published. They showed by mathematical modelling that parasites can in fact regulate their hosts if certain conditions are met. At around the same time, the role of parasites in the sexual selection of birds was highlighted by Hamilton and Zuk (1982). These ideas were soon adopted in grouse research. The interaction of red grouse and their intestinal parasites affecting the population dynamics was revealed (Hudson *et al.* 1998) and the negative effect of blood parasites on the quality of sexual traits of the male black grouse was found (Höglund *et al.* 1992). Parasites are now essential component of grouse ecology.

1.2 Intestinal parasites in the life-cycle of forest grouse

Parasites live at the expense of their host. Inevitably, parasitic infection will incur a cost on the host, whether it be a minor effect on energy balance or the ultimate cost, death. Avian intestinal helminth parasites are rarely lethal for the host but sublethal effects can be significant (Atkinson *et al.* 2008). The outcome of host – parasite interaction depends on many factors such as individual host factors, densities of both hosts and parasites or influence of other species. In the boreal forest grouse, requirements of breeding and the complex seasonal environment may affect parasite infections.

1.2.1 Breeding systems and sexual dimorphism

Spring is the intense breeding period of the capercaillie and the black grouse. They gather in leks where males display their vigour to females trying to choose a good mate (Koivisto 1965, Storch 1997). The mate choice of the female grouse in leks is based on several secondary sexual traits. Visual cues, such as colourful combs and quality of tail plumage draw female attention (Alatalo *et al.* 1991, Rintamäki *et al.* 2000). Honest signalling means that the production and maintenance of showy sexual traits is costly for the male and only individuals in good condition can maintain high-quality traits. When selecting a male with a costly display the female would get “good genes” for her offspring (Krebs & Davies 1997). Parasites can mediate sexual selection as they may negatively influence the quality of secondary sexual traits. Males with good abilities to resist parasites and diseases would also look or sound best (Hamilton & Zuk 1982, Møller 1990). Fighting ability is important and the strongest males will dominate the lek receiving most copulations (Alatalo *et al.* 1991). A large body size usually means large ornaments which promote success in leks (Höglund & Alatalo 1995). Consequently, sexual selection will favour larger males and promote sexual size dimorphism (Andersson & Iwasa 1996).

In sexually dimorphic tetraonids, sex-biases in parasite infections are anticipated. Male-bias in nematode infection prevalences seems to be a general phenomenon in birds even though the bias is not seen in cestode infections (Poulin 1996). Sex differences in parasite infections may result from ecological or physiological causes (Zuk & McKean 1990). Diets and habitats are not fundamentally different in male or female grouse but male body size is bigger and the growth rate of the male capercaillie chicks is faster than that of the females (Lindén 1981a). Higher energy requirements of the larger sex make it more exposed to orally acquired parasite infections (Zuk & McKean 1990). Physiological factors involve genetic or hormonal differences. The male androgen, testosterone, often has immunosuppressive effects in birds (Owen-Ashley *et al.*

2004) and leads to more severe parasitic infections (Mougeot *et al.* 2006). On the other hand, high blood testosterone level is connected with good mating success in black grouse male (Alatalo *et al.* 1996) which creates a possible trade-off between breeding effort and disease resistance in males.

1.2.2 Juvenile grouse and intestinal parasites

Grouse chicks hatch in June, and in less than six months they should reach a sufficient body size in order to survive the harsh winter conditions. Juvenile mortality of the dimorphic species is high, with mean survival of 7% for the capercaillie and 11% for the black grouse during the first year (Lindén 1981b). In the black grouse, juvenile survival was lower than adult survival also in England (Warren & Baines 2002) and the French Alps (Caizergues & Ellison 1997). The growth period is particularly demanding in the males of the capercaillie and the black grouse, and juvenile mortality is higher in males than in females. In the capercaillie, juvenile males have a longer growth period and higher energy requirements than juvenile females. (Lindén 1981a).

The grouse chicks are exposed to orally transmitted intestinal parasite infections from the very beginning of their lives. The parasite burden could be particularly detrimental to a young bird in the vulnerable stages of growth. In the willow grouse, the infection of the cestode (tapeworm) *Hymenolepis microps* affected negatively the body condition of both juveniles and adults and was negatively correlated with breeding mortality (chick losses) (Holmstad *et al.* 2005). Nematode (roundworm) infection may affect growth: the body weight of the juvenile willow grouse is negatively connected to the intensity of nematode infection (Dæhlen 2003).

1.2.3 Genetic diversity and parasitism

Capercaillie population experienced a dramatic decline in Finland from the 1960’s to 1990’s (Lindén 2002). The genetic effects of the recent population decline are not evident in the Finnish capercaillie population which seems to be continuous in the whole country (Liukkonen *et al.* 2004). However, in Central Europe, isolated capercaillie populations show differentiation and reduced genetic variation (Segelbacher *et al.* 2003). Small, isolated populations are at risk of losing genetic diversity and suffer from inbreeding depression (Keller & Waller 2002, Keyghobadi 2007).

The loss of genetic diversity may increase susceptibility to infectious diseases and parasites in host populations (King & Lively 2012). In addition to sudden decline in population density, genetic diversity decreases when inbreeding, i.e. mating among relatives, occurs in the population (Keller & Waller 2002). Inbreeding depression means decreased fitness as a result of increased homozygosity and the expression of deleterious alleles (Charlesworth & Charlesworth 1999, Keller & Waller 2002). The level of inbreeding can be inferred from known pedigrees but in wild populations, indirect methods are usually the only options.

Multilocus heterozygosity measured by a set of microsatellite markers has been used as a surrogate for genome-wide heterozygosity and inbreeding when studying the effects of inbreeding on various components of fitness (e.g. Coulson *et al.* 1998, Slate *et al.* 2000, Höglund *et al.* 2002). These studies found positive heterozygosity-fitness correlations (HFC's) suggesting inbreeding depression in natural populations. However, HFC's are often weak and thus difficult to detect (Coltman & Slate 2003). In order to obtain relevant results on HFC's and inbreeding depression in the population sample size should be adequate, analyses appropriate and population structure favourable (Szulkin *et al.* 2010). For example, the polygamous mating system of the capercaillie can increase the correlation between multilocus heterozygosity and inbreeding coefficient (Balloux *et al.* 2004). The study of HFC's may reveal risks of continuous population decline and fragmentation.

