The effects of parasites and food on red grouse (*Lagopus lagopus scoticus*)

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Thesis submitted for the degree of
Doctor of Philosophy
in the
Department of Biological Sciences
University of Stirling

February 2000

ABSTRACT

The interaction between the parasite *Trichostrongylus tenuis* and food quality was investigated in red grouse *Lagopus lagopus scoticus*, to determine the cause of variation in population cycles between different areas (Scotland and England). Analysis of long-term data, field experiments and population modelling were carried out.

Food quality, in terms of nutrient content of heather, was lower on Scottish grouse moors than on English moors. Parasite burdens were also lower in Scottish grouse populations, than in English grouse populations.

A three-way interaction, between food, parasites and area (Scotland/England), acting on breeding production, could explain the variation in population cycle period between areas. However, body condition of grouse was not affected by a food-parasite interaction. Experimental manipulation of food quality and parasite burden did not influence the breeding production of female grouse.

Modelling the effects of a food-parasite interaction on grouse populations provided evidence that such an interaction could explain variation in cycle period between areas, although other factors are likely to be important in some cases.

Red grouse are not unique, as other species also have cycles driven by food and parasites. Other species do not show cyclic population fluctuations because of having shared parasites, and a strong immune response. There is a specialist predator-prey relationship between red grouse and *T. tenuis*.

Statement of authorship:

Appendix 2 – entitled 'The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks' is a paper in press. I am a co-author, as I carried out fieldwork and data collection for the paper.

All other parts of this thesis are the result of analysis and authorship which is wholly my own.

Acknowledgements

I would like to thank the University of Stirling for providing me with a studentship, and the Game Conservancy Trust for part funding it, meeting all field costs, and providing long term data. John and Eira Drysdale kindly allowed me to traipse over their land every day to torment their grouse, let me keep a horse in their field, and maintained an interest in my work to this day!

Thanks to everyone at Stirling who provided support at some time, Dan Tompkins, Laura Saunders (for looking after my larvae) and Peter Hudson for supervising my project. Sue Haysom and Mandy Fox get a special mention for being completely mad like myself.

Thanks to everyone at Crubenmore who provided support at some time, Adam Smith, Silver Sheldon, Howard Colmer, Steve Campbell, Gilly, Emily and Ruth Howarth. I'm eternally grateful to David Howarth for making me go grouse beating, and for all his help with fieldwork and persuading me that it was worthwhile to get out the land rover and plod up the hill again! Karen Blake, thank you for performing miracles at the end!

Thanks to the dogs. Mull found the chicks, and Hammy and Rosie kept me company on long drives, boring days on the hill, and in the office.

I'll take this opportunity to thank my Mum and Dad, which I don't do often enough. They never questioned my career choice, which I am grateful for.

I met my husband, Kirk Taylor, on Drumochter when I was grouse beating. He helped with fieldwork, listened to my problems and gave better advice about grouse than any one, but then he is the best gamekeeper in the world!

And last but not least, thanks to the grouse. They are the real stars. I just hope that one day I get to shoot one.

CONTENTS

CHAPTER 1

INTRODUCTION

Ecologists have been studying population cycles in animals for many years, and are still trying to explain why some animals show these cyclic fluctuations in density. Since early work by Elton (1924), several texts have been entirely devoted to addressing this field of ecology (Elton 1942, Keith 1963, Krebs & Myers 1974, Finerty 1980, Tamarin *et al* 1990).

The existence of fluctuations in animal numbers is widespread, occurring in many different birds and mammals. This is particularly true of species that live in northern temperate zones, and many of these species exhibit regular periodic fluctuations in numbers (Elton 1924). Changes in animal density and populations can be caused by different factors. These can be both extrinsic factors (environmental factors such as food quality and food supply, predators and parasites) and intrinsic factors (demographic factors such as immigration and birth and death rates). Most extrinsic factors affecting animal populations work in a density dependent manner. Workers now generally agree that populations must be regulated by density-dependent factors that increase relative mortality as density increases. Immediate density-dependence is stabilising, but when this acts with a time delay it can become destabilising and generate damped or even sustained oscillations.

Most hypotheses that account for population cycles need more than one factor to operate. The environmental factors that are most likely to be responsible for cyclic fluctuations in animal populations are predation, food and social behaviour (Batzli 1996).

Population fluctuations and the factors that regulate them have been studied in many species including lemmings (Elton 1924, Krebs *et al* 1995a) and voles (Boonstra 1994, Krebs 1996) where spacing behaviour, predation and food have been found to be important. Parasites are though to cause population fluctuations in Soay sheep (Gulland 1992), whereas predation and food act on snowshoe hare populations (Erickson 1944, Krebs *et al* 1995b). Canadian lynx

populations, which prey on snowshoe hares (Stenseth *et al* 1997) also cycle depending on food.

Red grouse have also been the subject of many studies on population fluctuations and the factors that regulate them, including spacing behaviour, food, predation and parasites (Jenkins *et al* 1963, Jenkins *et al* 1967, Watson *et al* 1984a, Moss & Watson 1991, Hudson *et al* 1992).

1.1. Economic importance of red grouse

The red grouse *Lagopus lagopus scoticus* is a gamebird of both economic and conservation importance in Scotland and Northern England (Hudson 1992). The economic importance of red grouse increased with the development of intensive grouse management and driven grouse shooting during the middle of the 19th century (Hudson 1992, Dobson & Hudson 1994). The economic importance of red grouse as a game species led to the first detailed study of them which was published in 1911 (Lovat 1911).

Grouse shooting and grouse moor management maintains a multiple land-use system where grouse, sheep, deer and other wildlife benefit, and grouse moors are internationally important in terms of conservation, as well as being of major economic benefit.

