

Population Fluctuations in Mountain Hares: A Role for Parasites?

Scott-John Newey
Faculty of Forest Sciences
Department of Animal Ecology
Umeå

Doctoral thesis
Swedish University of Agricultural Sciences
Umeå 2005

Acta Universitatis Agriculturae Sueciae

2005:26

ISSN 1652-6880

ISBN 91-576-7025-0

© 2005 Scott-John Newey, Umeå

Tryck: SLU Service/Repro, Umeå 2005

Abstract

Newey, S.J. 2005. Population Fluctuations in Mountain Hares: A Role for Parasites? Doctor's dissertation. ISSN: 1652-6880. ISBN: 91-576-7025-0

Throughout their circumpolar distribution mountain hares *Lepus timidus* show unstable population dynamics characterised by regular and sometimes dramatic changes in abundance. The periodicity, amplitude and degree of cyclicity are different in different regions. The reasons for these fluctuations and geographic differences are not fully understood.

In Fennoscandia there is experimental and correlative evidence that some mountain hare populations are limited by predators, but the experiments needed to conclusively demonstrate the role of predators, or of other potential factors have not been undertaken. In Scotland the rigorous control of predators means that the role of predators is largely dismissed, but this has not been experimentally tested. The most promising line of enquiry suggests that intestinal parasites have the potential to destabilise some mountain hare populations. There is paucity of literature from Asia and central Europe and no firm conclusions could be drawn.

Time-series analysis of hunting bag records from Scotland largely confirmed the dominance of weak cycles with a mean periodicity of around 9 years found in earlier studies. The analysis of bag records from Fennoscandia found a number of differences compared to earlier studies. We found only limited evidence for the presence of 4-year cycles, and found that the pattern and distribution of cycles has changed in the last 20 years since the fox mange epizootic. Data coverage from central Europe and Asia was very limited and no meaningful conclusions could be drawn.

Populations of mountain hares in Scotland show unstable dynamics with 7-12 year fluctuations in abundance. I describe the findings of three studies which tested the hypothesis that intestinal parasites i) reduce female survival, body condition and fecundity, and ii) are randomly distributed within the host population. Parasite reduction experiments suggested that the intestinal parasite *Trichostrongylus retortaeformis* had little affect on female survival, but reduced female body condition and fecundity. A large scale cross-sectional study revealed that *T. retortaeformis* was loosely aggregated within the hare population and had a negative affect on body condition. These results are consistent with the hypothesis that parasites may destabilise some mountain hare populations in Scotland.

Key words: mountain hare, *Lepus timidus*, population dynamics, limitation, regulation, macroparasites, cycles.

Author's address: Scott Newey, Department of Animal Ecology, Swedish University of Agricultural Sciences, S-901 83 UMEÅ, Sweden.

To my Grandad, Ken Cutler

Contents

Introduction, 7

Limiting and regulating factors of mountain hare populations, 7

Do mountain hare populations cycle?, 8

The role of parasites in Scottish mountain hare population dynamics, 8

Macro-parasites, 9

The Anderson & May model, 10

The role of parasites in vertebrate host population dynamics, 13

Population assessment of Scottish mountain hare populations, 14

Objectives, 15

A review of limiting and regulating factors, 15

Do mountain hare populations cycle?, 18

Methods, 18

Results, 20

Discussion, 22

The role of parasites in Scottish mountain hare populations, 23

Methods, 24

Parasite reduction experiments, 24

Cross-sectional study, 26

Results, 27

Spring parasite reduction experiment, 27

Winter parasite reduction experiment, 28

Cross-sectional study, 28

Discussion, 29

Population assessment of Scottish mountain hare populations, 31

Methods, 31

Results and Discussion, 31

Conclusions, 32

References, 33

Acknowledgements, 39

Appendix

Papers I-VI

I base my thesis on the following papers, which I refer to by their Roman numerals.

- I.** Newey, S., Dahl, F. Willebrand, T. & Thirgood, S.J. Mountain hare populations in Eurasia: A review of limiting and regulating factors. (Manuscript).
- II.** Newey, S., Haydon, D.T., Willebrand, T., Aebischer, N.J., Dahl, F., Smith, A.A. & Thirgood, S.J. Are mountain hare populations cyclic? (Manuscript).
- III.** Newey, S., Thirgood, S.J. & Hudson, P.J. (2004) Do parasites burdens in spring influence condition and fecundity of female mountain hares *Lepus timidus*? *Wildlife Biology* **10**: 171-176.
- IV.** Newey, S. & Thirgood, S.J. (2004) Parasite-mediated reduction in fecundity of mountain hares. *Proceedings of the Royal Society of London. B.* **271**: S413-S415.
- V.** Newey, S., Shaw, D.J., Kirby A., Montieth, P., Hudson, P.J., & Thirgood S. J. (2005). Prevalence, intensity and aggregation of intestinal parasites in mountain hares and their potential impact on population dynamics. *International Journal for Parasitology* **35**: 367-373.
- VI.** Newey, S., Bell, M., Enthoven, S., & Thirgood, S.J. (2003) Can distance sampling and dung plots be used to assess the density of mountain hares? *Wildlife Biology* **9**: 185-192.

Papers III and VI are reproduced with kind permission from the publisher. Papers IV and V are reproduced within the publishers copyright agreement.

Introduction

Studies of the cyclic fluctuations of northern vertebrate species have played a central role in the development and understanding of population dynamics (Royama 1992). They have allowed examination of the nature of density dependence, the mechanisms and scale of synchrony and the role of stochastic factors in maintaining instability (Stenseth 1999; Lindstrom *et al.* 2001). However, even though it is three quarters of a century since Elton (1927) first described cycles in lynx fur returns, there is still no clear consensus on what causes cycles (Stenseth 1999; Berryman 2002; Turchin 2003). The difficulty of conducting experiments at suitably large spatial scales is one factor contributing to the lack of progress in this field (May 1999).

Throughout their circumpolar range mountain hare populations show apparently regular and sometimes dramatic changes in population density (Angerbjorn & Flux 1995). The amplitude, periodicity, propensity and nature of these fluctuations differ between countries and regions (Linden 1988; Angerbjorn & Flux 1995; Ranta *et al.* 1997). For example; mountain hare populations in Scotland are widely believed to show high amplitude, 10-year quasi-cycles (Tapper 1987); hare populations in northern Fennoscandia are often cited as showing highly synchronous, low amplitude 4-year cycles, while in the south they appear not to be cyclic (Angelstam *et al.* 1985); populations in Russia are documented as showing regular, high amplitude 8-12 year cycles in the taiga zones of Europe, Siberia and the Siberian forest-steppe, but shorter and less distinct 4-9 year cycles in the regions of mixed and insular forest zones and European forest-steppe (Naumov 1947; Keith 1981, 1983). The differences, nature and causes of these fluctuations are poorly understood.

Limiting and regulating factors of mountain hare populations (Paper I)

Unstable, or cyclic dynamics, have fascinated ecologists for decades (Lindstrom *et al.* 2001). Regular fluctuations in abundance have been reported for many vertebrate and invertebrate taxa (Royama 1992; Berryman 2002; Turchin 2003). One time-series study based on 694 time-series held in the Global Population Dynamics Database (NERC Centre for Population Biology 1999) revealed that fully 220 species exhibited cyclic dynamics (Kendall *et al.* 1998). Cyclic dynamics were particularly prominent among fish and mammal species, and there was a tendency for the degree of cyclicity to increase with latitude in mammal populations only (Kendall *et al.* 1998).

Although the wide spread occurrence of and interest in populations that show unstable or cyclic dynamics has led to a large number of explanations and mechanisms being proposed, there is still no clear consensus as to what causes cyclic dynamics (Berryman 2002; Turchin 2003). In looking for an explanation of mountain hare population dynamics it is tempting to look to the snowshoe hare

system for insights. In the boreal zone of north America the snowshoe hare shows well defined, persistent cyclic changes in abundance that are synchronised over large areas and are concurrent with cyclic changes in a suit of other predatory species (Krebs *et al.* 1995). Three large scale studies; one at Rochester and two at Kluane that have undertaken large scale correlative and manipulative studies of food availability and predator manipulation, singularly or combined, suggest that the 10-year cycle of snowshoe hares is driven by food and predation that interact in such a way that few hares die of starvation and most succumb to predation (Krebs *et al.* 1995; Krebs *et al.* 2001; Boutin *et al.* 2002). However, despite representing one of the most intensely studied systems what drives the 10-year snowshoe hare cycle is still not entirely clear (Krebs *et al.* 2001; Boutin *et al.* 2002). In Paper I we undertake a literature review of the factors that have been proposed to regulate or limit mountain hare populations in Eurasia.

Do mountain hare populations cycle? (Paper II)

Despite the widespread interest in mountain hare dynamics and the oft cited; 10-year cycle of Scottish mountain hare populations, the 4-year Fennoscandia cycle, and the 8-12-year cycle of northern Russia, no study has undertaken a rigorous and thorough analysis of time-series from different areas and sources. The current state of knowledge is based on a wide number of different exploratory and analytical methods. Indeed, the oft purported cyclic nature of many of the Russian hare populations appears to be based on a visual assessment of hunting records (Naumov 1947). The variable periodicity and amplitude exhibited by mountain hare populations complicates the characterisation of their dynamics and precisely when a fluctuating population can be usefully termed cyclic is unclear (Nisbet & Gurney 1982). One of the aims of this thesis was therefore to undertake a time-series analysis of as much available data as possible and, by virtue of treating all data the same and using standard analytical techniques, to present the first comprehensive characterisation of mountain hare dynamics.

The role of parasites in Scottish mountain hare population dynamics (Papers III, IV and V)

Populations of mountain hares in Scotland show unstable dynamics with 7-12 year fluctuations in abundance (Hewson 1976; Tapper 1976, 1992). The one time-series analysis to date suggests that these fluctuations represent phase-forgetting quasi-cycles with a mean periodicity of 9.5 years (range 7-12). The mechanisms causing these fluctuations are currently unknown. While predators such as fox are thought to play a significant role in driving mountain hare population fluctuations in Fennoscandia (Lindstrom *et al.* 1986; Danell & Hornfeldt 1987; Marcstrom *et al.* 1989; Lindstrom *et al.* 1994), the high level of predator control practiced on the sporting estates where most Scottish mountain hares occur make it unlikely that predation is an important driver of these fluctuations (Hewson 1976, 1985). Mountain hares are, however, known to be susceptible to high intensities of the gastrointestinal nematodes *Graphidium strigosum* and *Trichostrongylus retortaeformis* (Boag & Iason 1986; Iason & Boag 1988). Since hares carry a

significant helminth infection and host-parasite interactions are known to be destabilising (May & Anderson 1978; Anderson & May 1978) they have been proposed as a possible causal mechanism for the observed instability. We undertook two parasite reduction experiments of wild free living mountain hares to investigate the effect of parasite reduction on survival, body condition and fecundity of adult female hares. In addition, we investigated the prevalence, intensity, and aggregation of the two most common helminth parasites in a large sample of shot hares and also investigate the relationship between intensity of infection and body condition.

Macro-parasites

The traditional ecological perception of parasitic helminths is of a rather obscure group of “wormy” creatures that make their living by feeding on excess food in the guts of their hosts (Dobson *et al.* 1992). As such, even though the role of macro-parasites in influencing the dynamics of their host population has been a central question in the study of wildlife diseases, ecologists and wildlife managers have typically dismissed the role of such parasites as unimportant (Tompkins *et al.* 2001) - rather believing parasites to be normally benign and specialised predators that live in a delicate balance with their host (Lack 1954). The host mortality associated with epidemic outbreaks of disease were either explained as cases where the delicate balance had been disturbed, rationalised as unusual events, or were dismissed as not having any long term influence as the disease agent died out with decreasing host density (Tompkins *et al.* 2001). It has even been argued that parasites were unlikely to have a negative effect on host dynamics because if the parasite caused the death of the host, then the parasite would also die.

Parasites are generally defined as organisms that show a degree of habitat and nutritional dependency on host species and that also have a harmful effect on the host individual. Parasites exhibit a wide degree of variability in the degree of harm they cause. At one extreme, parasites merge into the parasitoid type association, with similarities, in population terms, to predator-prey interactions. At this end of the spectrum parasite infection is invariably associated with the death of the host and, in contrast to parasitoids, the death of all parasites living off that host individual. At the other end of the spectrum are the symbiont like parasites that live in nutritional and habitat dependency on the host, but have little if any impact on the individual host. At the population level a parasite is perhaps best regarded as an organism which in addition to exhibiting a degree of habitat and, or nutritional dependency, adversely influences the birth and, or mortality rates of its host which can be summarised in terms of the host populations’ intrinsic rate of increase (Anderson 1978). The functional relationship between the intensity of parasitic infection and the host population growth rate provides a precise and succinct way of quantifying the harmful effects of a parasite on the growth rate of its host population (Anderson 1978). An important consequence, which will be revisited later, is that the net growth rate of a host population will depend critically on the statistical distribution of the number of parasites per host (Anderson 1978).