1.2.4 Predation and parasites

Predation is the major cause of mortality in the forest grouse (e.g. Marcström *et al.* 1988, Tornberg *et al.* 2006, Wegge & Kastdalen 2007) in all developmental stages from egg to adult. Since intestinal parasites may infect young chicks as soon as they start to feed, the interaction of parasitic infection and susceptibility to predation may be present in grouse of all ages. Predators are often thought to catch substandard prey, individuals with some sort of ailment that would make them easier to find and catch (Temple 1987). Parasites themselves can influence host behaviour and increase vulnerability to predation if it serves the completion of the parasite life-cycle (Moore 2002). For example, the moose *Alces alces* is the intermediate host for the canine tapeworm *Echinococcus granulosus* and the wolf *Canis lupus*, the definitive host, gets infected from eating infective larvae in moose organs. Study of *E. granulosus* distribution in different moose populations showed that high predation pressure from wolves decreased parasite aggregation in moose population indicating parasite-induced mortality (Joly & Messier 2004).

A parasite infection may induce behavioural changes even when there is no apparent advantage of the behaviour for the parasite (Poulin 1994). In the red grouse, the nematode *Trichostrongylus tenuis* causes change in the odour of the host through pathological intestinal lesions which makes the host easier for a mammal predator to detect (Hudson *et al.* 1992). The end result is the death of both the host and the parasite leaving only the predator benefiting of the situation. Parasites might affect the general host condition negatively and this way increase vulnerability to predation (e.g. Murray *et al.* 1997). Apparently, parasite-induced behavioural changes of the host are not always adaptive for the parasite (Moore 2002) and therefore the parasite life-cycle as such does not predict infected host's susceptibility to predation.

1.2.5 Parasite and host populations – coupled dynamics?

The multiple effects of parasites on their host may lead to large-scale effects on the host population dynamics. Population regulation is usually a density-dependent process that limits the population growth by increasing mortality or reducing birth rate (Krebs 2009). Since parasites can affect both the mortality and the fecundity of the host, they have the potential to regulate host population. Modelling shows that regulation is possible if the birth rate of the parasite exceeds the sum of parasite death rate, host birth rate and parasite-induced host death rate (Anderson & May 1978). This basic result applies in a simplified scenario where parasite-induced host mortality is linearly proportional to the numbers of parasites per host. Also, parasite transmission is assumed instantaneous (no time-delays in reaching infectivity) and parasite distribution in hosts random. In this situation, both populations will oscillate indefinitely, parasite abundance following the host abundance with a time-lag, unless some conditions are altered. On the other hand, if parasite fecundity is too low, the host population will escape the regulation and grow until other factors influence the growth (Anderson & May 1978).

The assumptions behind the basic rule formulated by Anderson & May (1978) do not often apply in nature and if these assumptions are not met there are consequences for the host-parasite interaction. Some factors stabilize population dynamics while others cause instability and population fluctuations. For instance, the parasite distribution among hosts is typically not random but aggregated in nature (Anderson & Gordon 1982). Aggregation tends to stabilise the dynamics of parasite and host populations and dampen the oscillation (Anderson & May 1978). If the parasite-induced mortality rate and parasite burden had a non-linear relationship and mortality effect increased faster than the actual number of parasites, it would be harder for the parasite to retain the regulatory effect. In this situation, if there was regulation, population dynamics would be stable in case of aggregated parasite distribution (Anderson & May 1978). Regulation by aggregated parasite population would be even more difficult to achieve if there was a density-dependent mechanism (e.g. host immune response, crowding) limiting the parasite population (Anderson & May 1978).

In addition to causing mortality among their hosts, parasites can potentially reduce host reproduction. If the effect on reproduction is small compared to mortality effect and parasites are distributed in the typical aggregated way, the host population may be regulated on a stable level (May & Anderson 1978). More random distribution of parasites in a similar situation can lead to unstable regulation and population cycles.

It is very typical of macroparasites to have time-delays in their transmission. Many nematodes produce eggs that need to develop further in the environment in order to become infective, and this period may take days or weeks (Anderson 2000). Time-delays in transmission tend to have a destabilising effect on population dynamics although parasite distribution and the relative length of the time-delay influence the outcome, too (May & Anderson 1978).

The host-parasite interaction models reveal a complex and interesting array of possible outcomes. When modelling natural populations multiple factors must be taken into account before rational predictions based on models can be made. Many of these factors, such as parasite-induced reduction in host fecundity or parameters of parasite development need to be evaluated experimentally. Not surprisingly, well-founded bird-parasite interaction models that have natural premises are still rare (e.g. Dobson & Hudson 1992, Rosà *et al.* 2011).

1.3 The host species – forest grouse

The three forest grouse species belonging to the subfamily Tetraoninae (family Phasianidae) share some common features. They inhabit forested areas in the whole of Finland although each favour different types of forest. The capercaillie is generally known as a species of mature (> 90 years old) pine-dominated coniferous forests (Swenson & Angelstam 1993). The black grouse, on the other hand, prefers early-successional forests whilst the hazel grouse habitat is typically a dense mixed young to middle aged forest with a reasonable proportion of deciduous trees (Swenson & Angelstam 1993). All species nest on the ground and the precocial chicks leave the nest soon after hatching.

The Finnish grouse populations have fluctuated in a synchronous cyclic manner with 6-7 year frequency (Lindén 1989, Lindström *et al.* 1996), a pattern which has been traced back to the late 19th century (Lindström *et al.* 1995). However, since the 1990's the fluctuation has been fairly irregular (Ranta *et al.* 2004). The disappearance of regular cycles coincided with a clear decline in the density of all three grouse species (Ranta *et al.* 2004). Reductions by 40% or more were observed from the early 1960's to the late 1980's and the declining trend continued in the 1990's (Lindén 2002). Multiple explanations for the decline and the loss of cycles and synchrony have been put forward. The deterioration of the habitat due to human interference and forestry has most likely affected negatively all species, maybe most notably the capercaillie, the old forest species (Ranta *et al.* 2004). Landscape changes can lead to increased predation by generalist predators on the grouse (Henttonen 1989, Kurki 1997, Ludwig 2007). Climate change has led to poor breeding success as chicks hatch earlier than optimal; a phenomenon that could even account for the collapse of cycles (Ludwig 2006). In the 2000's the population trend in most parts of the country has been relatively stable (Wikman 2010). It seems now that the capercaillie has to some extent adjusted to the changing forest environment and can breed in managed younger forests too (Miettinen 2009, Sirkiä *et al.* 2011, Wegge & Rolstad 2011)

There are no specialist predators of the forest grouse, although the northern goshawk *Accipiter gentilis* certainly prefers grouse (Tornberg *et al.* 2006). Grouse, mostly the capercaillie and the black grouse, constitute a large part (ca. 40% in the 1990's) of the diet of the golden eagle *Aquila chrysaetos* (Sulkava *et al.* 1999). The eagle-owl *Bubo bubo* preys on grouse mainly in poor vole years (Korpimäki *et al.* 1990). Important mammal predators, also on chicks and eggs, are the red fox *Vulpes vulpes* and the pine marten *Martes martes* (Kurki *et al.* 1997).