1.2. Red grouse

Red grouse are territorial gamebirds which inhabit moorland where heather *Calluna vulgaris* is the predominant vegetation. Heather makes up over 90% of the diet of the red grouse, and their distribution within Great Britain is constrained by the availability of suitable heather dominant habitat. Male red grouse establish territories in the autumn, which can break down during the winter months and are then re-established in spring. Females start laying eggs during April. Clutch size usually varies between 5 and 12, and hatching takes place after 22 days of incubation. For the first two weeks grouse chicks feed on insects before progressing on to heather. Appendix 2 is a paper (in press) about this area of grouse biology, to which I contributed the majority of the radio-tracking data. The grouse-shooting season starts on

August 12th and finishes on December 10th. Most grouse are shot early in the season by driven grouse shooting.

1.3. Changes in numbers of grouse

Red grouse show both short-term and long-term population fluctuations. Numbers of grouse in Scotland have shown a general downward trend (Hudson 1992) over several decades, including two major declines. The entire grouse population of Scotland was affected by the first major decline during World War Two, and in the mid 1970s the Central Highlands and the South West of Scotland were subject to a marked decrease in grouse numbers (Barnes 1987). Short-term fluctuations in grouse populations vary throughout Britain with the majority exhibiting regular cyclic fluctuations. Where cycles exist in England they generally last 4-5 years (Figure 1.1.), whereas in Scotland population cycles tend to be longer, mostly 5-8 years (Figure 1.2.) (Potts *et al* 1984, Hudson 1992).

Many theories have been put forward as to the cause of these population cycles, two of which have been the subject of detailed investigation. The first is that of intrinsic mechanisms acting through spacing behaviour (Watson *et al* 1984a), and the second is the effect of the parasite *Trichostrongylus tenuis* on fecundity and breeding success of grouse (Hudson *et al* 1992a).

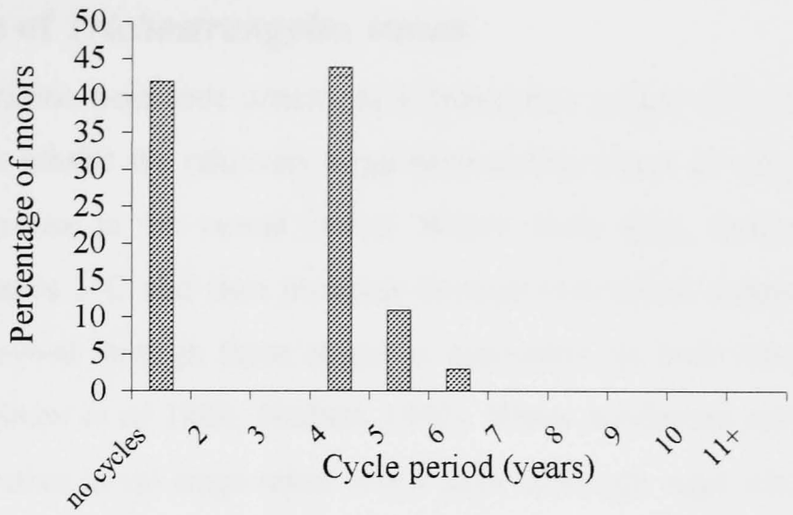

Figure 1.1. The cycle period of red grouse populations on English moors. (Figure from Hudson 1992). No cycles – where grouse populations are non-cyclic.

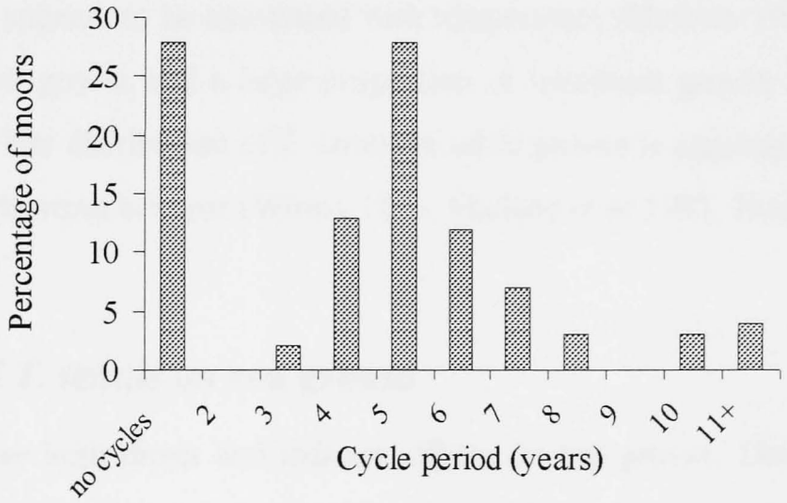

Figure 1.2. The cycle period of red grouse populations on Scottish moors. (Figure from Hudson 1992). No cycles – where grouse populations are non-cyclic.

1.4. Life cycle of *Trichostrongylus tenuis*

T. tenuis is a parasitic nematode which has a monoxenic (single host) life cycle (Figure 1.3.). The adult worms inhabit the relatively large blind-ending caeca of red grouse, and their eggs pass from the grouse in the caecal faeces. Within these eggs, embryos develop when the temperature exceeds 5°C and then progress through two larval stages to the infective third stage larvae. Survival through these stages is dependent on both temperature and moisture (Watson 1988, Shaw *et al* 1989, Hudson 1992). When conditions are optimal, development from egg to infective larval stage takes seven days, although eggs can remain unhatched for several months. These third stage infective larvae emerge from the caecal faeces and migrate to the growing tips of the heather on which grouse feed.