Macro-parasite pathology differs widely between species and systems. Many nematodes of veterinary importance produce significant reductions in the growth rate of individual hosts (*e.g.* Gulland 1992; Spedding & Brown 1992). Species that attach themselves to, for example the stomach or intestinal wall, can cause ulceration and haemorrhage; parasites that infect the lung or liver can damage these organs; while the intermediate stages of some cestode species produce cysts in the viscera or brains of their host (Dobson *et al.* 1992). Gastro-intestinal parasites can also reduce digestive efficiency of the host (Holmes 1985, 1987; MacRae 1993). Macro-parasites generally tend to decrease fecundity and/or increase morbidity rather than mortality (Dobson *et al.* 1992).

There appear to be few detailed studies that have attempted to quantify the energetic effects of macro-parasites on their hosts (Dobson *et al.* 1992). An experimental group of 18 Soay sheep kept under controlled conditions showed reduced growth rate when infected with *Ostertagia circumcincta* (Gulland 1992). Red grouse kept under experimental conditions showed reduced growth rates, loss of body mass, muscle loss, reduced digestive capacity and increase energy demands when infected with *T. tenuis* compared to non-infected control animals (Delahay *et al.* 1995).

The Anderson & May model

Theoretical work in the last quarter of a century shows that, depending on the circumstances and interaction between affects, macro-parasites can act to stabilise or destabilise their host dynamics (May & Anderson 1978; Anderson & May 1978). As three of the following papers (III, IV and V) set out to test different facets of the Anderson and May model that have been shown to destabilise host populations and potentially drive cycles, I will first introduce the model developed by Anderson and May, and then discuss how the population parameters of the host and parasite may affect the host dynamics.

Anderson and May used two differential equations to represent the host and parasite population growth rates (Anderson & May 1978);

$$dH / dt = (a - b) H - \alpha P$$

$$dP / dt = P(\lambda H / (H_0 + H) - (b + \mu + \alpha) - \alpha P / H)$$

Where H and P represent the host and parasite populations respectively, *a* and *b* are the birth and death rates of the non-parasitized hosts, α is the host death rate due to parasitism, λ is the birth rate of the parasites transmission stages, H_0 is a transmission efficiency constant, and μ is the death rate of parasites within the host.

The model framework assumes that the growth rate of the host population in the absence of parasitic infection is determined by constant birth and death rates. The death rate, *b*, represents mortality due to factors other than parasitism. The host population will grow exponentially as long as the birth rate is greater than the death rate. Density-dependant constraints on host population growth rate were omitted

from the model to simplify analysis and to shed light on the mechanism by which parasites regulate population growth (Anderson & May, 1978; May & Anderson, 1978). In the absence of parasitism or parasite regulated growth the host population would grow until it was limited or regulated by other factors.

The basic model assumes that parasite induced mortality is linear to the intensity of infection (May & Anderson 1978; Anderson & May 1978). Parasite induced mortality is therefore critically dependant on the distribution of parasites within the host population. The basic model assumes that parasites are independently distributed. A large number of studies, however, show that parasites are usually aggregated within the host population with most individuals having none or only small infections and only a minority of the host population harbouring the majority of parasite population (Shaw & Dobson 1995). This distribution is statistically well described by the negative binomial distribution (Shaw & Dobson 1995; Wilson *et al.* 2001).

Many helminth parasites show direct life cycles, where the eggs are voided in the faeces of the host and develop through a series of free living larval stages before maturing into an infective stage that is ingested by the host. Only a proportion of eggs will mature to infective stages and only a proportion of these will successfully establish within a host. Environmental factors such as temperature and humidity interact to determine egg and larval survival and maturation time. However, a key factor in determining the rate of transmission is the density of infective stages in the habitat in relation to the density of hosts (Anderson 1978). The transmission factor in the model represents losses of infective stages and the relative densities of the two populations. Populations of nematode parasite species that show direct life cycles that include free living stages will also have a developmental lag or time delay in the recruitment of new adults into the breeding population.

Parasite mortality is broken down into three distinct components; losses due to natural host mortality, losses due to parasite induced mortality, and natural parasite mortality due to the immunological response of the host and parasite senescence.

Assuming parasites are distributed independently within hosts, parasite mediated mortality is linear to the intensity of infection, and instantaneous transmission of parasites, parasites will stabilise the host population if the birth rate of the parasites transmission stages (λ) is greater than the sum of the death rate of parasites within the host (μ), the host death rate due to parasitism (α) and the host population birth rate (a); $\lambda > \mu + \alpha + a$ (Anderson & May 1978). If this condition is not met the host population “escapes” parasite regulation and grows exponentially until some other factor (not included in the model) contains growth. If the condition is fulfilled and the parasites regulate the host population growth rate, the model gives rise to equilibrium states for both host and parasite populations. In the basic model, however, the equilibrium state is not stable, *i.e.* neutral stability, and once perturbed the parasite and host populations will oscillate with a periodicity determined by the values of the rate parameters and an amplitude that is dictated by the size of the initial displacement (Anderson & May 1978; Anderson 1978).

Anderson and May (May & Anderson 1978; Anderson & May 1978) demonstrate that three characteristics; over-dispersion of the parasites in the host population, density-dependence in parasite mortality or fecundity, and parasite induced host mortality that increases faster than linearly with intensity of infection, will tend to stabilise the interaction. Conversely, parasite mediated reduction of host fecundity, a random distribution in the host population such that the death of an infected host does not remove a large proportion of the parasite population, and time-delays in the development of transmission stages of the parasite will tend to destabilise the interaction (May & Anderson 1978; Anderson & May 1978). Although Anderson and May highlight a number of factors that will either act to stabilise or destabilise a parasite-host interaction the overall result will depend on the interaction between stabilising and destabilising influences and the nature of the density-dependant relationship between parasite mediated effects and host density (May & Anderson 1978; Anderson & May 1978; Scott & Dobson 1989).

While micro-parasites, such as viruses and bacteria, reproduce and increase rapidly within a susceptible host, generally the pathology of an infection is not critically dependant on the level of infection, so there is little point in considering the precise number of infective agents (Pugliese *et al.* 1998). For this reason micro-parasite epidemiology is often modelled using the susceptible-infected (SI) or susceptible-infect-recovered (SIR) modelling framework. Macro-parasites however usually show little or no reproduction or increase in the host and instead tend to reproduce and infect hosts via free living larvae. Host mortality and morbidity are dependant on the level of infection. Moreover, parasites tend to show an aggregated distribution such that only a minority of hosts harbour the majority of parasites. Thus the impact of the parasite on the host population is dependant on the mean level of infection and is critically dependant on the distribution of parasites within the host population. These two considerations are incorporated into the Anderson and May model by use of k of the negative binomial distribution.

The use of k , although convenient, is not entirely satisfactory as it is not a biological parameter but rather a population statistic that does not necessarily reflect the processes that lead to parasite aggregation. Moreover, the value of k may not reflect the biological importance or effect, *i.e.* a k of 1 may not have half the affect of a k of 0.5. Furthermore, in the Anderson and May model k is a fixed quantity which runs against empirical observations that show that k varies within segments of the population, season and year (see Rosa & Pugliese (2002) for a recent review of these issues). Variations of the Anderson and May model have been proposed that, for example; explicitly model mechanisms that can give rise to aggregated distributions, let k vary, or include co-infection with more than one macro-parasite (Pugliese *et al.* 1998; Pugliese 2000; Rosa & Pugliese 2002). In a review and assessment of different deterministic models (Rosa & Pugliese 2002) found that all the models were remarkably consistent and the results from Anderson and May model were indistinguishable from other models that utilised different methods of representing the aggregated distribution of parasites within the host population. The different methods of modelling the aggregated distribution of parasites did, however, suggest that, in some circumstances, the fixed k used in the Anderson and May model underestimates the parameter region that gives rise to

sustained cycles, while under other circumstances the region of stability is underestimated (Rosa & Pugliese 2002).

The role of parasites in vertebrate host population dynamics

Despite the theoretical support experimental evidence for the role of parasites in regulating wildlife populations is limited. Experimental evidence is restricted to the red grouse-*T. tenuis* system. In northern England and Scotland red grouse exhibit regular 4-10 year cycles (Haydon *et al.* 2002) which have been attributed to the effects of the intestinal nematode parasite *T. tenuis* found in the ceca of infected birds (Hudson *et al.* 2002). Field and modelling studies showed that *T. tenuis* had little effect on host survival, reduced host fecundity, was loosely aggregated in the host population, and thus had the potential to destabilise red grouse populations and drive cycles (Dobson & Hudson 1992; Hudson *et al.* 1992). Parasite reduction experiments using anthelmintic drugs reduced the rate of population decline when administered to experimental populations prior to a predicted population crash, relative to untreated populations that underwent the predicted crash (Hudson *et al.* 1998). Based on the evidence that reducing parasites burdens limited the population crash Hudson *et al.* (1998) concluded that *T. tenuis* was responsible for driving population cycles of red grouse. Although the conclusions of the Hudson *et al.* study have been questioned (Lambin *et al.* 1999) the *T. tenuis*-red grouse system remains the only experimental evidence that parasites can destabilise host population dynamics (Tompkins & Begon 1999; Turchin 2003).

Parasite mediated affects on survival, body condition and fecundity have also been demonstrated in two ungulate population; Soay sheep on St. Kilda and Svalbard reindeer in Spitzbergen, arctic Norway. Feral Soay sheep on the St. Kilda archipelago of the east coast of Scotland exhibit unstable dynamics with population crashes every 3-4 years (Clutton-Brock *et al.* 1997). There are no predators nor competing herbivores on the islands and the dramatic population declines are characterised by overcompensating density-dependant winter mortality (Grenfell *et al.* 1992) associated with food limitation, poor weather and possibly macro-parasites (Clutton-Brock *et al.* 1991; Gulland & Fox 1992; Catchpole *et al.* 2000). Parasite reduction, achieved using an intraruminal anthelmintic bolus, suggested that parasites may play a role in inducing mortality in certain age and sex classes of wild Soay sheep during a population crash and that parasite induced mortality was additive to other causes (Gulland 1992).

Population densities of populations of Svalbard reindeer of Spitzbergen in arctic Norway fluctuate over a twofold range, birth and death rates also co-vary (Solberg *et al.* 2001). A significant part of these fluctuations has been attributed to stochastic weather events where winters with high precipitation are characterised by poor survival and low birth rate in the subsequent summer (Solberg *et al.* 2001). Parasite reduction experiments, cross-sectional and modelling studies suggest that intestinal helminth parasites reduce body condition, body fat and thus reduce fecundity of female reindeer and population growth rate (Albon *et al.* 2002; Stien *et al.* 2002).

The role of parasites in lagomorph population dynamics remains contentious due to the lack of conclusive experimental evidence. Although temporal changes in the prevalence and intensity of helminth infections have been reported in cyclic populations of snowshoe hares (Keith *et al.* 1985, 1986), experimental reduction of parasites have produced no detectable effects on snowshoe hare body condition, fat deposits, male sexual development or female fecundity (Bloomer *et al.* 1995; Murray *et al.* 1997, 1998). However, these studies have demonstrated that parasite reduction increased the survival rates of snowshoe hares principally due to reduced predation on individuals with low intensities of parasite infection (Murray 2002). Models of hare, predator and parasite dynamics demonstrate that parasite-induced vulnerability to predation acts in a destabilizing manner and makes population cycles more likely (Ives & Murray 1997).