The summer diet of the forest grouse consists of diverse plant material, such as the stems, leaves and berries of e.g. bilberry and lingonberry (Cramp & Simmons 1980). The chicks eat plenty of invertebrates such as spiders (Araneae), beetles (Coleoptera) and ants (Formicidae) especially in their first few weeks but also in autumn (Helminen & Viramo 1962, Cramp & Simmons 1980, Wegge & Kastdalen 2008). Winter diets differ between species. The capercaillie feeds in scots pine trees *Pinus sylvestris* eating needles and buds whilst the black grouse feeds mainly on birch *Betula* spp. catkins and buds. The hazel grouse favours catkins and buds of alder *Alnus* spp. and birch in winter (Cram & Simmons 1980).

The most obvious differences between grouse species can be seen in the appearance and breeding systems. The capercaillie and the black grouse are strongly sexually dimorphic, polygamous, lekking species. The difference between large glossy males and smaller cryptic females is so distinct that they might be suspected for separate species. On the contrary, the hazel grouse is monogamous, territorial and only weakly sexually dimorphic (Johnsgard 1983). Size differences between species are striking as a hazel grouse weighs only ca. 10% and a male black grouse ca. 32% of the weight of an adult male capercaillie (Koskimies 1958, Cramp & Simmons 1980).

1.4 The intestinal helminth parasites of Finnish forest grouse

Parasites of three taxonomic groups have previously been found in faecal or intestinal samples of Finnish grouse: coccidians (Apicomplexa, Coccidia), cestodes (Cestoda) and nematodes (Nematoda) (Lampio 1948, Muroma 1955, Isomursu *et al.* 2004). Coccidians are microscopic single-cell parasites. In this thesis, the focus is solely on macroscopic helminths parasites, cestodes and nematodes.

1.4.1 Parasite species and basic morphology

Cestodes (class Cestoda, phylum Platyhelminthes), also known as tapeworms, are segmented parasitic worms. They are very common and diverse parasites in wild birds: Over 1,700 cestode species of avian hosts have been named (Atkinson *et al.* 2008). The adult worm consists of a head (scolex), a short neck region and the body (strobila). Cestodes attach to the intestinal mucosa with special organs of the head. The segments of the strobila grow from the neck region and are called proglottids. Each of them contains complete female and male reproductive organs and a mature, gravid proglottid is filled with eggs. (Taylor *et al.* 2007). Three species have been identified in Finnish grouse, namely *Paroniella* (*Raillietina*) *urogalli* (Lampio 1946, Muroma 1951), *Skrjabinia* (*Raillietina*) *cesticillus* and *Hymenolepis* sp. (Isomursu *et al.* 2004). Most early findings were not identified to genus or species level.

Cestodes have been reported from the Finnish capercaillie and black grouse (Lampio 1946, Muroma 1951, Isomursu *et al.* 2004) and in the hazel grouse (Isomursu *et al.* 2004).

Nematode parasites (phylum Nematoda) are the best known parasites of Finnish grouse. The most common genus found in the capercaillie, black grouse and hazel grouse is *Ascaridia* (Ascaridiidae). Early reports identified two species, *A. compar* and *A. magnipapilla* (Lampio 1946), but later research has shown that these two are actually synonymous and should both be included in *A. compar* (Vasilev 1987a). *A. compar* is a parasite of gallinaceous birds, found in e.g. the grey partridge *Perdix perdix*, the rock partridge *Alectoris graeca*, the ring-necked pheasant *Phasianus colchicus* and the ptarmigans *Lagopus* spp. as well as in the three forest grouse species (Atkinson *et al.* 2008). *A. compar* is a large worm that lives in the lumen of the small intestine of the grouse. The length of a mature female worm is ca. 5–8 cm while the male is notably smaller, ca. 2–4 cm, and also thinner. The shape is spear-like with cylindrical body tapering to both ends. As for other nematode species, Lampio (1946) reports one case of *Capillaria longicollis* infection in capercaillie and Muroma (1951) one case of *Trichostrongylus* sp. in hazel grouse.

The nematode *A. compar* was found in 27% of capercaillie, 45% of black grouse and 32% of hazel grouse (Muroma 1951). In a later paper, the prevalence of *A. compar* according to intestinal samples was 40% in capercaillie and 45% in black grouse (Raitis & Helminen 1969). *A. compar* occurs practically all over the country, wherever forest grouse are present (Muroma and Helminen 1956, Raitis & Helminen 1969, Isomursu *et al.* 2004). Worms are common in autumn during the hunting season, become rare during winter but are most frequently found in spring (April–May) (Raitis & Helminen 1969).

1.4.2 Life cycles of parasites

The life cycle of cestodes is complex and includes at least one intermediate host The adult worms live in the intestine of the definitive host. They produce eggs that are passed to the environment in faeces. The intermediate host then consumes the egg from which an embryo i.e. oncosphere emerges and develops into a larva inside the intermediate host. This stage is infective to the definitive host. When the definitive host eats the infected intermediate host (either intentionally or accidentally) the larva will be released into the host’s intestine. The larva attaches to the mucosa of the small intestine, develops into an adult worm and starts producing eggs. (Taylor *et al.* 2007). The intermediate hosts of avian cestodes of the family Davaineidae are typically insects: e.g. beetles (Carabidae, Scarabaeidae, Tenebrionidae) for *S. cesticillus* (Enigk & Sticinsky 1959) and ants (*Myrmica* spp.) for *P. urogalli* (Muir 1954).