Once inside the grouse, larvae normally develop into adult worms within ten to fourteen days. However, this does not always occur immediately and in some cases the larvae moult their outer sheath and cease development in an arrested stage. These arrested larvae are usually found only during the winter months, and although the factors affecting this arrestment are not clearly known it appears to be associated with temperature (Hudson 1992, Dobson & Hudson 1994). Most adult grouse and a large proportion of immature grouse carry some level of *T. tenuis* infection. The distribution of *T. tenuis* in adult grouse is aggregated, with a few grouse carrying very high worm burdens (Wilson 1983, Hudson *et al* 1985, Hudson 1992).

1.5. Effects of *T. tenuis* on red grouse

T. tenuis can have both direct and indirect effects on red grouse. Directly, *T. tenuis* causes damage to the caecal mucosa, causing disruption of the plicae and internal bleeding, which probably reduces digestive capability and affects the normal functioning of the caeca (Watson *et al* 1987). Body condition of grouse is affected by *T. tenuis*, resulting in lower relative body mass and also a reduction in ability to gain mass (Wilson & Wilson 1978, Hudson 1986a & b). Experiments on captive grouse show that high worm burdens cause grouse to eat less, and have lower energy consumption and expenditure than grouse with little or no infection of *T. tenuis* (Delahay *et al* 1995).

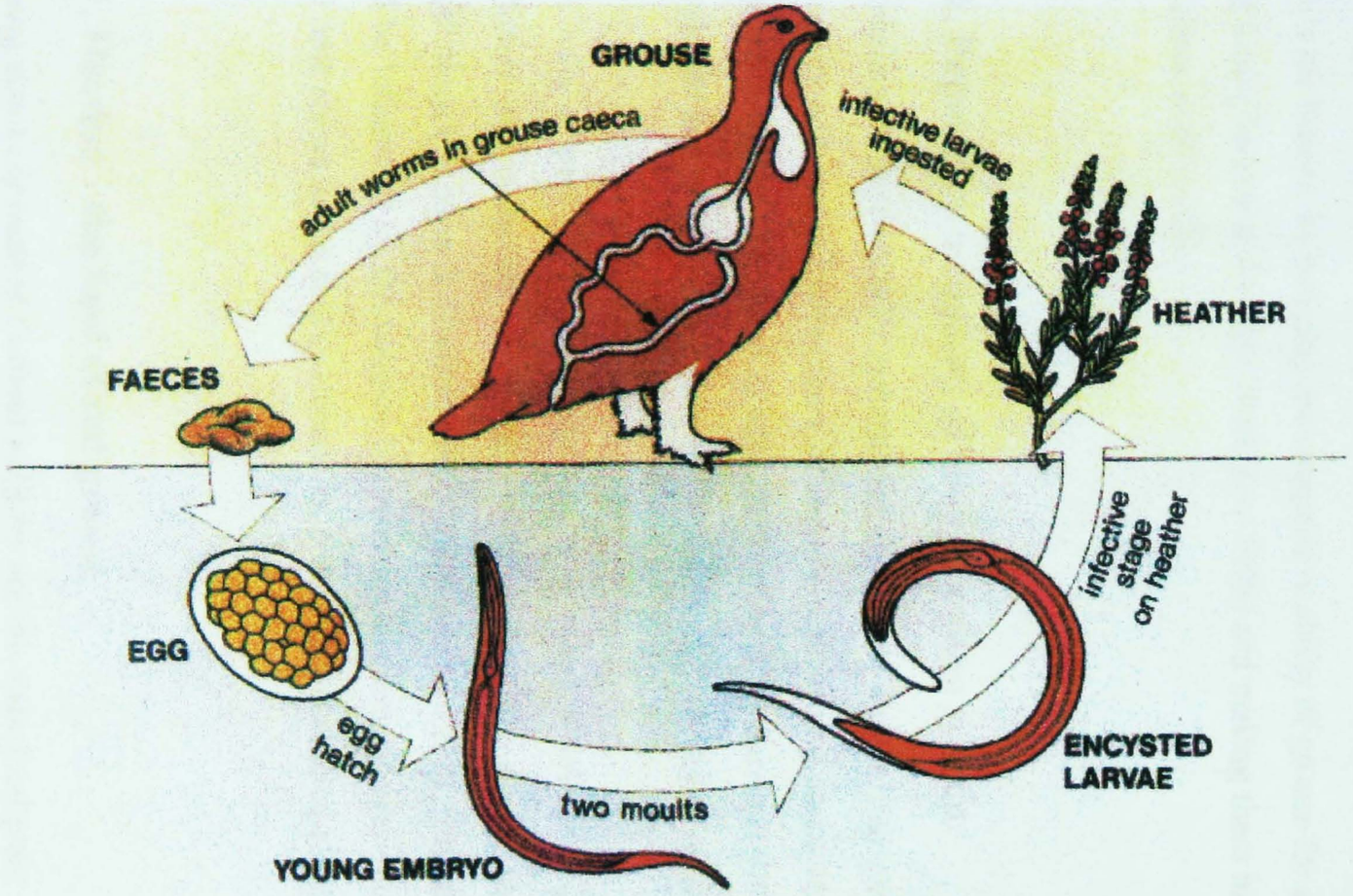

Figure 1.3. The life cycle of *Trichostrongylus tenuis*, a nematode parasite of red grouse. Two features of the life cycle are important. First, any increase in the number of worms inside a bird results from direct infection. Second, this is a direct life cycle with no intermediate hosts, so rates of infection will increase with the density of the grouse population. (Figure from Hudson 1992).