Population assessment of Scottish mountain hare populations (Paper VI)

The reliable estimation of population abundance is the cornerstone of most ecological research. Methodological texts all suggest that census techniques must be tailored to the species in question and to the level of precision required by each study (Sutherland 1996; Krebs 1999; Southwood & Henderson 2000). Mountain hare densities have been estimated using capture-recapture techniques (Flux 1970; Hewson 1976; Angerbjorn 1986) but such studies require considerable investment in time and resources. Less intensive census techniques such as vantage point counts, line transects and total counts using dogs have also been used for mountain hares, as have indirect methods based on dung plots (Flux 1970; Watson & Hewson 1973; Angerbjorn 1983; Hewson 1989; Gilbert *et al.* 2001). These studies did not, however, evaluate the effectiveness of the methods used. In this paper we critically test the use of distance sampling methods to estimate densities of mountain hares in the Scottish highlands and compare derived estimates with those arrived at by other methods. Estimates of population density may not be required for all research or management purposes and in some cases an index of relative abundance may be sufficient (Caughley & Sinclair 1994; Krebs 1999). Indirect surveys of animal abundance may be cheaper and easier than direct counts of the animals themselves and in this paper we also assess the use of dung plots as an indirect index of the abundance of mountain hares.

With careful planning, sufficient effort, a short sampling period and a reliable method of marking, the assumptions of capture-recapture methods can be effectively met and sufficient animals trapped to generate reliable estimates (Krebs 1999). Capture-recapture methods are labour intensive, however, and are also intrusive to the study animals. Because of these logistic and welfare considerations, capture-recapture techniques are usually limited to detailed ecological research rather than as a quick method for assessing abundance. Distance sampling offers a potentially useful technique for estimating mountain hare density as counts from line transects are less intrusive and labour intensive than capture-recapture techniques, offer the advantage of being able to quickly cover large study areas, and allow estimates of precision to be attached to density estimates. In this study

we evaluate distance sampling and dung plots as cost effective methods of estimating hare density in the Scottish highlands. We compared density estimates derived from these methods to estimates derived from capture-recapture techniques.

Objectives

1. Review limiting and regulating factors for mountain hare populations in Eurasia (Paper I).
2. Address the question of whether mountain hare populations cycle or merely fluctuate? (Paper II).
3. Based on the Anderson and May macro-parasite model assess the role of nematode parasites in destabilising mountain hare population dynamics in Scotland (Papers III, IV and V).
4. Develop cost effective methods to assess population density of mountain hares in the Scottish highlands (Paper VI).

A review of limiting and regulating factors (Paper I)

In paper I we undertake a literature review of the mechanisms that have been proposed as limiting or regulating mountain hare populations. While we are able to offer an exhaustive review of the literature relating to northern Europe our assessment of the literature pertaining to Asia and central Europe is restricted due to the limited availability of English language literature.

Although the early theoretical work of Lotka (1932) and Volterra (1926) demonstrated that simple predator-prey systems were inherently unstable and prone to cycles, the role of predators in driving their prey population dynamics was questioned by the influential opinions of Errington (1946). Errington (1946) proposed that predators only take a “doomed surplus” – those animals that were sick, dying or excluded from the breeding population and thus unlikely to contribute to further generations, and that prey population dynamics were driven by “... internal strife ...”. Errington’s views are no longer as influential as they were and there is now a widely accepted paradigm that predators can limit their prey populations (Krebs *et al.* 1995; Hanski & Korpimaki 1995; Korpimaki & Norrdahl 1998; Thirgood *et al.* 2000; Korpimaki *et al.* 2002; Ekerholm *et al.* 2004).

In Fennoscandia there appears to be a widely held belief that predation by foxes limits mountain hare populations. In Sweden at least there is a body of correlative and experimental evidence that fox predation plays an important role in limiting mountain hare populations; i) the widely observed increase in hare and other small

game species in response to a large scale decline in fox numbers following an epizootic of sarcoptic mange (Danell & Hornfeldt 1987; Lindstrom *et al.* 1994), and ii) the classic predator manipulation experiments of Marcstrom and co-workers (Marcstrom *et al.* 1988, 1989) on two islands in the northern gulf of Bothnia that were alternately subject to predator control or predator protection that demonstrated that small game populations increased when foxes were controlled.

The role of fox predation in Norway and Finland is less certain. One study in Norway showed that small game, including mountain hare, numbers increased as fox numbers declined due to an epizootic of sarcoptic mange and that small game numbers declined as fox numbers recovered at both the regional and national scale (Myrberget & Lund-Tangen 1990). In Finland, stomach analysis of foxes suggests that foxes prey on large numbers of hares, however, high predation in itself is not sufficient to limit a prey population. Predator reduction experiments that reduced over winter mammalian predator numbers undertaken by Kauhala *et al.* (1999, 2000) failed to demonstrate that predation was limiting mountain hare populations. However, the authors suggest that predator control which was confined to the winter months failed to reduce the numbers of breeding pairs due to high immigration rates and that breeding success may have been higher than normal due to reduced competition (Kauhala *et al.* 1999) thus confounding the results. A correlative study on the association between hare and fox numbers assessed from snow track data were also inconclusive (Kauhala & Helle 2000).

The role of predators in driving mountain hare population dynamics in Russia is largely dismissed due to the low density of predators combined with low predation pressure relative to the number of hares hunted by people (Naumov 1947; Labutin 1960; Naumov 1960b). None of these studies however present any data on cause specific mortality or demonstrate that predation is compensatory, and have to be treated with some scepticism. Predators, are assumed to increase in density as hare populations increase and are attributed with accelerating, deepening and lengthening the decline and low phases of the population cycle, but again there is no evidence presented for this (Naumov 1947; Labutin 1960; Naumov 1960b).

Fox, wild cats, stoat, buzzard, hen harrier, and golden eagle prey on mountain hares in Scotland (Hewson 1976; Watson *et al.* 1993; Watson 1997). But due to the rigorous control of mammalian predators (fox, weasel and stoat), crows and the illegal persecution of raptors (golden eagle, hen harrier and buzzard) on Scottish grouse moors (Hudson 1992; Etheridge *et al.* 1997; Redpath & Thirgood 1997; Whitfield *et al.* 2003), where most mountain hares occur, predators are not thought to play an important role in limiting mountain hare populations in Scotland (Hewson 1976, 1985). The role of predators has not been experimentally tested, and out with areas of grouse moor production the role of predators is entirely unknown.

To date the only hypothesis to receive experimental attention in Scotland has been the potential role of parasites in destabilising hare population dynamics. In only the second experiment of its kind to experimentally manipulate individual parasite intensities of wild, free living lagomorphs Newey *et al.* (Papers III, IV, V)

investigated three features of the host-parasite association that the Anderson and May macro-parasite model (May & Anderson 1978; Anderson & May 1978) suggests can destabilise host population dynamics. The experimental and cross-sectional studies of Newey *et al.* (Papers III, IV, V) show the intestinal nematode parasite *Trichostrongylus retortaeformis* reduces fecundity, has little effect on female survival, and is mildly aggregated in the mountain hare population. These are all features that theoretical studies (May & Anderson 1978; Anderson & May 1978) have demonstrated act to destabilise host dynamics.

The role of parasites and pathogens in Fennoscandia appears to be largely unexplored. Outbreaks of tularemia, a bacterial disease common in rodents caused by the bacterium *Francisella tularensis*, is highly infectious spreading via inhalation of infected aerosols or by arthropod bites and has been associated with declines in hare numbers (Borg *et al.* 1969; Hornfeldt 1978). The prevalence and intensity of tularemia is, however, dependant on many factors including climate, rodent and vector density and thus, Hornfeldt (1978) suggest that tularemia is unlikely to play an important role in the long term population dynamics of mountain hares.

The favoured explanation for hare cycles in Russia is a build up of parasites as hare density increases (Naumov 1947, 1960b). However, as we review in Paper I there is actually very little evidence to support this hypothesis. This conjecture is largely based on the concurrent increase of parasite infections with increasing hare numbers, along with the observation that the intensity of parasite infection increases with hare population density and peaks two years later than the start of the decline in hare numbers.

Population declines in hare abundance have been associated with food shortage associated with severe weather, in particular heavy or prolonged snowfall, both in the highlands of eastern Scotland and Baltic islands (Hewson 1965, 1970; Angerbjorn 1981). Both the highlands of Scotland and Baltic are characterised by low lying ericaceous vegetation that is readily buried by snow, and high density populations. It is therefore unclear whether the observed population declines are caused directly by or in association with inclement weather, food shortage, or high population density. Whatever the causes, such events appear to be uncommon occurrences that are unlikely to drive long term population dynamics. Mountain hares occur at low densities in boreal Fennoscandia (< 3 hare km²) and food availability and quality are dismissed as limiting factors (Keith 1983) in mainland populations, although this has not been experimentally tested. Similarly in Russia the role of food quantity is largely dismissed (Naumov 1947; Popov 1960; Naumov 1960a) but this view is not entirely consistent with all of the available evidence and what is known from similar systems elsewhere (Keith 1983). Although food limitation is dismissed, Naumov (1947) speculates that food quality at peak hare density might have an important influence on population growth rates by reducing fecundity and survival, but there is no firm evidence to support this conjecture. Overall the role of food has not been well studied and much more work is needed to elucidate the role of food in mountain hare population dynamics.

Date of first breeding and thus the length of the breeding season is influenced by air temperature (Naumov 1947, 1960a; Angerbjorn 1986) and in one study in eastern Scotland first litter size was found to be closely related to air frost (Hewson 1970). Based on two years observations Flux (1970) suggested that first litter prenatal mortality was associated with harsh weather in spring however the data are far too limited to draw any conclusions. Thus weather, in particular air temperature, in late winter or early spring has the potential to limit female productivity and population growth rate. But weather and annual seasonal temperatures are generally considered to fluctuate around a mean and so it is difficult to see how air temperature could limit hare populations in the long term. It is also unclear whether the reduced litter size is due to reduced fecundity due to lower female body condition or resorption of embryos in response to environmental stress. Moreover, there was no indication that weather affected annual productivity or whether smaller first litters were compensated for by better survival of leverets or larger second litters. Given the strong link between date of birth, adult size, survival and fecundity, environmentally mediated life-history characteristics have the potential to propagate cohort or maternal effects. Perhaps not surprisingly there appears to have been little work done on the role of weather and climate in limiting or regulating mountain hare populations and there is very little that we can conclude from the published literature.

Summary and conclusions

There is good evidence that some hare populations in Fennoscandia are limited by predation. There is little evidence that nutrition or parasitism are important but the key experiments looking for interactions have not been conducted. There is emerging evidence that some hare populations in Scotland are regulated by parasites and that parasites contribute to population instability. Predation is unlikely to be important because predator populations are reduced by game managers. Large scale experiments are required to consolidate this work and also to investigate interactions with nutrition and climate. Access to Russian research literature is severely limited. Based on the literature reviewed here the limitation and regulation of mountain hare populations in Russia is unclear and accessing the Russian research material should be a priority. Similarly there is a paucity of English language research material available on Central European hare populations and making this information available to the wider scientific community should also be a priority.

Do mountain hare populations cycle? (Paper II)

Methods

Time-series

There is currently no national monitoring scheme for wild mammals in the UK and here we rely on game bag statistics that are collected by private hunting estates and

collated into the National Game Census (NGC) by The Game Conservancy Trust. The NGC data base currently holds mountain hare time-series for 212 estates dating from 1850 to 2002 but most series were too short or incomplete to be used. Our analysis is based on 57 series from 51 estates in Scotland and range in length from 20 to 109 years (Table 1; Paper II).

Although the Statistics Service of Norway have compiled hunting statistics on small game since 1971 data collection, processing, analysis and presentation have changed a number of times (Statistics Norway, 2002) and we considered the data unsuitable for analysis. Our assessment of Norwegian populations is limited to a reanalysis of three published time-series which ranged in length from 13-22 years; Moksnes (1972), Hjelford (1980), and Myberget & Lund-Tangen (1990) (Table 1; Paper II).

National game bag statistics for the whole of Sweden are collected by the Association for Hunting and Wildlife Management (Wildlife Monitoring) and the current database contains records from 25 hunting administrative areas from 1960 to 2002. Mountain hare populations in large areas of Sweden and Norway were affected by a drastic decline in fox numbers during the 1980's due to an epizootic of sarcoptic mange (Danell & Hornfeldt 1987; Lindstrom *et al.* 1994; Smedshaug *et al.* 1999). We therefore split the series into two shorter time-series; 1960-1980 to represent pre-mange period and 1981-2002 to coincide with post-mange period. Although there is a rich mountain hare literature for Sweden only three studies included usable and unique time-series; Hornfeldt, Lofgren & Carlson (1986), Danell & Hornfeldt (1987), and Small, Marcstrom & Willebrand (1993) (Table 1; Paper II).