The life cycle of the grouse ascarid, *A. compar*, is simple with no intermediate hosts or tissue migrations (Vasilev 1987b). The adult worms copulate in the lumen of the host's small intestine and consequently female worms produce eggs. The eggs are voided in the faeces to the environment. Outside the host, the embryo in the egg has to develop into a third-stage (L3) larva before being infective to a bird. The next bird is infected when it consumes infective eggs in feed. The larvae in the eggs are released in the digestive system and they develop through further two larval stages into maturity in the intestinal lumen (Vasilev 1987b).

Many avian capillarid parasites (Trichuridae, Capillarinae) have an essentially similar life cycle as ascarids (Atkinson *et al.* 2008). However, some species require an intermediate host for the development of the infective larva. In these cases, earthworms serve as intermediate hosts. Adult *Capillaria longicollis* (syn. *C. caudinflata*) occur in the small intestine (Taylor *et al.* 2007). The life cycle of *Trichostrongylus* sp. (Trichostrongylidae) resembles the ascarid life cycle with one major difference: the eggs hatch in the environment and the emerged larvae develop into infective L3 stage in vegetation (Taylor *et al.* 2007). Intermediate hosts are not required and birds are infected when they eat infective larvae with plants. Adult worms reside typically in the bird's ceca.

1.5 Objectives

The aim of this study is to provide new information on the interactions between grouse hosts and their intestinal helminth parasites taking into account both individual host factors and population level consequences. Due to the different life histories of the two parasite taxa, nematodes and cestodes, their effects on the host can be expected to vary. Cestode parasites of Finnish grouse have mainly been neglected in ecological research but they are now included in the study. The problem of grouse population fluctuations can be addressed from a new perspective when data on parasite infections is combined with grouse census data.

My study questions are:

a) How do host factors (sex, age class and body size) affect the occurrence of intestinal parasites? (I) The distribution of parasites in host population is typically not random but aggregated due to e.g. host age, sex or ecological features. Especially in species with notable sexual dimorphism biases in distribution can be expected.
b) Does genetic diversity influence the resistance to intestinal helminth infections? (II) Reduced fitness caused by inbreeding depression may be a threat in small or isolated populations. Genetically diverse population is more capable to fight parasitic infections. The least heterozygous individuals would be more likely to harbour parasites.
c) Does intestinal parasite infection affect the host bird's susceptibility to predation? (III) Indirect effects of parasitism include e.g. increased vulnerability to other infectious agents or predation. The parasite load of a grouse hunted with a trained dog, a surrogate for a natural canine predator, is compared to that of a grouse hunted without a dog. Finding more parasitized grouse in the bag hunted with dog would suggest parasite-induced vulnerability to canine predation.
d) Do intestinal parasites regulate grouse populations? (IV) In coupled dynamics of host and parasite populations, the population densities and growth rates are correlated. Analysing the connections between annual parasite loads and host population indices (growth rate, survival and juvenile proportion) explains the role of parasites in the complex dynamics of the grouse population. Under parasitic regulation, the grouse population growth would be negatively affected by parasite abundance.

2 Material and methods

All the material was collected voluntarily by grouse hunters in 1995–2002. The grouse were shot during regular hunting season in autumn (September 10th – October 31st). According to written instructions and pictures, the hunter removed the whole intestine (including caeca) which was then stored frozen in a plastic bag until examination. One of the wings was also included in the sample for the determination of age class and sex. Background information was recorded for each bird. This included the place of origin (game management district), date, method of hunting (with dog or no dog) and type of weapon used.

In total, samples from 1120 birds from which both sex and age could be determined were received. Black grouse were the most numerous species (607), followed by capercaillie (267) and hazel grouse (246). All these were included in the study of the effect of host sex and age on intestinal helminth infections (I). A subset of 623 samples was selected for the study of parasitism and susceptibility to hunting (III). The selected birds were all shot with a shotgun which requires a closer shooting distance (≤ 40 m) than a rifle. The subset included 277 black grouse, 184 capercaillie and 162 hazel grouse. The genetic study was conducted using 196 capercaillie samples collected in 1996–2002 (II). This included all the capercaillie from which the DNA could be successfully extracted. In the population dynamics study (IV), 943 birds from four game management districts had the necessary background information (age class, sex and sampling month). The fifth district (Oulu) was omitted because of the small number of annual samples.

In the laboratory, the intestines were dissected and inspected for macroscopic helminth parasites as in Raitis & Helminen (1969). The smallest nematode species (e.g. *Capillaria* sp., *Trichostrongylus* sp.) would probably remain undetected using this method unless the infection was very intense. However, the method reveals the species considered the most significant in Finnish conditions. All observed parasites were extracted, rinsed and then stored in 10% formalin solution for later identification. Nematodes were counted and identified microscopically. Cestodes were dyed with carmine red (Sigma Chemicals) and identified microscopically (Khalil *et al.* 1994). Cestodes could not be counted reliably due to the fragmentation of most of the worms.

Parasitological terms are used according to Margolis *et al.* (1982). Abundance is the relative density of infection in all hosts examined i.e. the total number of parasites from all infected hosts divided by the number of all hosts (infected and uninfected) examined. Intensity means the number of parasites per infected host. Prevalence is the number of infected hosts divided by the number of all hosts examined (times 100%).

The associations between host sex, age and species on the occurrence of intestinal helminths were studied using hierarchical loglinear modelling using backward selection procedure (P = 0.01). The sex differences in nematode abundances were analyzed for both age groups separately using nonparametric Mann-Whitney U-test because of the skewed distribution of the nematodes among birds.

To examine the effect of heterozygosity on parasitism FSTAT for Windows version 2.9.3.2 (Goudet 2001) was used. The level of inbreeding was estimated as the multilocus heterozygosity (MLH) and mean d^2 over eight microsatellite loci. Multilocus heterozygosity is the proportion of heterozygous loci within an individual. According to Coulson *et al.* (1998) mean d^2 is the squared distance in repeat units between the two alleles an individual had at a microsatellite locus, averaged over all loci at which an individual was scored. I used generalized linear modelling with a binomial distribution and logit link function in the analysis of both cestode and nematode infection occurrence (presence/absence data). Generalized linear modelling with a negative binomial distribution and log link function was applied in the analysis of nematode infection intensity. Host age and sex were included as factors and the two measures of heterozygosity were used as covariates. In model selection I used Akaike Information Criteria and Akaike weights (Burnham & Anderson 2002). Additionally, analysis of variance was used to assess differences in heterozygosity between age classes and sexes.

The associations between host sex, age, species, the month of sampling, the use of dog and the occurrence of intestinal helminths were analysed by hierarchical loglinear modeling with backward elimination procedure (P = 0.05). I calculated separate models for cestodes and nematodes (ascarids) and X^2 test was used to test the observed differences in detail.