T. tenuis also reduces both breeding production and survival of grouse (Hudson 1992). Previous population studies have shown that poor breeding success is associated with high worm burdens (Potts *et al* 1984) and that treatment of grouse with anthelmintic to remove infections of *T. tenuis* increases both breeding production and survival (Hudson 1986, Hudson *et al* 1992a).

Through its impact on condition, *T. tenuis* also has indirect effects on other aspects of the bird's life history, by reducing the competitive ability of grouse for resources such as territories and food (Hudson & Dobson 1994, Fox 1999) and making them more vulnerable to predation (Hudson *et al* 1992b).

1.6. Population modelling of the red grouse system

Modelling of host-parasite systems has previously shown that parasite induced reduction in fecundity will destabilise numbers of the host and, within limits set by other factors, generate population cycles (Anderson & May 1978, May & Anderson 1978). These models have been developed and applied specifically to the red grouse - *T. tenuis* system.

The level of parasite induced reduction in breeding production has been proved to be both sufficient and necessary to generate cyclic fluctuations similar to those seen in red grouse populations (Dobson & Hudson 1992, Hudson *et al* 1998). The period of a population cycle will be influenced by the balance between the intrinsic growth rate of the grouse population and time delays in the density-dependent processes influencing population growth (May 1981).

1.7. Heather - the food of red grouse

Young shoots of heather *Calluna vulgaris* are the main food plant of red grouse. Heather is a high fibre, low protein food source. Grouse feed selectively on heather plants that are high in nutrients, especially nitrogen and phosphorus (Gimingham 1972, Moss *et al* 1975, Savory 1983). The nutritive value of heather varies naturally in different areas and is influenced by underlying rock type together with climatic conditions. Higher quality heather, in terms of

nutrients, is found on 'rich' moors over base-rich underlying rock such as limestone, and lower quality heather found on 'poor' moors over underlying acidic rocks such as granite. More species of plants grow on 'rich' moors, and the soil is more fertile. Grouse stocks have been shown to be generally higher on 'rich' moors than on 'poor' moors in north-east Scotland (Jenkins *et al* 1967, Picozzi 1968, Moss *et al* 1975) although more extensive work has found that quality is less important than predation pressure (Hudson 1992).

Food quality has been shown to affect the breeding production of red grouse (Moss *et al* 1975) and according to Jenkins *et al* (1967) may do this in three ways. The first is heather growth in the previous summer, which will affect the amount of green heather available for grouse in the winter, and is correlated with breeding success in the following summer. Secondly, the amount of heather browning over the winter, which reduces the amount of green heather available in the spring and is also correlated with subsequent breeding success, and lastly, the timing of heather growth in the spring for providing fresh growth for grouse to feed on. Maternal nutrition of female grouse both before and during egg-laying is related to breeding production and could be important for breeding success (Moss *et al* 1975).

Previous studies have shown that manipulation of food quality by application of nitrate fertiliser increases nitrogen content of heather and heather growth, and in some cases increased breeding production (Watson *et al* 1984b). Heather is not only a food source for grouse, but also provides cover and shelter. The structure of the heather sward has to be carefully maintained in order to provide for all the requirements of the grouse.

1.8. Food-parasite interaction

Both food and parasites have a major influence on the reproductive success of animals (Lack 1954). In red grouse, independent field studies have shown that both these factors can influence breeding production (Moss *et al* 1975, Hudson 1986). Lack (1954) suggested that food availability had a dominating role in limiting the numbers of an animal, but would interact with parasites where these were abundant.

A number of studies have been undertaken to investigate the combined effects of food and parasites (Scrimshaw *et al* 1968, Solomons & Keusch 1981, Keymer *et al* 1983), and some

studies have looked at the effects of an interaction between food and parasites on population dynamics (Gulland 1992, Murray *et al* 1997, Murray *et al* 1998). However, although a food-parasite interaction has been suggested as a possible cause of population cycles in red grouse (Hudson 1986), this has never been subject to a detailed investigation.

There are many factors that are important in terms of grouse moor management. Weather, predators, level of keepering, and muirburn all have a part to play in maintaining numbers of red grouse. However, this study is concerned with two main factors, namely food and parasites.

1.9. Study sites

During this study, data were collected from grouse moors throughout Scotland, and long-term data used were collected over twenty years from more than 120 grouse moors in Scotland and England by the Game Conservancy Trust and Peter Hudson. These study sites were all areas of heather moorland, managed for grouse shooting to varying degrees.

Intensive fieldwork (Chapters 4 & 5) was carried out on two main study sites, located on Ralia Estates, Inverness-shire. Both South Drumochter and Crubenmore were moors where the grouse population was managed for driven grouse shooting. A more detailed description can be found in Chapter 4.

1.10. Aim and thesis outline

The aim of this study was to investigate the interaction between food and parasites in red grouse *Lagopus lagopus scoticus* to determine the mechanisms and potential causes of the variation in population cycles between different areas.

To achieve this, I investigated the effect of a food-parasite interaction on breeding production (Chapter 2) and body condition of red grouse (Chapter 3) using long-term data. I tested the hypothesis of a food-parasite interaction experimentally (Chapter 4), and designed a technique

for estimating the biomass of heather (Chapter 5). In Chapter 6, results from previous chapters were used to model grouse populations. Finally the findings of this study and questions arising from it were discussed, and suggestions made for future work (Chapter 7). This thesis has been written in paper format where possible. Therefore there may be some degree of repetition between chapters.