Abundance data of small game species has been collected by the Finnish authorities by questionnaire surveys sent to a network of permanent observers. The observers provide an estimate of relative abundance using a scale of 0-3. Questionnaire responses are averaged by province to provide a density category, or index, for each area (Linden 1988). Although care is needed interpreting such indices the questionnaire data is considered suitable for time-series analysis and has been used in other time-series studies (Linden 1988; Ranta *et al.* 1997). We also used two time-series published by Siivonen (1948) and one by Pulliainen (1982) (Table 1; Paper II).

Mountain hares in central Europe are restricted to the high European alps of Switzerland, Italy and France (Mitchel-Jones *et al.* 1999). Switzerland keeps official hunting statistics for each of the country's 26 Cantons, which are in the public domain (Table 1; Paper II). Mountain hares are not hunted everywhere in Switzerland, the hunting season is very short and in some years no hares are shot, so only 10 Cantons yielded time-series long enough to be analysed. Four series were found in the literature from northern Italy (Scherini & Tosi 1990)(Table 1; Paper II).

Only four time-series from Russia, all longer than 20 years, were found in the literature; Naumov (1972), Bulmer (1974), and Jedrzejewski *et al.* (1996)(Table 1; Paper II).

Reliance on hunting statistics assumes that the number of animals taken parallels the true population. Two studies have attempted to validate the use of bag records; Brand & Keith (1979) concluded that although fur returns of Canadian lynx exaggerated the cycle they were a reliable index of lynx numbers, and Cattadori *et al.* (2003) found a strong association between number of grouse counted using trained pointing dogs and the number of red grouse shot.

Analysis

In order to assess the temporal nature of population fluctuations, long-term data are essential (Stenseth 1999). In paper II we take advantage of four long term data sets of mountain hare abundance indexed from hunting records or questionnaire data from Scotland, Sweden, Finland and Switzerland (Table 1; Paper II). While some studies of these data sets have been undertaken before (Hornfeldt 1978; Tapper 1987; Linden 1988; Ranta *et al.* 1997), comparison between studies is hindered due to differences in data preparation, analysis and classification and these data series remain to be fully explored. To further investigate and understand the range of dynamics of mountain hare populations we also collated and reanalysed time-series from published studies (Table 1; Paper II).

Time-series were first transformed to natural logarithms to stabilise variance and to convert linear additive processes to multiplicative processes. We used LOESS regression (Cleveland 1979; Cleveland & Devlin 1988; Trexler & Joseph 1993) to detrend and smooth all the time-series prior to analysis. Time-series were then subject to autocorrelation analysis to identify whether the series exhibited a statistically significant periodicity (Turchin 2003).

Identifying the density-dependant structure of a series can serve as a guide for identifying plausible candidates for the mechanisms producing the observed dynamics. First order density-dependence may arise due to direct resource competition within the species, whereas second or higher order feedback in density-dependence is usually considered a sign of trophic interactions like predator-prey or parasite-host relationships (Royama 1992; Stenseth 1999; Turchin 2003). We used the partial rate correlation function (Berryman & Turchin 2001) to identify the processes order and significance.

Results

Scotland. Overall 56% of the series examined were classified as cyclic (12%) or weakly cyclic (44%) with a mean periodicity of 8.7 years, but there is considerable variation and periodicity rages from 5-15 years (Table 2; Paper II).

Norway. The time-series from Moskness (1972), from the south-west of Norway, revealed cyclic behaviour with a 3-year periodicity. Hjelford's (1970) and Myrberget & Land-Tagen's (1990) studies both from Nordland in central Norway were classified as non-cyclic and weakly cyclic with a 7-year periodicity respectively (Table 2; Paper II).

Sweden. None of the 25 series of Swedish game bag statistics analysed were classified as cyclic in either the pre- or post-mange time periods. Both the pre- and post-mange series are predominantly non-cyclic with only around a third showing weak cyclic dynamics (Table 2; Paper II). The series from the 1960-1980 pre-mange period show a shorter periodicity of 3.9 years compared to the post-mange period of 6.5 year (Table 2; Paper II). The characteristic consistent low amplitude fluctuations of the 1960-80 pre-mange period are replaced by more variable and higher amplitude fluctuations in the 1980-2002 time period (Table 2; Paper II). Although the proportion of non-cyclic time-series is the same in both time periods there is a change in the distribution of weakly cyclic series. Of the eight counties that are weakly cyclic in both time periods only three are the same (Figure 1; Paper II). The central counties that exhibited 3-4 year cycles in the pre-mange period are non-cyclic after the mange epizootic, while there is an increase in weak cyclic series in southern Sweden and in the central-eastern areas around Stockholm (Figure 1; Paper II).

Finland. None of the series from the nine provinces were classified as cyclic in our analysis, six were classified as showing weak cyclic dynamics with a mean periodicity of 5.3 years, and the remaining three were regarded as non-cyclic (Table 2; Paper II). With the exception of Lapland in the very north of Finland all of the weak cyclic series are in the south-west and central Finland (Figure 1; Paper II).

Alpine hare populations. Six of the ten series we analysed from Switzerland were classified as non-cyclic and four were weakly cyclic with a mean periodicity of 6.2 years (Table 2; Paper II). Only one time-series from Italy; Bolzano was classified as weakly cyclic with a periodicity of 6-years, the other series was non-cyclic (Table 2; Paper II).

Russian Federation. One of the two series from the Kommi Republic (NW Russia) published by Naumov (1972) exhibited an 8-year weak cycle, the second series, however, was non-cyclic. The series from the Borovichi Central Forest Reserve, Novgorodskaya, also in north-west Russia (Jedrzejewski *et al.* 1996) was non-cyclic. The series from Bulmer (1972) from Yakutskaya in far eastern Russia showed an 11-year cycle (Table 2; Paper II).

The seven cyclic series identified in this study all come from Scotland and although influenced by a range of time lags appear to be most affected by delayed density-dependence operating at time lags of two and more years (Table 3; Paper II). The weakly cyclic series show a more even distribution between first and higher order processes and while 69% of the series are influenced by a combination of direct and delayed density-dependence processes 41% are only

influenced by first order direct density-dependence. Ninety-three percent of the non-cyclic series are most strongly influenced by direct density-dependence.

The 1960-80 time-series from Sweden show a distinct pattern with weakly cyclic series dominated by delayed density-dependent processes while the majority (83%) of non-cyclic series show no evidence of density-dependence or only direct density-dependence (Table 3; Paper II). The later, 1981-2002 series show a similar pattern with the weakly cyclic series being largely driven by higher order, delayed, processes and while some 41% of the non-cyclic series are driven by first order, direct density-dependence, processes there is large proportion (47%) that do not show any significant time lag affect (Table 3; Paper II).

The Finnish time-series show a very clear cut with all of the weakly cyclic series showing only delayed density-dependent processes and none of the non-cyclic series revealed any significant process order (Table 3; Paper II). The weakly cyclic series from Switzerland are influenced by direct and delayed density-dependent processes, while the non-cyclic series are dominated by first order processes only (Table 3; Paper II).

Discussion

The one previous time-series analysis of mountain hare bag records from Scotland based on 20 series suggested that mountain hare populations were best described as phase-forgetting quasi-cyclic with a mean periodicity of 9.5 years (Tapper 1987, 1992). Despite differences in methodology and data coverage the results from this study are remarkably similar both in terms of characterising the nature of the cycles and in the estimated periodicity.

From our analysis of Swedish game bag statistics, hare populations in Sweden are less cyclic than our analysis suggests is the case in Scotland. Swedish hare populations are characterised by higher frequency and lower-amplitude dynamics compared to the mean 9-year period and higher-amplitude dynamics identified in the Scottish game bag data. The later bag records from the post-mange period however exhibit a longer, approximately 6-year periodicity. Hornfeldt's (1986) opinion, based on a visual assessment of the time-series, that mountain hare populations exhibit 4-year cycles is confirmed by our reanalysis of those data. The occurrence of true cyclic dynamics in Hornfeldt's (1986) series, however runs contrary to the results of our analysis of the longer-term hunting statistics which revealed no true cyclic time-series.

Our analysis of the long term Swedish time-series shows that the amplitude and periodicity both increase in the 1980-2002 period compared to the 1960-1980 period. Furthermore, although there is no change in the proportion of weakly cyclic and non-cyclic series, there is a marked change in the distribution of weakly cyclic populations. The central counties that were classified as weakly cyclic in the 1960-80 period are non-cyclic in the 1980-2002 period. These counties correspond to the areas most heavily affected by the fox mange epizootic in the late 1970's and early

1980's. Intriguingly the areas in the very north and south of Sweden that were non-cyclic in the 1960-80 pre-mange period are classified as weakly cyclic in the later 1980-2002 post-mange period.

Previous time-series studies of changes in mountain hare abundance in Finland based on winter game enquiry questionnaires have shown the widespread occurrence of cycles ranging from 4-11 years with shorter cycles in the north giving way to longer cycles in the south (Linden 1988; Ranta *et al.* 1997). The results from our analysis largely concur with the results of earlier studies, however the current study does differ in the distribution of cycles which we found to be concentrated in central and southern provinces where as previous studies (Linden 1988; Ranta *et al.* 1997) found more cyclic series in the northern provinces.

To our knowledge there are few published studies on mountain hare population dynamics in central Europe. It is therefore difficult to put our findings into context, especially given the limited geographic coverage and small number of series available. Similarly investigations of population cycles in Asia have been hampered by the shortage of suitable long-term data (Keith 1981, 1983) and it is difficult to assess our results. In the west, our understanding of mountain hare ecology is largely confined to few studies that have been translated into English and our understanding of Asian mountain hare ecology is limited. As Asia represents a substantial proportion of the mountain hare's range we suggest that accessing the Russian, and other non-English, literature should be a priority.

Although cyclic and weakly cyclic series are predominantly driven by second and higher order processes indicative of delayed density-dependent affects, with the exception of Finland, first order direct density-dependent processes also appear to play an important role in these series. The series from Finland are an interesting exception as there is a clear dominance of second and higher order processes in the weakly cyclic series and no significant density-dependent affect in the non-cyclic series. The time-series from Finland are the only series in the long-term data not derived from hunting statistics.

The role of parasites in Scottish mountain hares (III, IV and V)

Models of parasite-host interactions have identified three features that can lead to instability; i) a high level of parasite-induced reduction in host fecundity compared to impact of parasites on host survival, ii) time delays in parasite recruitment, and iii) a random distribution of parasites within the host population (May & Anderson 1978; Anderson & May 1978). Here we describe two parasite reduction experiments designed to asses the effect of a) parasite removal in early spring on female mountain hare body condition and fecundity, referred to as the *spring parasite reduction experiment*, and b) over winter parasite reduction on survival,

body condition, and reproduction, referred to as *the winter parasite reduction experiment*.

The outcome of host-parasite interactions is critically dependant on the distribution of parasites within the host population. In paper V, we describe a *cross-sectional study*, in which we investigate the prevalence, intensity of infection and degree of aggregation of the most common helminth parasites found in mountain hares and assess whether the degree of aggregation is low so that either *G. strigosum* or *T. retortaeformis* have the potential to destabilise the host-parasite equilibrium density as identified by the Anderson and May macro-parasite model (May & Anderson 1978; Anderson & May 1978). We also investigated the effect of parasite intensity on reproduction, indirectly by examining the effects of parasites on body condition, since body condition during the winter months is known to affect fecundity in a range of lagomorph species (Vaughan & Keith 1981; Angerbjorn 1986).

Methods

Parasite reduction experiments

Both experiments were carried out on private hunting estates in the central highlands of Scotland; near Newtonmore (57.0635°N, 4.1207°W). Both study areas were managed for red grouse production and consisted of a mosaic of different aged stands of heather giving way to lichens and grasses at higher altitudes. The study sites were in mountainous areas and the altitude of the study sites ranged from 500 to 900 m. Both experiments were undertaken on moors with high densities of mountain hares as assessed by capture-recapture and distance sampling (Paper VI). Avian and mammalian predators were killed by gamekeepers, but were present at low density on both sites in all years.

The spring parasite reduction experiment was undertaken over two years (2000 and 2001) and hares were caught in spring. The winter parasite reduction experiment was carried out over the winter 2002-2003. Hares were caught in early winter and so the sample of animals caught included adults (> 1 year) and young of the year which, were distinguished by apophyseal notch at the head of the tibia and were not included in the study. In both studies mountain hares were caught in cage traps set over night or by driving hares into long nets. Captured animals were sexed and female hares were weighed, hind foot length measured and fitted with a radio-collar. Alternate females were administered 1 ml of Ivermectin by subcutaneous injection. Ivermectin is a broad spectrum anthelmintic that has been shown to remove helminth parasites in other wildlife studies (Murray *et al.* 1996; Sovell & Holmes 1996).