When examining the effect of parasites on grouse population dynamics, birds were assigned to one of four population growth phases — low, increase, peak or decline phase — according to the annual combined grouse density of the district (Table 1). Generalized linear modelling was then used to assess the effects of population phase, sampling month, host age class, host sex and host species on the abundance and occurrence of *A. compar* and the occurrence of cestodes. This method was chosen because the distribution of *A. compar* was close to negative binomial distribution. Selection of the best model was based on Akaike information criteria and Akaike weights (Burnham & Anderson 2002). General linear models (multivariate analysis of variance) were used to study the effects of parasite indices on host population indices. Variance-to-mean ratio was used to assess the degree of aggregation of *A. compar* in grouse population.

Statistical analyses were calculated with SPSS (versions 11.5–21.0).

Table 1. Definitions of the grouse population growth phases.

Phase	Definition
low	$\mathbf{Density_t}$ < $density_{t-1}$ and $density_{t+1}$
increase	$Density_{t-1}$ < $\mathbf{density_t}$ < $density_{t+1}$
peak	$\mathbf{Density_t}$ > $density_{t-1}$ and $density_{t+1}$
decline	$Density_{t-1}$ > $\mathbf{density_t}$ > $density_{t+1}$

3 Results

3.1 The parasites

Four parasite species were identified: one ascarid nematode *Ascaridia compar* (Ascarididae) and three species of cestodes, namely *Skrjabinia* (*Raillietina*) *cesticillus* (Davaineidae), *Paroniella* (*Raillietina*) *urogalli* (Davaineidae) and *Hymenolepis* sp. (Hymenolepididae).

All parasite species were found in every bird species. Cestode species had a similar distribution as regards host age and sex, *S. cesticillus* being the most prevalent species whilst *Hymenolepis* sp. was quite rare. Also, the life cycles of all cestode species are essentially alike and different from that of the nematode species. Therefore all three cestode species are pooled in the statistical analyses.

3.2 Host factors affecting parasite distribution (I)

Occurrence of cestodes was related to age class (Fig. 1). Cestodes were much more prevalent in juveniles than in adults in all three bird species, especially in the capercaillie (juveniles 38%, adults 4.7%) and the black grouse (juveniles 33%, adults 2.9%). On the other hand, *A. compar* was less common and less abundant in juveniles than in adults in the capercaillie and the black grouse. In the hazel grouse, such difference was not observed. The degree of sex-biased ascarid parasitism was higher in juveniles than in adults.

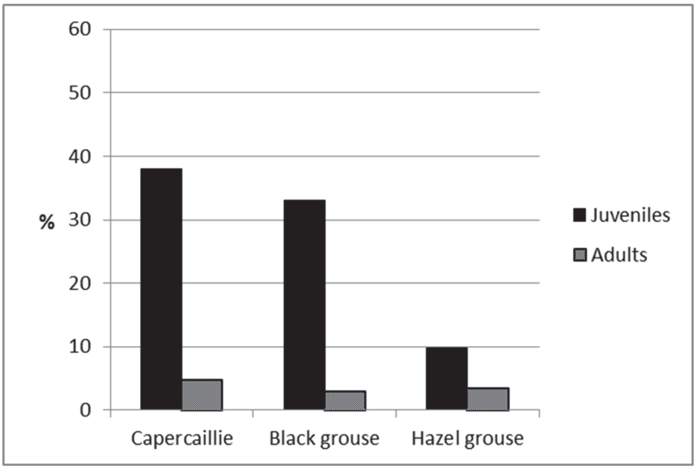

Fig. 1. The prevalence of cestodes by age class and host species.

The occurrence of the *A. compar* was associated with host sex as worms were more common in male birds (Fig. 2). The male-bias in prevalence was largest in the capercaillie and the black grouse whilst in the hazel grouse the difference between sexes was very small (Fig. 2). Sex difference was also found in ascarid abundance: a significant male-bias was found in juvenile capercaillie, adult capercaillie and juvenile black grouse. In adult black grouse, the observed male-bias in abundance was not quite statistically significant. However, the occurrence of cestodes was not related to host sex.

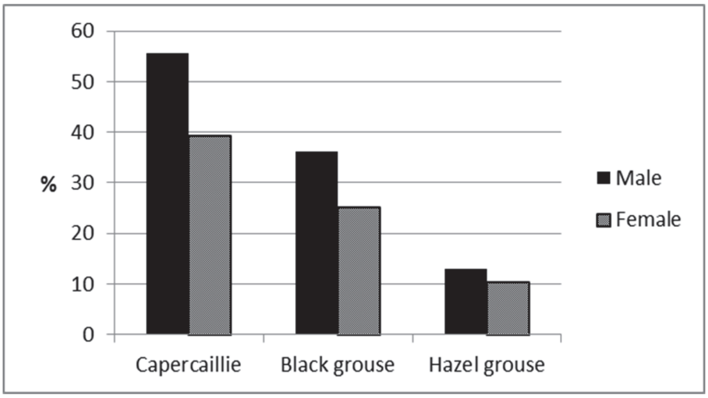

Fig. 2. The prevalence of *A. compar* in males and females in adult grouse.

The size of the host species affected both the prevalence and the abundance of *A. compar*. Both increased from the smallest species to the biggest species among adult birds (Fig. 3). The capercaillie had the highest prevalence and the highest load of *A. compar* whilst the hazel grouse had the lowest values in both sexes. This difference between species was also seen when looking at males and females separately. In juveniles, a similar size-related difference between species was not found, although in the smallest species, hazel grouse, the abundance of *A. compar* was lower than in the two larger species. Among adults, the sex-bias in parasitism and in body weight was of the same magnitude in the dimorphic species (I, Table 2).

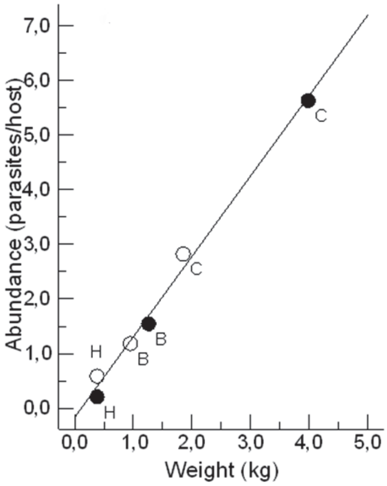

Fig. 3. The relationship between the average host weight (adults) and the abundance of *A. compar*/ host. H = hazel grouse, B = black grouse, C = capercaillie. Closed dot = male, open dot = female.