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CHAPTER 2

VARIATIONS IN RED GROUSE POPULATION DYNAMICS: FOOD-PARASITE INTERACTION AND BREEDING PRODUCTION

2.1. Introduction

The regular fluctuations in animal numbers known as population cycles have been studied and documented in a range of species. The red grouse *Lagopus lagopus scoticus* exhibits such population cycles and two major mechanisms have been proposed to explain these fluctuations. The first is that of intrinsic mechanisms acting through spacing behaviour (Watson *et al* 1984a), and the second is the influence of the parasitic nematode *Trichostrongylus tenuis* on survival and breeding production (Hudson *et al* 1992). This study is concerned with the second mechanism.

Lack (1954) was one of the first to propose that food and parasites would act together to cause the fluctuations in populations of red grouse. More recently, independent field studies on red grouse have shown that both food (Moss *et al* 1975) and parasites (Hudson 1986) influence breeding production.

High numbers of the gut parasite *T. tenuis* have been found to be associated with low breeding production in red grouse (Potts *et al* 1984). Experiments carried out in northern England have shown that breeding success can be increased when parasite burdens are reduced through treatment with anthelmintic (Hudson 1986, Hudson *et al* 1992).

Modelling of this host-parasite system has shown that *T. tenuis* reduces breeding production in red grouse. This is sufficient and necessary, in combination with other factors, to generate the type of population fluctuations observed in grouse populations (Anderson & May 1978, May & Anderson 1978, Dobson & Hudson 1992, Hudson *et al* 1998).

Food quality has also been shown to have an effect on the breeding production of red grouse. Their diet consists mainly of heather *Calluna vulgaris,* which is a high-fibre, low-protein food. Grouse feed selectively on heather that is high in nutritive value, choosing to eat plants that have high nitrogen and phosphorus content (Moss *et al* 1975, Savory 1983). Nutrition of female grouse before and during egg laying is positively related to breeding production, and could be an important factor in determining breeding success (Moss *et al* 1975). Increasing nitrogen through application of nitrate fertiliser to manipulate food quality has experimentally demonstrated an increase in breeding production in some cases, although this effect was unable to prevent a population decline (Watson *et al* 1984b). Nutrient content of heather varies naturally between grouse moors in north-east Scotland, depending on the underlying rock structure (Jenkins *et al* 1967, Picozzi 1968, Moss *et al* 1975).

Grouse population cycles differ between areas. In Scotland, grouse populations cycle over 6-12 years, whereas in Northern England cycles are shorter in length, of 4-5 years (Potts *et al* 1984, Hudson 1992). The period of a population cycle can be influenced by the intrinsic growth rate of the grouse population and by environmental effects that cause time delays in population growth (May 1981). As both food quality and parasites influence the breeding production of grouse, the parsimonious hypothesis could be that the two interact synergistically and have a combined effect on breeding production. Experimental studies on captive grouse have suggested that grouse suffer a greater impact of *T. tenuis* when they are eating poor quality food (Delahay & Moss 1996). The difference in grouse population cycles between areas could be due to a variation in food quality, with this influencing the way in which *T. tenuis* affects grouse breeding production, and therefore influencing the grouse population growth rate and so the period of population cycles.

This study examines the hypothesis that food quality and parasites interact, and that the effects of this interaction on breeding production could explain variations in population cycles between different areas. This hypothesis is examined by using long-term data to look at the effects of parasites and food quality on the breeding production of grouse, and a possible interaction between them.

2.2. Methodology

2.2.1. Long-term data

Data on red grouse have been collected by the Game Conservancy Trust (GCT) and Peter Hudson over twenty years, from grouse moors in both Scotland and England, to form a large database containing long term data. This study used data obtained from this database, concerning counts of grouse and worm burdens. Counts of grouse using dogs have been undertaken in July of each year by the GCT on 1 km^2 study sites within each grouse moor (Hudson & Newborn 1995). Shot grouse have also been collected over the same period and worm burdens estimated from these by the GCT. During this study (1996-1998) I added to this data by collecting shot grouse from Scottish estates and estimating worm burdens from them.

2.2.2. Worm burdens

T. tenuis infections in shot grouse were estimated by performing worm counts (Hudson 1986, Hudson & Newborn 1995). Their caeca were removed, cut into five sections, opened out and the contents rinsed with water over a 210 μm gauze. The adult worms were washed into a solution of 300 ml of water. Four subsamples of 10 ml were taken, and the worms in these were counted. The number of worms were added together, then multiplied by 15 to give the total number of worms per grouse.

2.2.3. Heather quality and weather variables

The GCT collected heather samples from study sites within grouse moors in 1997. These heather samples were analysed by the GCT for nitrogen and phosphorus concentration to provide an estimate of heather quality (Smith *et al* 1999). These data were used in this study to provide an estimate of grouse food quality. Weather variables were also used in this study. Temperature, taken as the average in July across a range of years (Hudson 1992) and rainfall, taken as the average number of wet days across a range of years (Hudson 1992) were included in the analysis.

2.2.4. Breeding production estimates

Breeding production was estimated from grouse count data for study sites within each grouse moor for individual years, as no direct measurement of breeding production, such as clutch size

or hatching success, was available. The ratio of young-to-old grouse (total young grouse counted/total old grouse counted), and the ratio of young per female grouse (total young grouse counted/total female grouse counted) as obtained from grouse counts during July each year were used as a measure of breeding success.

2.2.5. Statistical analysis

Data were analysed with Minitab 11. All results of statistical tests were tested for normality using an Anderson Darling normality test. For statistical analysis the long-term data used did not include worm burden data on young grouse as worm burdens in young grouse when counted in August are usually very low and not representative of the population as a whole. As numerous different people have collected the GCT data over 20 years, some records were incomplete, with missing values or zeros entered where values were unknown. For this reason, records with missing values and records showing worm burdens as zero were not included in the analysis. Data were only included in the analysis where worm burden, breeding production and heather quality were available (Sites included in the analysis are listed in Appendix 1A). As heather quality was only estimated in one year (1997), data was reduced to an average for each site.