During the course of the winter parasite reduction experiment each radio-collared female was found by radio-tracking every 2-4 weeks to monitor survival. We estimated survival probability using the Kaplan-Meier method where females alive at the end of each experiment prior to culling were right censored.

In 2000 and 2001 radio-collared females caught that spring and a random sample of unhandled hares were shot in autumn. For the winter parasite reduction experiment the radio-collared females and a sample of unhandled hares were shot in May 2003. We included a sample of unhandled hares as a control group to investigate the possible effects of handling and radio-collaring. No hare has ever been recorded to breed in the year of their birth and because our sample of control animals shot in autumn 2000 and 2001 included juvenile females we only included females that we positively identified as having bred that year.

To compare the body condition of hares at the time of capture we used body mass, and controlled for the affect of size by including hind foot length as a covariate. We used the same method to compare body condition for hares shot in autumn 2000 and 2001. However, hares shot in May 2003 for the winter parasite reduction experiment were in the middle of the breeding season and due to the changes in body weight associate with pregnancy and lactation we considered any measure of body condition based on body mass to be inappropriate. Instead we used the kidney fat index (mass of kidney divided by mass of fat around the kidney) as measure of body condition.

Parasite burdens were assessed by removing the stomach, duodenum and small intestine of shot hares and washing the contents through sieves. We searched the stomach residue by eye and recorded the total number of *G. strigosum*. The contents of the small intestine and duodenum were washed into 400 ml of water and four 10 ml sub-samples removed. We counted the number of *T. retortaeformis* in each sub-samples and estimated the total number of *T. retortaeformis* using the regression equation: total count ~ 0.82 (sum of 4 sample counts from duodenum) + 0.57 (sum of 4 sample counts from small intestine) ($F_{3,2}=277.3$, $p<0.001$, adjusted $r^2=0.993$). The sampling regime and regression equation were derived from a pilot study comprising a series of sample and total counts from the small intestine, duodenum, appendix, and large intestine. The four sub-samples counted for each section of the intestine were summed and entered into a multiple regression against the total count. The model, presented above, was derived by backward stepwise deletion of non-significant variables until the best model was found.

Fecundity was estimated by counting the number of corpora lutea and corpora albicantia in ovary cross-sections after culling. Ovaries were removed and frozen to -20 °C before being sectioned by hand into 1 mm sections. Sections were examined under a 10x stereomicroscope and the number of corpora lutea and corpora albicantia were summed to give a measure of fecundity. In the analysis of fecundity we include hind foot length as a covariate to control the effects of age and size on reproductive performance (Iason 1990).

We analysed the data using analysis of variance fit using the General Linear Model function in SYSTAT (v. 9). Data were normalised by log transformation if examination of residuals indicated this was necessary. We derived the minimal acceptable model by backward stepwise deletion from a maximal model that included all terms and interactions. Examination of the residuals of the kidney fat index indicated the data could not be normalised by transformation and

Generalised Linear Models (GLMs) also failed to provide an adequate fit. We, therefore, analysed these data using a Kruskal-Wallis test, a non-parametric technique that makes no assumption regarding the data distribution.

Cross-sectional study

From each of 30 (only 4 in winter 1998/1999) moors in the central Highlands of Scotland we culled approximately 20 hares during the winters of 1998/1999 (N=79) and 1999/2000 (N=510) providing us with a total sample of 589 hares (Paper V; Table 1). Samples were examined within 24 hours of hares being shot and we recorded sex, body weight, hind foot length and noted the breeding status of females. The stomach and intestines were removed and the intensity of infection of *G. strigosum* and *T. retortaeformis* was determined as already described (Paper III).

We present prevalence, intensity and aggregation data for both winters but as the data from the two winters are not strictly comparable, all statistical analyses were restricted to the more extensive 1999/2000 data set (Paper V; Table 2). Prevalence is expressed as the percentage of hares infected and intensity of infection as the arithmetic mean number of parasites per hare. In all cases, data are blocked by moor.

Differences in the prevalence of *G. strigosum* infection between groups of hares were tested using GLMs with binomial errors. The effects of sex, month and moor were added into a full model and the minimal acceptable model was derived by backward stepwise deletion from a full model that included all terms and interactions. Almost all hares were infected with *T. retortaeformis* (see results; Table 2; Paper V), thereby precluding any analysis of prevalence.

We used a GLM with negative binomial error terms to investigate the effect of sex, month and moor on intensity of infection of *T. retortaeformis* (Wilson *et al.* 1996; Wilson *et al.* 2001). We derived the minimal acceptable model by backward stepwise deletion from a maximal model that included all terms and interactions. Due to the highly aggregated distribution and large number of zeros in the *G. strigosum* distribution we were unable to fit an adequate model when we included *G. strigosum* intensity in the full model. We were thus unable to investigate the response of *T. retortaeformis* intensity to co-infection with *G. strigosum*.

Examination of residual plots showed counts of *G. strigosum* to be too highly aggregated for fitting GLMs to be appropriate when using *G. strigosum* as a response variable. Despite the advantages of using GLMs to model parasite data being widely advocated (Crawley 1993; Wilson *et al.* 1996; Wilson & Grenfell 1997) GLMs with negative binomial errors can encounter problems in fitting a single common dispersion parameter to all the different combinations of the terms in the model, especially when the data is highly aggregated and with a low prevalence (Shaw *et al.* 1998). Therefore, to investigate the effects of moor, month and sex on *G. strigosum* intensity we utilised an extension of analysis of variance termed analysis of dispersion (Shaw *et al.* 1998), in which the degree of aggregation

is explicitly fitted by searching through parameter space via maximum likelihood, to obtain the best fit. The degree of aggregation may vary between groups as well as the mean. However, this technique only permits one dependent variable to be entered at a time, and therefore does not permit the production of a minimal acceptable model. Rather it identifies dependent variables which are influencing both the degree of aggregation and mean burden. For all analyses of dispersion the data was checked for its fit to the negative binomial distribution (following the methodology of Shaw *et al.* (1998)), and despite the highly aggregated data adequate fits were found.

We estimated the exponent k of the negative binomial distribution using least biased estimating method (Wilson *et al.* 2001) obtained from the analysis of dispersion (Shaw *et al.* 1998). Estimates of dispersion are exaggerated by grouping (*e.g.* males and females) of data (Shaw & Dobson 1995) so here we provide common k estimates (which take into account heterogeneities in host data) when describing the overall degree of aggregation.

We used the residuals from a non-parametric, LOESS regression (Cleveland 1979; Cleveland & Devlin 1988; Trexler & Joseph 1993; R Development Core Team 2004), of body mass on hind foot length as an index of body condition. While this approach has been criticised (Green 2001) the large sample sizes involved in this study prohibited a more detailed assessment of body condition, and by using LOESS we avoided any assumptions about the scaling of the allometric relationship between body mass and a linear measure of body size. Furthermore, mass-structural size residuals have been shown to have a significant relationship with percent body fat in snowshoe hares (Wirsing *et al.* 2002). Our data consisted of fixed and random terms, were non-orthogonal and unbalanced and we therefore used Residual Maximum Likelihood models (ReML, GenStat v.6.) to examine the effect of intensity of infection on body condition. *Graphidium strigosum* and *T. retortaeformis* intensity, sex and month were entered as fixed terms in the maximal model along with moor as a random term. The minimal acceptable model was found by backward stepwise deletion from the maximal model, which included all term and interactions. Pregnant and lactating females were excluded from this analysis.

Results

Spring parasite reduction experiment

There was no significant difference in body size or condition between hares assigned to treated and untreated groups at time of capture in April. Hares treated with Ivermectin had significantly lower intensities of *T. retortaeformis* than untreated hares when culled in autumn (Figure 1a; Paper III). Treated hares were in significantly better condition when killed in autumn than either untreated hares or unhandled hares and treatment was the most significant explanatory factor (Figure 1b; Paper III). Although hares treated with Ivermectin tended to have more corpora bodies than untreated or unhandled hares the differences were not statistically significant (Figure 1c; Paper III). The lack of statistical significance was most

likely due to small sample size and associated low statistical power ($\beta=0.48$ (S-Plus v.6.)).

The lack of a significant effect of anthelmintic treatment on fecundity may also have been influenced by the timing of the treatment. Female mountain hares become pregnant with their first litter in March and experimental parasite removal in April may have a limited effect on fecundity. Previous research has shown that pregnancy rates, birth dates and litter size in both mountain hares and snowshoe hares are closely related to nutritional status in winter (Vaughan & Keith 1981; Pehrson & Lindlof 1984; Angerbjorn 1986).

Winter parasite reduction experiment

Forty-one female hares were captured in October 2002. There was no significant difference in hind foot length or body mass between females assigned to the two experimental groups. There was no significant difference in survival probability of hares treated with Ivermectin (0.77 ± 0.10) and untreated hares (0.76 ± 0.09). When killed in May 2003 the intensity of *T. retortaeformis* was significantly lower in female hares that had been treated with Ivermectin than in either the untreated or unhandled hares and treatment was the only significant factor (Figure 1a; Paper IV). There was no significant effect of treatment or handling on body condition as measured by the kidney fat index (Figure 1b; Paper IV). Female hares that had been treated with Ivermectin had significantly higher fecundity as measured by the counts of corpora albicantia than either of the control groups and treatment was the only significant factor (Figure 1c; Paper IV).

Cross sectional study

The prevalence, intensity of infection and level of aggregation for *G. strigosum* and *T. retortaeformis* are presented in Table 2 (Paper V). The prevalence of *G. strigosum* was low in both years compared to *T. retortaeformis* which was found in not less than 99% of individuals and populations sampled. Both moor and the moor*month interaction had a significant affect on the prevalence of *G. strigosum*. Intensity of infection of *G. strigosum* was determined by moor, month and sex, with females generally being more severely infected. Although the mean monthly intensity of infection of *T. retortaeformis* showed monthly changes with an over winter decline and an increase in late spring, month had no significant effect on intensity. While females tended to be more severely infected, the difference between sexes was not significant. Only moor and the moor*sex interaction were identified as significant terms in describing mean *T. retortaeformis* intensity. Both *G. strigosum* and *T. retortaeformis* were aggregated with variances greater than means, but *G. strigosum* was consistently more aggregated than *T. retortaeformis*. Analyses of dispersion revealed significant differences in the degree of aggregation of both *G. strigosum* and *T. retortaeformis* between hares from different moors and months but not sex (Paper V; Table 2).

Analysis of body condition, based on mass-structural size residuals, revealed that month and sex had a significant affect on recorded body condition and the

month*sex interaction was also highly significant. While the intensity of infection of *G. strigosum* and *T. retortaeformis* did not influence body condition independently, there was a highly significant interaction between month**T. retortaeformis* intensity suggesting that *T. retortaeformis* had a negative effect on body condition.

Discussion

The results from the two parasite reduction experiments and the extensive cross-sectional study demonstrate that the intestinal nematode parasite *T. retortaeformis* i) has an insignificant effect on host survival, ii) has a significant and relatively large negative effect on host fecundity compared to the effect on survival, and iii) shows a relatively low degree of aggregation compared to many parasites. These three characteristics along with the time-delay inherent in the life cycle of *T. retortaeformis* means that the *T. retortaeformis*-mountain hare interaction exhibits a number of features which Anderson and May have demonstrated can lead to instability (May & Anderson 1978; Anderson & May 1978). However, the final outcome will be dependant on the interaction between those factors that tend to destabilise and those factors that tend to act in a stabilising manner. Furthermore, as with other forms of regulatory processes, the role of parasites in host population regulation can only be demonstrated if parasite mediated reduction in host survival or fecundity increases with host abundance (Scott & Dobson 1989). Although the density-dependant relationship is the source of an ongoing study, we are currently unable to speculate whether the detrimental affect of parasites is density dependant or not.

Experimental treatment with Ivermectin reduced the intensity of *T. retortaeformis* infection. In both parasite reduction experiments the effects of Ivermectin were still apparent five and seven months after dosing in May or October respectively (Papers III and IV). This was some what surprising as Ivermectin has no prophylactic effect and hares are reinfected either from the environment or from arrested larvae emerging after the removal of the gut fauna. In snowshoe hares reinfection may lead to levels of infection similar to non-treated animals within six weeks of anthelmintic treatment (Murray *et al.* 1996; Sovell & Holmes 1996). The prolonged effect of parasite reduction suggests that reinfection of mountain hares in the Scottish Highlands is rather slow, but to our knowledge there is no data on reinfection rates of mountain hares and this is an obvious area for future research.