3.3 Genetic diversity (II)

The microsatellite loci of capercaillie were highly variable with number of alleles ranging from 8 to 21. Generally, loci showed heterozygote deficiency which was probably due to non-random mating.

Indices of heterozygosity explained the intensity of *A. compar* infections. Both heterozygosity indices (mean d^2 and MLH) were included into the best models to explain *A. compar* infection intensity: the number of *A. compar* was higher among more homozygous individuals (II, Fig. 4). Occurrence of *A. compar* infection was only connected with one index, mean d^2. Low mean d^2 predicted a higher probability to have *A. compar* infection.

Heterozygosity did not explain the occurrence of cestodes.

MLH was higher in adult capercaillie than in juveniles.

3.4 Parasitism and susceptibility to predation (III)

Grouse hunted with a trained dog were more often infected with cestodes than grouse hunted without a dog. The prevalence of cestodes in the dog-assisted bag was 27% while in the bag with no help from dog the prevalence was only 14%. The difference was of the same direction in all bird species. Cestodes were more common in juvenile birds. When analysis was made on juvenile birds alone, the interaction between cestode infection and the use of dog was still significant. There was also a temporal aspect as cestode infections became less frequent later in the hunting season. This had no effect on the basic finding: the dog-assisted bag contained more birds infected with cestodes in both September and October (Fig. 4).

On the contrary, *A. compar* infection was not found to be associated with the hunting method in any grouse species.

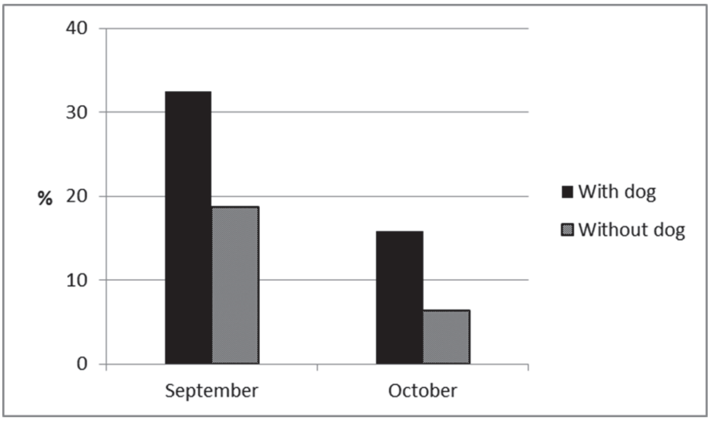

Fig. 4. The prevalence of cestodes in grouse (all species, both age classes) according to hunting method.

3.5 Population dynamics of hosts and parasites (IV)

In the decline phase of grouse population, the prevalence and abundance of *A. compar*, as well as variance-to-mean ratio were higher than in any other phase. Grouse population growth was negatively affected by *A. compar* abundance and prevalence (Fig. 5). Annual survival was also negatively correlated with abundance and prevalence of *A. compar* while breeding success was not.

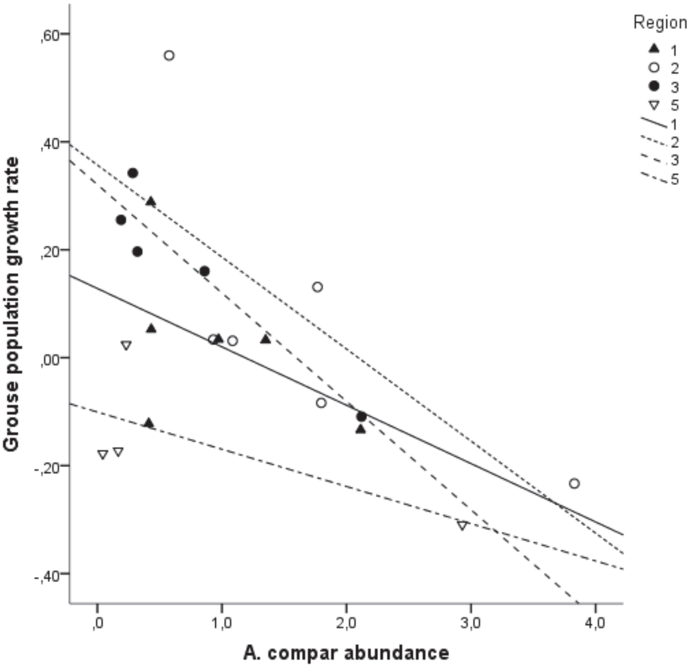

Fig. 5. The effect of the abundance of *A. compar* on the grouse population growth rate in different sampling regions. 1 = Satakunta, 2 = Keski-Suomi, 3 = Kainuu, 5 = Lappi

Cestodes were most common in the population increase phase. When comparing the two months of data collection, a decrease of prevalence of cestodes from September to October was seen in every grouse population growth phase. Cestode prevalence was not related to grouse population growth rate, survival or breeding success.

Distribution of *A. compar* changed notably in juvenile grouse during the autumn. Parasites were less aggregated in October compared to September. In adults, the direction of change was the opposite: aggregation increased.

4 Discussion

The population dynamics of the forest grouse do seem to be under the influence of parasites according to the results: *A. compar* affected negatively the grouse population growth. Especially the two dimorphic species, the capercaillie and the black grouse, are important for the dynamics because they harbour most of the *A. compar* population. Results also suggest that a loss of genetic diversity makes grouse more susceptible to *A. compar*. Inbred populations would therefore have higher parasite loads and suffer more of negative population-level effects. Cestodes are parasites of juvenile grouse and may not be involved in host population regulation but they may influence the bird's chances of being found by canine predators.

4.1 Sex-bias in parasitism – size matters

The prevalence and abundance of *A. compar* was clearly male-biased in the sexually dimorphic grouse species. Male-bias in parasitism is a known phenomenon in birds and mammals, particularly regarding nematode parasites (Poulin 1996, Moore & Wilson 2002). In some avian parasite taxa, general sex-biases have not been found. Cestodes seem to infect both sexes similarly (Poulin 1996) and some blood parasites are more common in female birds (McCurdy *et al.* 1998).