Although grouse counts were performed on study sites within grouse moors, worm burdens were obtained over the entire moor. Where there was more than one study site within a grouse moor, the same worm burden data was used for each study site, as it was impossible to separate worm burden data into study sites from the GCT database.

As the distribution of worms within a site was known not to be normally distributed (Hudson 1992) the mean value of worms would not necessarily describe the data very well, so the median value of worms was used for each site.

2.3. Results

2.3.1. Differences in worm burdens between areas

Median worm burdens were lower in Scottish grouse populations than in English populations (Table 2.1, Figure 2.1.) and this difference was significant (Mann Whitney W=1039.0, Df = 1, 54 $P < 0.001$).

2.3.2. Food quality and weather

Food quality, in terms of nitrogen and phosphorus concentration in heather, was lower on Scottish moors (Table 2.1, Figure 2.2.) than on English moors (Table 2.1, Figure 2.2.). This difference in nutrient concentration was significant (GLM on arcsine square root transformed data Nitrogen $F_{1,54} = 56.43$, $P < 0.001$; Phosphorus $F_{1,54} = 17.00$, $P < 0.001$).

Mean rainfall is lower on moors in England than on moors in Scotland (Table 2.1, Figure 2.3.) and mean July temperature is higher on English moors than on Scottish moors (Table 2.1, Figure 2.3.). When these weather variables were added to the analysis, the differences in food quality between Scotland and England could be explained.

There was a negative relationship between rainfall and food quality in terms of both nitrogen (GLM $F_{1,54} = 9.56$ $P = 0.003$) and phosphorus (GLM $F_{1,54} = 11.33$ $P = 0.001$). July temperature showed a positive relationship with both nitrogen concentration in heather (GLM $F_{1,54} = 65.28$ $P < 0.001$) and phosphorus concentration (GLM $F_{1,54} = 15.20$ $P < 0.001$).

2.3.3. Breeding production

Breeding production was lower on Scottish sites than on English sites for both young to old ratio (Table 2.1, Figure 2.4.) and for number of young per female grouse (Table 2.1, Figure 2.4.). This difference in breeding production between Scotland and England was significant for both young to old ratio (GLM $F_{1,54} = 12.50$, $P = 0.001$) and young per female grouse (GLM $F_{1,54} = 4.36$, $P = 0.042$).

Table 2.1. Mean values of variables entered in analysis (± 1 SE) for both Scotland and England. n = 28 for all Scottish variables, n = 27 for all English variables.

Variable	Scotland	England
Median worm	829 ± 113	2054 ± 163
% P	0.074 ± 0.0022	0.086 ± 0.0020
% N	1.267 ± 0.0305	1.561 ± 0.023
July temperature	14.13 ± 0.049	15.07 ± 0.058
Rainfall (wet days)	165.36 ± 2.54	157.41 ± 3.48
Young to old ratio	1.99 ± 0.098	2.46 ± 0.084
Young per female	4.48 ± 0.218	5.059 ± 0.168

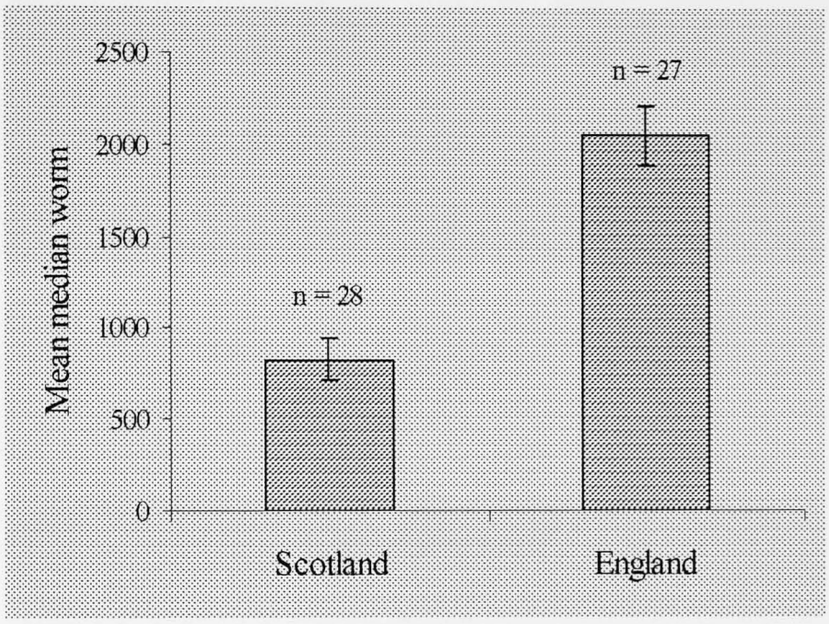
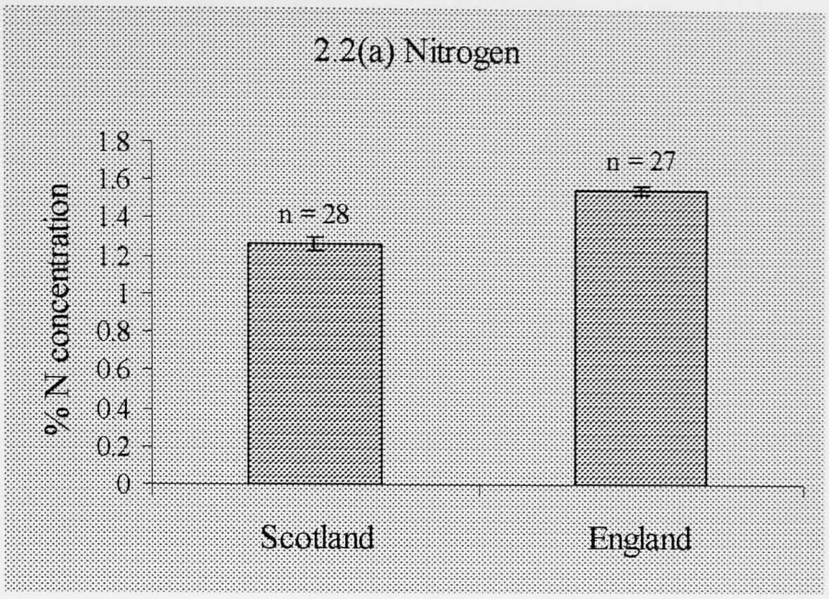