Parasites could reduce the reproductive output of mountain hares either by reducing female body condition and subsequent ability to reproduce or by reducing the quality or survival of offspring. Here we have only investigated the effect of parasites on female body condition and fecundity. However, female hares in better body condition are likely to breed earlier in the season and produce heavier young (Iason 1989b, 1990). Leverets born earlier in the year tend to go into their first winter larger and with greater body mass (Hewson 1968; Keith & Windberg 1978; Iason 1989a) and larger, heavier individuals are less susceptible to over winter

mortality (Keith & Windberg 1978; Boutin 1984; Iason 1989b, 1990). Furthermore, given that larger females tend to produce more offspring (Iason 1990) there is a significant advantage to early breeding females as not only are her offspring likely to survive better, but also to breed better. I believe that this could be a rewarding area of future research.

An individual's fitness is not only dependant on its current environment but is also a product of its past environment, such as early development, or even of its parental environment. Such maternal effects, also known as cohort or delayed life-history effects, are increasingly recognised as potentially important factors in determining population dynamics (Benton *et al.* 2001; Beckerman *et al.* 2002; Beckerman *et al.* 2003). It is widely appreciated that unstable dynamics are more likely in systems where there is a time lag in density-dependence, and the transmission of maternal environmental conditions to offspring phenotype is a potential cause of such a lag (Benton *et al.* 2001). Recent theoretical studies have shown that maternal effects caused by for example poor weather over the course of a breeding season can increase instability (Benton *et al.* 2001; Beckerman *et al.* 2002; Lindstrom & Kokko 2002). Larger females have been shown to breed earlier in the year and to produce more young annually than smaller females (Iason 1990). Early born young grow to be bigger and enter their first winter larger and heavier (Iason 1989a). The link between maternal size and the subsequent potentially better survival and greater fecundity of young born to larger females provides a link between maternal environment and offspring fitness. Thus any factor that influenced the maternal environment of a cohort has the potential to infer a time lag and thus decrease the stability of the system. In their correlative study on the effects of intestinal helminths on body condition and fecundity, Iason & Boag (1988) failed to find any correlation between intensity of infection and body condition or fecundity. This led them to speculate that the possible role of parasites in generating cyclic changes in abundance was more likely to be affected by parasite induced reduction in adult body condition and fecundity.

To date the role of parasites in lagomorph population dynamics has been contentious due to the lack of conclusive experimental evidence. Although parasite infections have been associated with increased susceptibility to predation in snowshoe hares the role of parasites in limiting or regulating lagomorph populations has largely been dismissed. On Scottish grouse moors, where predators are intensely controlled, and heather - the dominant vegetation, is burnt on a rotational basis to promote the growth of young, nutritious heather, mountain hare populations can reach very high densities. In less intensively managed areas mountain hare populations may be limited or regulated by predation or some other factor, but at the high densities found on grouse moors, and in the absence of serious predation pressure, parasites might play a more important role than has been previously demonstrated through experiments in less intensively managed environments.

Population assessment (Paper VI)

Distance sampling techniques, where density estimates are derived from the distribution of sighting distances of individual animals from transect lines, have become widely used (Thomas *et al.* 1998). The reliable use of distance sampling is bound by three critical assumptions (Buckland *et al.* 2001); i) all individuals are detected on the transect line, ii) individuals are detected before they move appreciably in relation to the observer; and iii) measurements of distance from the transect line are accurate.

Methods

The study was conducted during March-May 2000 and 2001 and August-September 2001 on four moors managed for red grouse production. Study areas were 4-6 km² and were demarcated by natural features. The study areas were chosen to represent high, medium and low density. We used distance sampling (Buckland *et al.* 2001) and capture-recapture (Otis *et al.* 1978; White *et al.* 1982; Pollock *et al.* 1990) techniques to estimate density. Dung plots were used as an index of relative abundance (Putman 1984). The methods applied to each study area are shown in Table 1 (Paper VI).

Results and Discussion

Although the different techniques gave different density estimates, the rank order of sites was consistent, and mean dung density showed a consistent relationship with the estimated hare densities (Figure 2; Paper VI). Estimates from distance sampling were higher than those derived from capture-recapture at the high-density sites. While the density estimates are all comparable, precision was dependant on the analysis used and the density. The data here do not allow us to identify whether the poor precision at the two high-density sites was density-dependant or site dependant as both high-density sites were steep hillsides with complex topography.

With careful study design, distance sampling offers a good compromise between accuracy, precision and effort as a technique to estimate the density of mountain hares. Distance sampling can give accurate density estimates across a range of hare densities, although there are methodological problems associated with hare behaviour particularly at high density. Discrepancies between density estimates derived from distance sampling and from capture-recapture techniques at high density are more likely the result of underestimation by capture-recapture due to trap saturation than overestimation by distance sampling, as suggested by the increase in dung density with increasing distance sampling estimates. A further difficulty is that density estimates at low hare densities are only possible by pooling survey data that require unverifiable assumptions about detection functions. However, distance sampling is considerably less labour intensive in comparison to capture-recapture techniques and offers a cost-effective method for estimating mountain hare density when a high degree of precision is not critical. Dung plots

are a rapid and reliable alternative technique where estimates of relative mountain hare abundance are all that are required.

Conclusions

1. There is good evidence that some hare populations in Fennoscandia are limited by predation. There is little evidence that nutrition or parasitism are important but the key experiments looking for interactions have not been conducted. There is emerging evidence that some hare populations in Scotland are regulated by parasites and that parasites contribute to population instability. Predation is unlikely to be important because predator populations are reduced by game managers. Large scale experiments are required to consolidate this work and also to investigate interactions with nutrition and climate. Access to Russian research literature is severely limited. Based on the literature reviewed here the limitation and regulation of mountain hare populations in Russia is unclear and accessing the Russian research material should be a priority.

2. Based on our analysis of hunting records and indices of abundance mountain hare populations can at best be described as “weakly-cyclic”. Only 12% of Scottish populations showed true cyclic dynamics, 44% were classified as weakly cyclic and the remainder as non-cyclic. The mean periodicity was 9 years, but ranged from 5-15. The results from our analysis concurred with previous studies of Scottish game bag data. None of the national game bag statistics from Sweden showed true cyclic dynamics and only a third showed weakly cyclic dynamics. Our finding contrasted with the widely held view that mountain hares in Sweden show 3-5 year cycles. The geographic distribution of weakly cyclic series in Sweden showed a marked change after the fox mange epizootic of the late 1970’s-early 1980’s. Our analysis of the Finnish winter game enquiry time-series failed to identify any series showing true cycles. However, 67% showed weak cycles with a mean periodicity of 4.7 years. We have too few time-series to make any meaningful inference about mountain hare population dynamics in central Europe and the former USSR. Again accessing non-English literature from eastern and central Europe should be priority for future research.

3. Experimental and cross-sectional studies show that *T. retortaeformis*, a nematode intestinal parasite, exhibits a weakly aggregated distribution within the hare population, has relatively little effect on host survival, reduces female fecundity, and as a direct life-cycle parasites has a delay in recruitment into the adult parasite population. Based on the Anderson and May macro-parasite model *T. retortaeformis* could act to destabilise mountain hare populations in Scotland. However, the final effect will be dependant on the interplay between stabilising and destabilising factors, whether or not there is a density-dependant relationship between parasite effects and host density, and whether those detrimental affects are additive to other losses.

4. Distance sampling offers a cost-effective method of estimating mountain hare density in the Scottish Highlands, although distance sampling is not very effective at low and very high hare density. An estimate of pellet density based on dung plots offers a cheap and effective method of estimating relative density.

References

- Albon, S. D., Stien, A., Irvine, R. J., Ropstad, R. & Halvorsen, O. (2002) The role of parasites in the dynamics of a reindeer population. *Philosophical Transactions Royal Society of London Series B. Biological Sciences*, **269**, 1625-1632.
- Anderson, R. M. (1978) The regulation of host populations growth by parasite species. *Parasitology*, **76**, 119-157.
- Anderson, R. M. & May, R. M. (1978) Regulation and stability of host-parasite populations I. Regulatory processes. *Journal of Animal Ecology*, **47**, 219-247.
- Angelstam, P., Lindstrom, E. & Widen, P. (1985) Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. *Holarctic Ecology*, **8**, 285-298.
- Angerbjorn, A. (1981) Winter food as a limiting factor of dense mountain hare populations on Islands. (eds Meyers, K. and MacInnes, C. D.), pp. 529-535, Proceedings of the 1st World Lagomorph Conference, University of Guelph.
- Angerbjorn, A. (1983) The reliability of pellet counts as density estimates of mountain hares. *Finish Game Research*, **41**, 13-20.
- Angerbjorn, A. (1986) Reproduction of Mountain Hares (*Lepus timidus*) in Relation to Density and Physical Condition. *Journal of Zoology, London.*, **208**, 559-568.
- Angerbjorn, A. & Flux, J. E. C. (1995) *Lepus timidus*. *Mammalian Species*, **495**, 1-11.
- Beckerman, A., Benton, T. G., Ranta, E., Kaitala, V. & Lundberg, P. (2002) Population dynamic consequences of delayed life-history effects. *Trends in Ecology and Evolution*, **17**, 263-269.
- Beckerman, A. P., Benton, T. G., Lapsley, C. T. & Koesters, N. (2003) Talkin' 'bout my generation: Environmental variability and cohort effects. *American Naturalist*, **162**, 754-767.
- Benton, T. G., Ranta, E., Kaitala, V. & Beckerman, A. P. (2001) Maternal effects and the stability of population dynamics in noisy environments. *Journal of Animal Ecology*, **70**, 590-599.
- Berryman, A. & Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos*, **92**, 265-270.
- Berryman, A. A. (2002) Population cycles: Causes and analysis. *Population cycles* (ed A. A. Berryman), pp. 3-28. Oxford University Press.
- Bloomer, S. E. M., Willebrand, T., Keith, I. M. & Keith, L. B. (1995) Impact of helminth parasitism on a snowshoe hare population in central Wisconsin: A field experiment. *Canadian Journal of Zoology*, **73**, 1891-1898.
- Boag, B. & Iason, G. R. (1986) The occurrence and abundance of helminth parasites of the mountain hare *Lepus timidus* (L.) and the wild rabbit *Oryctolagus cuniculus* (L.) in Aberdeenshire, Scotland. *Journal of Helminthology*, **60**, 92-98.
- Borg, K., Hanko, E., Krunajevic, T., Nilsson, N.-G. & Nilsson, P. O. (1969) On tularemia in the varing hare (*Lepus timidus* L.). *Nord.Vet.Med.*, **21**, 95-104.
- Boutin, S. (1984) The effect of conspecifics on juvenile survival and recruitment of snowshoe hares. *Journal of Animal Ecology*, **53**, 623-637.
- Boutin, S., Krebs, C. J., Boonstra, R., Sinclair, A. R. E. & Hodges, K. E. (2002) Understanding the snowshoe hare cycle through large-scale field experiments. *Population Cycles* (ed A. A. Berryman), pp. 69-91. Oxford University Press, Oxford.
- Brand, C. J. & Keith, L. B. (1979) Lynx demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management*, **43**, 827-849.

- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. (2001) Introduction to Distance Sampling: Estimating abundance of biological populations. Oxford University Press.
- Bulmer, M. G. (1974) A Statistical Analysis of the 10-Year Cycle in Canada. *Journal of Animal Ecology*, **43**, 701-718.
- Catchpole, E. A., Morgan, B. J. T., Coulson, T. N., Freeman, S. N. & Albon, S. D. (2000) Factors influencing Soay sheep survival. *Applied Statistics Journal of the Royal Statistical Society Series C*, **49**, 453-472.
- Cattadori, I. M., Haydon, D. T., Thirgood, S. J. & Hudson, P. J. (2003) Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. *Oikos*, **100**, 439.
- Caughley, G. & Sinclair, A. R. E. (1994) Wildlife Ecology and Management. Blackwell Science.
- Cleveland, W. S. (1979) Robust Locally Weighted Regression and Smoothing Scatterplots. *Journal of the American Statistical Association*, **74**, 829-836.
- Cleveland, W. S. & Devlin, S. J. (1988) Locally Weighted Regression: An Approach to Regression Analysis by Local Fitting. *Journal of the American Statistical Association*, **83**, 596-610.
- Clutton-Brock, T. H., Illius, A., Wilson, K., Grenfell, B. T., MacColl, A. D. C. & Albon, S. D. (1997) Stability and instability in ungulate populations: an empirical analysis. *The American naturalist*, **149**, 195-219.
- Clutton-Brock, T. H., Price, O. F., Albon, S. D. & Jewell, P. A. (1991) Persistent instability and population regulation in Soay sheep. *Journal of Animal Ecology*, **60**, 593-608.
- Crawley, M. J. (1993) GLIM for Ecologists (Methods in Ecology S.). Blackwell Scientific, UK.
- Danell, K. & Hornfeldt, B. (1987) Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. *Oecologia*, **73**, 533-536.
- Delahay, R. J., Speakman, J. R. & Moss, R. (1995) The energetic consequences of parasitism: Effects of a developing infection of *Trichostrongylus tenuis* (Nematoda) on red grouse (*Lagopus lagopus scoticus*) energy balance, body weight and condition. *Parasitology*, **110**, 473-482.
- Dobson, A. P. & Hudson, P. J. (1992) Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *Journal of Animal Ecology*, **61**, 487-498.
- Dobson, A. P., Hudson, P. J. & Lyles, A. M. (1992) Macroparasites: Worms and Others. *Natural Enemies: The Population Biology of Predators, Parasites and Diseases* (ed M. J. Crawley), pp. 329-348. Blackwell Scientific Publications, Oxford.
- Ekerholm, P., Oksanen, L., Oksanen, T. & Schneider, M. (2004) The impact of short-term predator removal on vole dynamics in an arctic-alpine landscape. *Oikos*, **106**, 457-468.
- Elton, C. (1927) Animal Ecology. Sidgewick & Jackson, London.
- Errington, E. (1946) Predation and vertebrate populations (concluded). *Quarterly Review of Biology*, **21**, 221-245.
- Etheridge, B., Summers, R. W. & Green, R. E. (1997) The Effects of Illegal Killing and Destruction of Nests by Humans on the Population Dynamics of the Hen Harrier *Circus cyaneus* in Scotland. *Journal of Applied Ecology*, **34**, 1081-1105.
- Flux, J. E. C. (1970) Life history of the mountain hare (*Lepus timidus scoticus*) in north-east Scotland. *Journal of Zoology, London.*, **161**, 75-123.
- Gilbert, L., Norman, R. A., Laurenson, M. K., Reid, H. W. & Hudson, P. J. (2001) Disease persistence and apparent competition in a three-host community: an empirical and analytical study of large-scale, wild populations. *Journal of Applied Ecology*, **70**, 1053-1061.
- Green, A. J. (2001) Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology*, **82**, 1473-1483.
- Grenfell, B. T., Price, O. F., Albon, S. D. & Clutton-Brock, T. H. (1992) Overcompensation and population cycles in an ungulate. *Nature*, **355**, 823-826.
- Gulland, F. M. D. (1992) Role of nematode parasites in Soay sheep mortality during a population crash. *Parasitology*, **105**, 493-503.

- Gulland, F. M. D. & Fox, M. (1992) Epidemiology of nematode infections in Soay sheep (*Ovis aries* L.) on St. Kilda. *Parasitology*, **105**, 481-492.
- Hanski, I. & Korpimäki, E. (1995) Microtine rodent dynamics in Northern Europe: Paramatised models for predator-prey interaction. *Ecology*, **76**, 840-850.
- Haydon, D. T., Shaw, D. J., Cattadori, I. M., Hudson, P. J. & Thirgood, S. J. (2002) Analysing noisy time-series: describing regional variation in the cyclic dynamics of red grouse. *Philosophical Transactions Royal Society of London Series B. Biological Sciences*, **269**, 1609-1617.
- Hewson, R. (1965) Population changes in the mountain hare, *Lepus timidus* L. *Journal of Animal Ecology*, **34**, 587-600.
- Hewson, R. (1968) Weights and growth rates in mountain hares *Lepus timidus scoticus*. *Journal of Zoology, London.*, **154**, 249-262.
- Hewson, R. (1970) Variation in reproduction and shooting bags of mountain hares on two moors in north-east Scotland. *Journal of Applied Ecology*, **7**, 243-252.
- Hewson, R. (1976) A population study of mountain hares (*Lepus timidus*) in north-east Scotland from 1956-1969. *Journal of Applied Ecology*, **45**, 395-414.
- Hewson, R. (1985) Long-Term Fluctuations in Populations of Mountain Hares (*Lepus timidus*). *Journal of Zoology, London.*, **206**, 269-273.
- Hewson, R. (1989) Grazing Preferences of Mountain Hares on Heather Moorland and Hill Pastures. *Journal of Applied Ecology*, **26**, 1-11.
- Hjelford, O. (1980) Viltbiologi. Landbruksforlaget, Oslo.
- Holmes, P. H. (1985) Pathogenesis of *Trichostrongylus*. *Veterinary Parasitology*, **18**, 89-101.
- Holmes, P. H. (1987) Pathophysiology of parasitic infections. *Parasitology*, **94**, S29-S51.
- Hornfeldt, B. (1978) Synchronous population fluctuations in voles, small game, owls, and tularaemia in Northern Sweden. *Oecologia*, **32**, 141-152.
- Hornfeldt, B., Lofgren, O. & Carlson, B.-G. (1986) Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden. *Oecologia*, **68**, 496-502.
- Hudson, P. J. (1992) Grouse in space and time. The Game Conservancy Trust Ltd..
- Hudson, P. J., Dobson, A. P. & Newborn, D. (1998) Prevention of population cycles by parasite removal. *Science*, **282**, 2256-2258.
- Hudson, P. J., Dobson, A. P. & Newborn, D. (2002) Parasitic worms and population cycles of red grouse. *Population Cycles* (ed A. A. Berryman), pp. 109-129. Oxford University Press, Oxford.
- Hudson, P. J., Newborn, D. & Dobson, A. P. (1992) Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. Monitoring and parasite reduction experiments. *Journal of Animal Ecology*, **61**, 477-486.
- Iason, G. R. (1989a) Growth and Mortality in Mountain Hares: The Effect of Sex and Date of Birth. *Oecologia*, **81**, 540-546.
- Iason, G. R. (1989b) Mortality of Mountain Hares in Relation to Body Size and Age. *Journal of Zoology, London.*, **219**, 676-680.
- Iason, G. R. (1990) The Effects of Size, Age and a Cost of Early Breeding on Reproduction in Female Mountain Hares. *Holarctic Ecology*, **13**, 81-89.
- Iason, G. R. & Boag, B. (1988) Do Intestinal Helminths Affect Condition and Fecundity of Adult Mountain Hares. *Journal of Wildlife Diseases*, **24**, 599-605.
- Ives, A. R. & Murray, D. L. (1997) Can sublethal parasitism destabilize predator-prey population dynamics? A model of snowshoe hares, predators and parasites. *Journal of Animal Ecology*, **66**, 265-278.
- Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A. N. & Milkowski, L. (1996) Population dynamics (1869-1994), demography, and home ranges of the lynx in Bialowieza Primeval Forest (Poland & Belarus). *Ecography*, **19**, 122-138.
- Kauhala, K., Helle, E. & Helle, P. (1999) Impact of predator removal on predator and mountain hare populations in Finland. *Annales Zoologici Fennici*, **36**, 139-148.
- Kauhala, K. & Helle, P. (2000) The interactions of predator and hare populations in Finland - a study based on wildlife monitoring counts. *Annales Zoologici Fennici*, **37**, 151-160.

- Kauhala, K., Helle, P. & Helle, E. (2000) Predator control and the density and reproductive success of grouse populations in Finland. *Ecography*, **23**, 161-168.
- Keith, I. M., Keith, L. B. & Cary, J. R. (1986) Parasitism in a declining population of snowshoe hares. *Journal of Wildlife Diseases*, **22**, 349-363.
- Keith, L. B. (1981) Population dynamics of hares. Myers, K. and MacInnes, C. D395-440. 1981. Guelph, University of Guelph. Proceedings of the World Lagomorph Conference.
- Keith, L. B. (1983) Role of Food in Hare Population-Cycles. *Oikos*, **40**, 385-395.
- Keith, L. B., Cary, J. R., Yuill, T. M. & Keith, I. M. (1985) Prevalence of Helminths in a Cyclic Snowshoe Hare Population. *Journal of Wildlife Diseases*, **21**, 233-253.
- Keith, L. B. & Windberg, L. A. (1978) A demographic analysis of the snowshoe hare cycle. *Wildlife Monographs*, **58**, 1-70.
- Kendall, B. E., Prendergast, J. & Bjornstad, O. N. (1998) The macroecology of population dynamics: taxonomic and biogeographical patterns in population cycles. *Ecology Letters*, **1**, 160-164.
- Korpimäki, E. & Norrdahl, K. (1998) Experimental reduction of predators reverses the crash phase of small-rodent cycles. *79*, 2448-2455.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N. C. (2002) Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society of London Series B. Biological Sciences*, **269**, 991-997.
- Krebs, C. J. (1999) *Ecological Methodology*. Longman.
- Krebs, C. J., Boonstra, R., Boutin, S. & Sinclair, A. R. E. (2001) Conclusions and Future Research Directions. *Ecosystem Dynamics of the Boreal Forest* (eds C. J. Krebs, S. Boutin & R. Boonstra), pp. 491-501. Oxford University Press, New York.
- Krebs, C. J., Boutin, S., Boonstra, R., Sinclair, A. R. E., Smith, J. N. M., Dale, M. R. T., Martin, K. & Turkington, R. (1995) Impact of food and predation on the snowshoe hare cycle. *Science*, **269**, 1112-1115.
- Labutin, Y. V. (1960) Predators as a factor in snow hare population changes. *Investigations into the causes and regularities of the population dynamics of the snow hare in Yukatia*. (ed S. P. Naumov), USSR Academy of Sciences Press, Moscow.
- Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Methuen, London.
- Lambin, X., Krebs, C. J., Moss, R., Stenseth, N. C. & Nigél, G. (1999) Population Cycles and Parasitism. *Science*, **286**, 2425.
- Linden, H. (1988) Latitudinal gradients in predator-prey interactions, cyclicality and synchronism in voles and small game populations in Finland. *Oikos*, **52**, 341-349.
- Lindström, E. R., Andren, H., Angelstam, P., Cederlund, G., Hoernfeldt, B., Jaederberg, L., Lemnell, P. A., Martinsson, B., Skoeld, K. & Swenson, J. E. (1994) Disease reveals the predator : sarcoptic mange, red fox predation, and prey populations. *Ecology*, **75**, 1042-1049.
- Lindström, E. R., Andren, H. & Widen, P. (1986) Influence of predators on Hare populations in Sweden: a critical review. *Mammal Review*, **16**, 151-156.
- Lindström, J., Ranta, E., Kokko, H., Lundberg, P. & Kaitala, V. (2001) From Arctic Lemmings to adaptive dynamics: Charles Elton's legacy in population ecology. *Biological Reviews*, **76**, 129-158.
- Lindström, J. & Kokko, H. (2002) Cohort effects and population dynamics. *Ecology Letters*, **5**, 338-344.
- Lotka, A. J. (1932) The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences*, **22**, 461-469.
- MacRae, J. C. (1993) Metabolic consequences of intestinal parasitism. *Proceedings of the Nutritional Society*, **52**, 121-130.
- Marcström, V., Keith, L. B., Engren, E. & Cary, J. R. (1989) Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Canadian Journal of Zoology*, **67**, 658-668.
- Marcström, V., Kenward, R. E. & Engren, E. (1988) The Impact of Predation on Boreal Tetraonids During Vole Cycles: An Experimental Study. *Journal of Animal Ecology*, **57**, 859-872.
- May, R. M. (1999) Population biology: Crash tests for real. *Nature*, **398**, 371-372.