In the capercaillie and the black grouse, the body size seemed to be an important factor. Large males consume more food and consequently are more exposed to orally transmitted parasites such as *A. compar*. The sex-bias both in size and parasite abundance was nearly the same in adult capercaillie and black grouse indicating the significance of host size for *A. compar* infection. When comparing the adult birds of the three grouse species, each sex separately, *A. compar* was found to be most common in the largest birds (male capercaillie) and least common in the smallest (hazel grouse). Two basic explanations exist for the male-bias: the immunosuppressive effects of the male androgen, testosterone, or sex difference in body size (Folstad & Karter 1992, Zuk & McKean 1996). Hormonal factors are probably of less significance in this context. Production of androgens in male capercaillie is highly seasonal with a single peak occurring during the breeding season in spring (Hissa *et al.* 1983). Juvenile birds have not yet experienced high androgen levels in the autumn but nevertheless the sex-bias was present in juveniles. On the other hand, the immunosuppressive effects of testosterone are not always self-evident in birds as reviewed by Roberts *et al.* (2004).

Juvenile males of size-dimorphic species grow faster than females which may demand different strategies and trade-offs in males and females. Large size may be of an advantage for a male grouse when competing for females (Rintamäki *et al.* 2001) but it involves costs as well. The fast growing males are constantly at the limit of their resources and any negative external effects, such as unfavourable weather, will affect males more than females (Lindén 1981a). Parasites may be more harmful in growing males than in growing females (Tschirren *et al.* 2003).

In this study, cestodes were predominantly parasites of juvenile grouse irrespective of sex. Grouse chicks are exposed to cestode infections because of their diet rich in invertebrates (Wegge & Kastdalen 2008) which can be intermediate hosts for avian cestodes. During this period of increased exposure physiological or ecological sex differences have not yet reached the level of mature birds and, as a consequence, sex-bias in cestode infection is not observed.

4.2 Parasite-mediated selection for heterozygosity

In the capercaillie, genetic diversity measured by multilocus heterozygosity explained the *A. compar* worm burden. The more heterozygous the bird was the less it had *A. compar* worms. In other words, genetically more diverse capercaillie seem to cope better with the infection. The occurrence, i.e. susceptibility to infection was not so clearly dependent on heterozygosity as only one index correlated with the probability of infection. Additionally, heterozygosity seemed to be connected with general survival because adult capercaillie were more heterozygous than juveniles suggesting selection for heterozygosity.

Heterozygosity-fitness correlations (HFC) in animals have been studied widely and it seems they generally do exist, although weak (Chapman *et al.* 2009). Parasite-mediated heterozygosity advantage has been found in e.g. in Soya sheep (Coltman *et al.* 1999), California sea lions (Acevedo-Whitehouse *et al.* 2003) and passerine birds (mountain white-crowned sparrow, MacDougall-Shackleton *et al.* 2005; great tit, Voegeli *et al.* 2012). These studies found correlations between both disease susceptibility and infection intensity.

The aim of HFC studies is to find out possible negative effects of inbreeding that may appear in small, declining or fragmented populations. Inbreeding generally means mating with relatives and it can lead to increased homozygosity and expression of deleterious alleles i.e. inbreeding depression (Keller & Waller

2002). The findings of negative HFC's underline the harmful effect of population decline. Genetic diversity is important in many respects, also for disease resistance (King & Lively 2012).

Technically, studying the often weak HFC's is challenging. Microsatellite diversity may not give true representation of the whole genomic diversity (DeWoody & DeWoody 2005) and evaluation of the level of inbreeding by heterozygosity is difficult in practice (Balloux *et al.* 2004). Small sample sizes and few analysed alleles are problematic in HFC studies and even the correlation between multilocus heterozygosity and inbreeding can be weak (Balloux *et al.* 2004, Slate *et al.* 2004, Chapman *et al.* 2009). However, since inbreeding depression is a known risk for population health (Keller & Waller 2002) and the present results tentatively show that grouse can be affected, too, further studies with more effort would be necessary. After all, forest grouse have suffered from recent population declines and habitat fragmentation.

4.3 Predation on parasitized grouse

In this study, grouse of all three species hunted with a hunting dog were more often infected with cestodes than those hunted without a dog. The dogs did not actually have to catch the grouse but only locate it and point it out to the hunter. Possibly something in the behaviour or the scent of the infected birds attracts dogs. The finding suggests that natural canine predators using the same cues as dogs may also find cestode-infected birds more easily.

Parasites sometimes affect the host's condition, physiology or behaviour in a way that makes the host more vulnerable to predation (Moore 2002). Tests with hunting dogs have also shown that red grouse with a high burden of the nematode *Trichostrongylus tenuis* are more easily found by dogs (Hudson *et al.* 1992). Parasite-induced vulnerability to predation in red grouse was further supported by the higher worm burden of predator-killed birds compared to hunted birds (Hudson *et al.* 1992). As in the case of grouse cestodes, *T. tenuis* does not benefit from the predation and the death of the host can be regarded as unwanted side-effect from the parasite's point of view.

Cestodes were mainly parasites of juvenile grouse being ca. ten times more common in young capercaillie and black grouse than in adults. The increased predation due to parasites would be focused at the juvenile proportion of the population. Predation caused by cestode infections can be one factor behind the observed high mortality of juvenile grouse (Lindén 1981b).

4.4 The role of intestinal parasites in grouse population dynamics

There was a significant negative correlation between adult survival and *A. compar* (abundance and prevalence). Also, the aggregation of *A. compar* in juvenile grouse decreased during autumn which can be a sign of mortality among the most heavily infected individuals. The proportion of cestode-infected birds decreased during autumn which may be a sign of cestode-induced grouse mortality but also the natural consequence of lower exposure and transmission rate. Intestinal parasites are associated with mortality of the red grouse when the infection intensity is high (Hudson *et al.* 1992). In the willow grouse, cestode and nematode parasite infections were related to reduced body mass and breeding mortality (Holmstad *et al.* 2005). In order to have regulatory effects on the host population, the parasite must cause mortality or reduction in fecundity in the hosts (Anderson & May 1978). Thus, the findings point to *A. compar* as a potential regulating factor in the forest grouse population.