Figure 2.1. Mean median worm burdens (± 1 SE) of grouse populations on moors in Scotland and England. n = sample size.



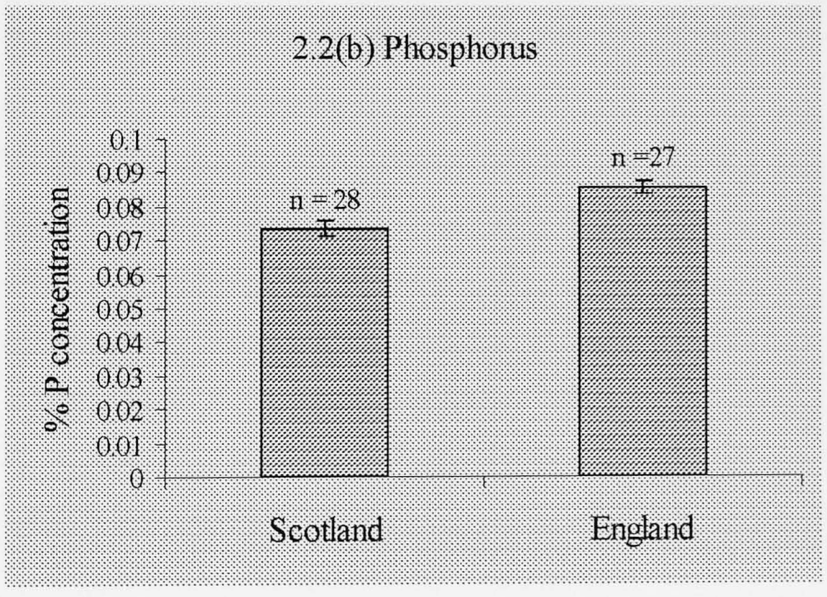
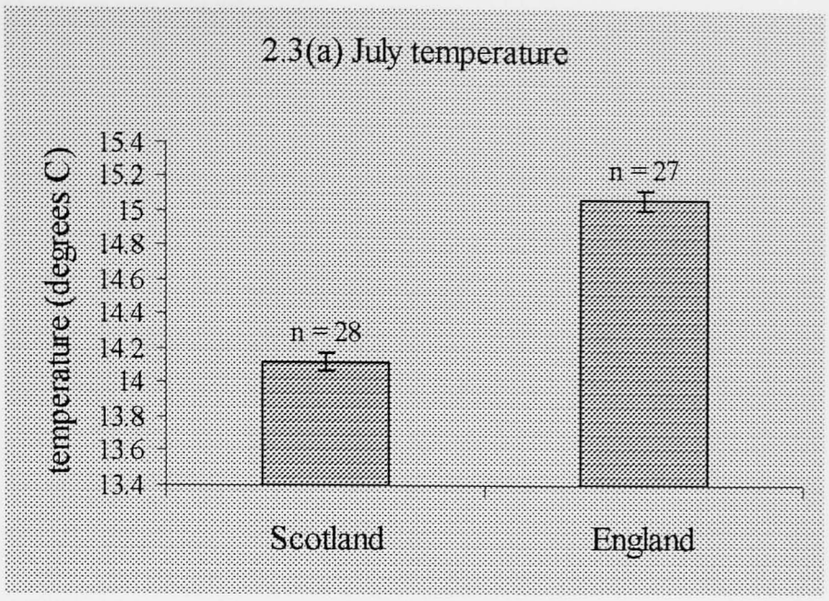


Figure 2.2. Mean nitrogen (Fig. 2.2(a)) and phosphorus (Fig. 2.2(b)) concentration in heather (± 1 SE) on Scottish and English moors in 1997. n = sample size.



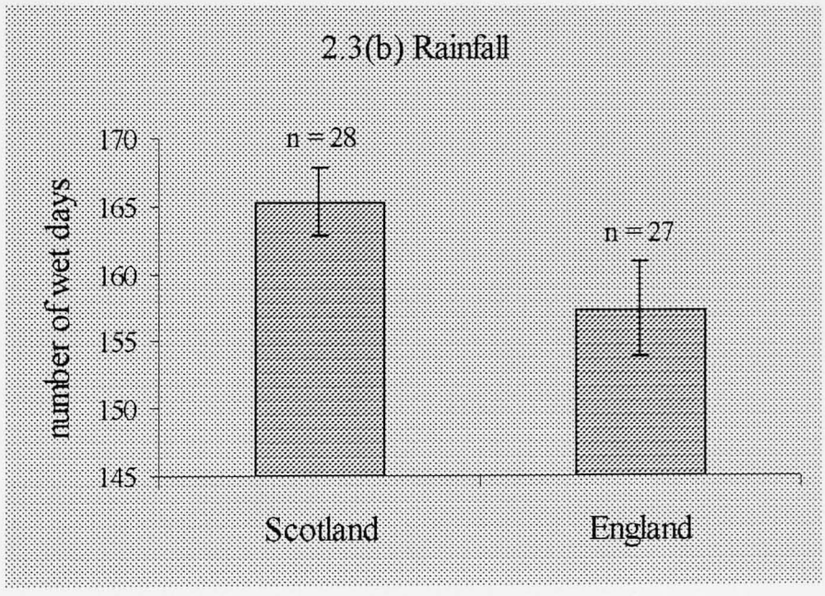


Figure 2.3. Mean July temperature (Fig. 2.3(a)) and mean rainfall (Fig. 2.3(b)) on moors in Scotland and England (± 1 SE). n = sample size.