- May, R. M. & Anderson, R. M. (1978) Regulation and stability of host-parasite population interactions II. Destabilizing processes. *Journal of Animal Ecology*, **47**, 249-267.
- Mitchel-Jones, A. J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P. J. H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralik, V. & Zima, J. (1999) The Atlas of European Mammals. Poyser.
- Moksnes, A. (1972) Bestandsvingninger hos småviltarter i Trollheimsområdet. *Naturen*, **5**, 319.
- Murray, D. L. (2002) Differential body condition and vulnerability to predation in snowshoe hares. *Journal of Animal Ecology*, **71**, 614-625.
- Murray, D. L., Cary, J. R. & Keith, L. B. (1997) Interactive effects of sub-lethal nematodes and nutritional status on snowshoe hare vulnerability to predation. *Journal of Animal Ecology*, **66**, 250-264.
- Murray, D. L., Keith, L. B. & Cary, J. R. (1996) The efficacy of anthelmintic treatment on the parasite abundance of free-ranging hares. *Canadian Journal of Zoology*, **74**, 1604-1611.
- Murray, D. L., Keith, L. B. & Cary, J. R. (1998) Do parasitism and nutritional status interact to affect production in snowshoe hares? *Ecology*, **79**, 1209-1222.
- Myrberget, S. & Lund-Tangen, H. I. (1990) Cyclic variations in small game populations in central Norway. Trondheim, NINA, Norwegian Institute for Nature Research. Transactions of the 19th International Union of Game Biologists Congress, Trondheim 1989.
- Naumov, S. P. (1947) Ecology of the snow hare *Lepus timidus* L.: Theoretical foundations for the prognosis of the species' population. Moscow Society of Naturalists, Moscow.
- Naumov, S. P. (1960a) General Regulation of the Species' Population and its Dynamics. *Investigations into the causes and Regularities of the Population Dynamics of the Snow Hare in Yukatia* (ed S. P. Naumov), USSR Academy of Sciences, Moscow.
- Naumov, S. P. (1960b) Investigations into the causes and Regularities of the Population Dynamics of the Snow Hare in Yukatia. USSR Academy of Sciences, Moscow.
- Naumov, S. P. (1972) The Ecology of Animals. The Board of Trustees of the University of Illinois. Originally published as *Ekologiya zhivotnykh* by the Higher School State Publishers, Moscow, 1963.
- NERC Centre for Population Biology (1999). The Global Population Dynamics Database.
- Nisbet, R. & Gurney, W. (1982) Modeling fluctuating populations. The Blackburn Press, Caldwell, New Jersey.
- Otis, D. L., Burnham, K. P., White, G. C. & Anderson, D. R. (1978) Statistical Inference from Capture Data on Closed Animal Populations. *Wildlife Monographs*, **62**.
- Pehrson, A. & Lindlof, B. (1984) Impact of Winter Nutrition on Reproduction in Captive Mountain Hares (*Lepus timidus*) (Mammalia, Lagomorpha). *Journal of Zoology, London.*, **204**, 201-209.
- Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E. (1990) Statistical inference for capture-recapture experiments. *Wildlife Monographs*, **107**.
- Popov, M. V. (1960) Food conditions and their significance in population dynamics. *Investigations into the causes and Regularities of the Population Dynamics of the Snow Hare in Yukatia* (ed S. P. Naumov), USSR Academy of Sciences, Moscow.
- Pugliese, A. (2000) Coexistence of macroparasites without direct interactions. *Theoretical Population Biology*, **57**, 145-165.
- Pugliese, A., Rosa, R. & Damaggio, M. L. (1998) Analysis of a model for macroparasitic infection with variable aggregation and clumped infections. *Journal of Mathematical Biology*, **36**, 419-447.
- Pulliainen, E. (1982) Habitat selection and fluctuations in numbers in a population of the arctic hare (*Lepus timidus*) on a subarctic fell in Finnish forest Lapland. *Zeitschrift für Säugetierkunde*, **47**, 168-174.
- Putman, R. J. (1984) Facts from Faeces. *Mammal Review*, **14**, 79-97.
- R Development Core Team . R: (2004) A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.
- Ranta, E., Linstrom, J., Kaitala, V., Kokko, H., Linden, H. & Helle, E. (1997) Solar activity and hare dynamics: A cross-continental comparison. *American Naturalist*, **149**, 765-775.

- Redpath, S. M. & Thirgood, S. J. (1997) Birds of Prey and Red grouse. HMSO.
- Rosa, R. & Pugliese, A. (2002) Aggregation, stability, and oscillations in different models for host-macroparasite interactions. *Theoretical Population Biology*, **61**, 319-334.
- Royama, T. (1992) Analytical population Dynamics. Chapman & Hall, London.
- Scherini, G. & Tosi, G. (1990) Correlation between grouse and mountain hare hunting bags. Myrberget, S. pp. 97-100. Trondheim, NINA, Norwegian Institute for Nature Research. 8-9-1989.
- Scott, M. E. & Dobson, A. P. (1989) The role of parasites in regulating host abundance. *Parasitology Today*, **5**, 176-183.
- Shaw, D. J. & Dobson, A. P. (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. *Parasitology*, **111**, 111-133.
- Shaw, D. J., Grenfell, B. T. & Dobson, A. P. (1998) Patterns of macroparasite aggregation in wildlife host populations. *Parasitology*, **117**, 597.
- Siivonen, L. (1948) Structure of short cyclic fluctuation in numbers of mammals and birds in the northern parts of the northern hemisphere. *Papers in Game Research*, **1**, 1-166.
- Small, R. J., Marcstrom, V. & Willebrand, T. (1993) Synchronous and Non-synchronous Population Fluctuations of Some Predators and Their Prey in Central Sweden. *Ecography*, **16**, 360-364.
- Smedshaug, C. A., Selas, V., Lund, S. E. & Sonerud, G. A. (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biology*, **5**, 157-166.
- Solberg, E. J., Jordhoy, P., Strand, O., Aanes, R., Loison, A., Saether, B.-E. & Linnel, D. C. (2001) Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography*, **24**, 442-451.
- Southwood, R. & Henderson, P. A. (2000) Ecological Methods. Blackwell Science.
- Sovell, J. R. & Holmes, J. C. (1996) Efficacy of Ivermectin against nematodes infecting field populations of snowshoe hares (*Lepus americanus*) in Yukon, Canada. *Journal of Wildlife Diseases*, **32**, 23-30.
- Spedding, C. R. W. & Brown, T. H. (1957) A study on the subclinical worm infestation of sheep 1. The effect of level of infestation on the growth rate of the lamb. *Journal of Agricultural Science*, **48**, 286-293.
- Stenseth, N. C. (1999) Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos*, **87**, 427.
- Stien, A., Irvine, R. J., Ropstad, R., Halvorsen, O., Langvatn, R. & Albon, S. D. (2002) The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. *Journal of Animal Ecology*, **71**, 937-945.
- Sutherland, W. J. (1996) Ecological Census Techniques: A Handbook. Cambridge University Press, Cambridge.
- Tapper, S. C. (1987) Cycles in game-bag records of hares and rabbits in Britain. *Symposia of the Zoological Society of London*, **58**, 79-98.
- Tapper, S. C. (1992) Game Heritage: An ecological review from shooting and game keeping records. The Game Conservancy Limited.
- Thirgood, S. J., Redpath, S. M., Rothery, P. & Aebischer, N. J. (2000) Raptor predation and population limitation in red grouse. *Journal of Animal Ecology*, **64**, 504516-516.
- Thomas, L., Laake, J. L., Derry, J. F., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Strindberg, S., Hedley, S. L., Burt, M. L., Marques, F. F. C., Pollard, J. H. & Fewster, R. M. Distance 3.5. (1998). Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.
- Tompkins, D. M. & Begon, M. (1999) Parasites can regulate wildlife populations. *Parasitology Today*, **15**, 311-313.
- Tompkins, D. M., Dobson, A. P., Arneber, P., Begon, M., Cattadori, I. M., Greenman, J. V., Heesterbeek, J. A. P., Hudson, P. J., Newborn, D., Pugliese, D., Rizzoli, A., Rosa, R., Rosso, F. & Wilson, K. (2001) Parasites and host population dynamics. *Wildlife Diseases* (eds P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek & A. P. Dobson), pp. 45-62. Oxford University Press, London.
- Trexler, J. C. & Joseph, T. (1993) Non-traditional Regression Analyses. *Ecology*, **74**, 1629-1637.

- Turchin, P. (2003) *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press.
- Vaughan, M. R. & Keith, L. B. (1981) Demographic response of experimental snowshoe hare populations to over winter food shortage. *Journal of Wildlife Management*, **45**, 354-380.
- Volterra, V. (1926) Variations and fluctuations of the numbers of individuals in animal species living together. *Journal du Conseil permanent international pour l'Exploration de la Mer*, **3**, 3-51.
- Watson, A. & Hewson, R. (1973) Population densities of mountain hares (*Lepus timidus*) on western Scottish and Irish moors and Scottish hills. *Journal of Zoology, London.*, **170**, 159.
- Watson, J. (1997) *The Golden Eagle*. T. & A.D. Poyser, London.
- Watson, J., Leitch, A. F. & Rae, S. R. (1993) The Diet of Golden Eagles *Aquila chrysaetos* in Scotland. *Ibis*, **135**, 387-393.
- White, G. C., Anderson, D. R., Burnham, K. P. & Otis, D. L. (1982) *Capture-Recapture and Removal Methods for Sampling Closed Populations*. LA-8787-NERP. New Mexico 87545, Los Alamos National Laboratory.
- Whitfield, D. P., McLeod, D. A. R., Watson, J. F., Fielding, A. H. F. & Haworth, P. F. (2003) The association of grouse moor in Scotland with the illegal use of poisons to control predators. *Biological Conservation*, **114**, 157-163.
- Wilson, K., Bjornstad, O. N., Dobson, A. P., Merler, S., Pogliayen, G., Randolph, S. E., Read, A. F. & Skorping, A. (2001) Heterogeneities in macroparasite infections -- patterns and processes. *The Ecology of Wildlife Diseases* (eds P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek & A. P. Dobson), pp. 6-44.
- Wilson, K. & Grenfell, B. T. (1997) Generalized linear modelling for parasitologists. *Parasitology Today*, **13**, 33-38.
- Wilson, K., Grenfell, B. T. & Shaw, D. J. (1996) Analysis of Aggregated Parasite Distributions: A Comparison of Methods. *Functional Ecology*, **10**, 592-601.
- Wirsing, A. J., Steury, T. D. & Murray, D. L. (2002) Noninvasive Estimation of Body Composition in Small Mammals: A Comparison of Conductive and Morphometric Techniques. *Physiological and Biochemical Zoology*, **75**, 489-497.

Acknowledgements

Firstly thank you to my supervisors; Simon Thirgood, Adam Smith and Tomas Willebrand. Simon Thirgood originally set up the hare project and employed me to catch hares. Simon's input, advice and support have been central to the success of the mountain hare project, my coming to Sweden, and the production of papers that support my thesis. Adam Smith has advised and assisted with many aspects of this work from the beginning, and critically found the funds to keep me gainfully employed to study mountain hares over the years it has taken to gather this data and complete my thesis. Tomas Willebrand came into the project much later but has more than made up for it since, and has helped and guided me through the Swedish higher education system, the horrors of time-series analysis and the R statistical language, and the final production of my thesis.

The department of animal ecology and all the denizens thereof made me very welcome. Their support throughout my time in Sweden is very much appreciated. A special thank you to Fredrik Dahl and Tuulikki Rooke for their help in all aspects of living and working in a foreign country, good company, some amazingly good food, and generally making my time in Sweden even more pleasant. A

personal thank you to Ylva, Patrik and Marcus Jonsson for giving me somewhere to live and free run of their home. Thank you to Ylva for help with organising the printing and proof reading my thesis. Also thanks to Jens Persson for advice on where to go to in Sarek – even though we didn't see any wild animal bigger than a lemming.

Many people have helped with field and laboratory work; David Howarth and Adam Smith have helped and given advice throughout; Marjorie Bell, Matt Davis, Siobhan Egan, Stephanie Enthoven, Paul French, David Howarth, Alan Kirby, Alice Labbe, Katja Neumann, Adam Smith, Leigh Stephen, and Helene Tourus all helped with laboratory or fieldwork. Matt, Alice, Katja and Helene all deserve special thanks for their help in chasing hares over Scottish Munros in the dark in winter!

I should also like to thank Nicholas Aebischer, Rachel Atkinson, Steve Buckland, Siobhan Egan, Ray Hewson, Isla Graham, Dan Haydon, Glenn Iason, Alan Kirby, Karen Laurensen, Kirsty Park, Shaila Rao, Darren Shaw, and Len Thomas for discussion, advice and commenting on draft manuscripts. This work would not have been possible without the cooperation and help of many land owners and game keepers. I should particularly like to thank; Ralia and Glen Banchor Estates and John Drysdale for hosting the experimental studies; Collin Niven, Ken Dakers, Kevin Binnington, and Steve McKinnon put up with me stamping all over their moors, disturbing their grouse and spooking their deer far more than they might have liked.

Finally, an immeasurably large thank you to Katja!

This work has been funded by; The National Research Council (UK), the British Ecological Society, The Scottish Research Trustees, The Game Conservancy Trust, and the Swedish Institute.