As further evidence of the importance of *A. compar* in grouse dynamics, I found that annual mean abundance and prevalence of *A. compar* affected negatively the annual grouse population growth rate. The effect was based on a decrease in survival rather than on a decrease in reproduction. In addition, *A. compar* abundance and prevalence were highest in the years of the grouse population decline phase. In the cyclic dynamics of the red grouse and the parasite *T. tenuis*, mean parasite abundance follows the density of red grouse and is highest after the grouse population peak (Dobson & Hudson 1992). In the forest grouse, the parasite abundance also seems to peak the year before the host population crash. The pattern resembles the classic predator-prey model or Lotka-Volterra equation describing cyclic dynamic (Krebs 2009). In general, coupled cyclic fluctuations of parasites and hosts can emerge when there is a negative correlation between the growth rate of the host population and the abundance of parasites and a positive correlation between the growth rate of parasite population and host density (Berryman *et al.* 2002). The forest grouse – *A. compar* interaction seemed to be missing this feedback as grouse density did not affect the growth of *A. compar* abundance. Cyclic host-parasite dynamics will not emerge in this situation.

Cestodes did not seem to have dynamic effects on grouse population. They were the most common in the increase phase of grouse population but less common in the peak and decline phases. Cestodes accumulate in the juvenile population which is usually largest in increasing grouse population (Lindén 1989).

Grouse population can escape regulation by cestodes because of strong decrease in transmission rate after chick period due to diet shift. Regulation would be difficult also because *Raillietina* sp. and *P. urogalli* seem to be relatively benign parasites that the birds can tolerate without losing condition (Thomas 1986, Delahay 1999).

Regular cyclic dynamics following the previously recognised pattern were not observed during the sampling period 1995–2000. The regular cycles disappeared in the whole country by the 1990's (Ranta *et al.* 2004). The change in population dynamics was preceded by notable decline of grouse densities, particularly the densities of the capercaillie and the black grouse (Lindén 2002). During the sampling period, the hazel grouse was the most numerous species of the three whilst earlier, during cyclic dynamics, the black grouse was the most abundant (Ranta *et al.* 2004). This must have influenced negatively the abundance and transmission of *A. compar* since the parasite is more abundant in the black grouse and the capercaillie than in the hazel grouse. Ranta *et al.* (2004) speculate that the black grouse may have been the key species for the maintenance of the grouse cycles. Since the black grouse apparently has been the most important host species for *A. compar* the decline of the black grouse population would lead to a considerable decrease of *A. compar*. As a consequence, strong coupling in host-parasite dynamics may have broken.

5 Concluding remarks

My results show that intestinal helminths parasites have a significant role in the life and population dynamics of the forest grouse. Intestinal parasites have adverse effects on grouse but the effects of the parasite species on the host are as different as their life-cycles. Cestodes can notably only influence the juvenile population and the main effect is indirect, increased risk of canine predation. Nematode parasites, namely *A. compar*, infect the whole grouse population, particularly the larger species and males of dimorphic species. Only *A. compar* seems to have the potential to regulate grouse population as it has a negative effect on the grouse population growth rate and survival. The key host species in the *A. compar* – grouse dynamics may be the black grouse, a relatively large species of high density and wide distribution that evidently harbours a large part of the *A. compar* population. More heterozygous individuals are better able to cope with *A. compar* infection suggesting that a population with reduced genetic diversity would have higher parasite load and suffer more of parasite-induced reduction in survival and growth rate.

Many aspects of the influence of intestinal helminths on the forest grouse still need further research. I found that *A. compar* is a suitable candidate for a grouse population regulator. Modelling the host-parasite interaction of *A. compar* and grouse would give theoretical foundation for testable hypothesis on the population dynamics. This approach has been used in studies of the red grouse (Dobson & Hudson 1992) and rock partridge (Rosá *et al.* 2011). However, modelling requires numerous parameters about the life-histories of both the host and the parasite, many of which are still unknown for these species in the boreal forest environment. Among the most important and interesting parameters are parasite-induced death rate of the host and parasite-induced reduction in the fecundity of the host.

This data consisted of birds sampled in the autumn but spring can be a more critical time because then *A. compar* prevalence is at the highest level (Raitis & Helminen 1969). At the same time, grouse are burdened by the demands of the breeding season which can make them particularly vulnerable to parasites and harm the breeding success. Indeed, *A. compar* infection can decrease the hatching success of eggs in rock partridge (Rosá *et al.* 2011). Comparison between parasite burdens in spring and autumn would give information on the annual changes in parasite distribution and possible mortality effects.

Study of grouse genetics and parasite-mediated selection for heterozygosity would benefit from using larger set of alleles. Also the black grouse and the hazel grouse deserve attention in the field of parasite resistance genetics. I used microsatellite heterozygosity to describe general genomic heterozygosity but a more specific parasite resistance study would examine the major histocompatibility complex (MHC) genes that code the proteins of cell surface that present antigens to lymphocytes. These extremely diverse genes are essential in the immune defence and inbreeding and decrease of MHC diversity would compromise parasite resistance (Apanius *et al.* 1997). During environmental changes both in global and local scale the multiple effects of a loss of genetic diversity in natural populations should be addressed.

The negative effect of the abundance of *A. compar* on the grouse population growth rate and the peak of *A. compar* population in the decline phase of the grouse population are findings that open up a new perspective on monitoring grouse population dynamics. Years of high *A. compar* abundance are the most likely years of grouse population decline when hunting pressure should be modified accordingly. Regular monitoring of intestinal parasite abundance might give additional tools for assessing the state of the grouse population and perhaps ultimately for the planning of grouse hunting. With suggested further studies on parasitological ecology of forest grouse, these tools would become more reliable and applicable.

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Original articles

- I Isomursu M, Rätti O, Helle P & Hollmén T (2006) Sex and age influence intestinal parasite burden in three boreal grouse species. J Avian Biol 37: 516–522.
- II Isomursu M, Rätti O, Liukkonen T & Helle P (2012) Susceptibility to intestinal parasites and juvenile survival are correlated with multilocus microsatellite heterozygosity in the Capercaillie (*Tetrao urogallus*). Ornis Fenn 89: 109–119.
- III Isomursu M, Rätti O, Helle P & Hollmén T (2008) Parasitized grouse are more vulnerable to predation as revealed by a dog-assisted hunting study. Ann Zool Fenn 45: 496–502.
- IV Isomursu M, Rätti O & Helle P (2013) Intestinal parasites as potential factors in the dynamics of fluctuating forest grouse populations in Finland. Manuscript.

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ISBN 978-952-62-0363-8 (Paperback)
ISBN 978-952-62-0364-5 (PDF)
ISSN 0355-3191 (Print)
ISSN 1796-220X (Online)

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