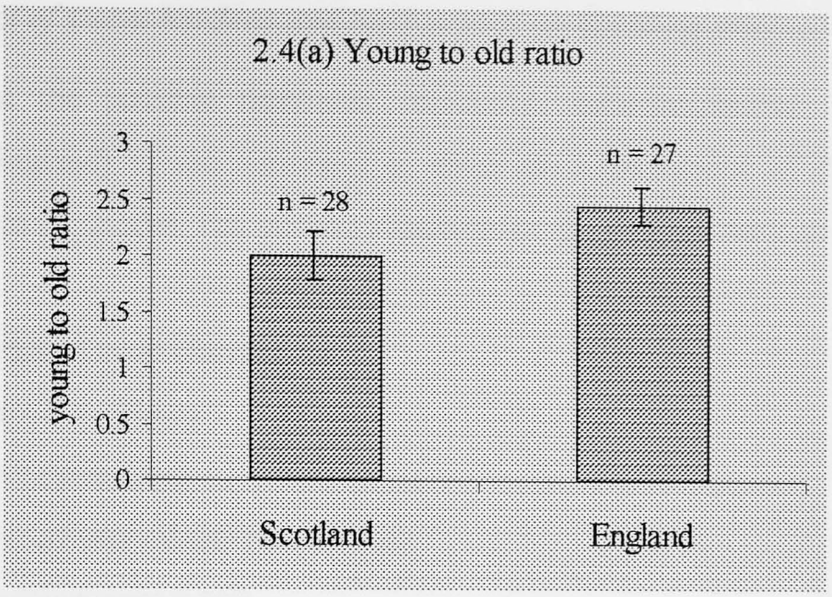


Figure 2.4. Mean young-to-old ratio (Fig. 2.4(a)) and young-per-female grouse (Fig. 2.4(b)) on Scottish and English moors (± 1 SE). n = sample size.

2.3.4. Effect of worm burdens and food quality on breeding production

To look at the possible three-way interaction between worms, food quality and area (Scotland/England) it was necessary to enter all combinations of the interactions between variables into the model. The starting variables for the analysis were as follows:

Scotland/England code (factor)
Median worm (covariate)
%P and %N (covariates)
July temperature and rainfall (covariates)
Scotland/England code * %P
Scotland/England code * %N
Median worm * %P
Median worm * %N
Median worm * Scotland/England code
Scotland/England code * median worm * %P
Scotland/England code * median worm * %N

There was a significant three-way interaction effect on breeding production in terms of young to old ratio. This interaction was between area (Scotland/England), worm burden and nitrogen concentration in heather (GLM on arcsine square root transformed data $F_{1,54} = 4.48$, $P = 0.040$). Other significant variables were phosphorus concentration in heather ($F_{1,54} = 17.99$, $P < 0.001$), July temperature ($F_{1,54} = 7.77$, $P = 0.008$) and rainfall ($F_{1,54} = 6.07$, $P = 0.018$).

This three-way interaction was also true for breeding production in terms of young per female grouse (GLM on arcsine square root transformed data $F_{1,54} = 4.12$, $P = 0.048$). Other variables that were significant in this case were phosphorus concentration in heather ($F_{1,54} = 8.84$, $P = 0.005$) and July temperature ($F_{1,54} = 8.65$, $P = 0.005$).

In both these cases the three-way interaction between area (Scotland/England), food quality and worms showed a very small but significant negative association with breeding production both in terms of young to old ratio and number of young per female grouse. The only difference between the two analyses was that rain had a significant effect on young to old ratio.

The coefficients for the effect of worms on breeding production appeared to show a positive relationship, but once the equation of the model was differentiated, the true coefficients for the effects of worms were all negative. Worms had a greater negative effect on breeding production, both in terms of young to old ratio and young per female, in Scotland than in England (Coefficients: Scotland young:old = -0.006907; young per female = -0.031; England young:old = -0.00076; young per female = -0.000196).

2.4. Discussion

This study investigated the hypothesis that food and parasites interact, and that the effects of this interaction could explain variations in population cycles between different areas. Analysis of long-term data showed that parasite burdens were lower in grouse populations in Scotland than in those in England. Food quality was lower on Scottish moors than on English moors, and this could be explained by weather conditions. Breeding production of grouse was lower in Scotland than in England.

There was a three-way interaction between food, parasites and area, which had a small negative association with breeding production. These findings will now be discussed in greater detail.

2.4.1. Parasite burdens

Parasite burdens were lower in Scottish grouse populations than in English populations. As grouse population densities are generally lower in Scotland than England (Hudson 1992, Smith *et al* 1999) we would expect this to be the case.

The way in which parasite burdens have been estimated for each moor in this study may have introduced some error. Parasite burdens used were median values, calculated for each year for each moor and then averaged to give a value for each moor. Breeding production estimates and food quality estimates were both obtained from study sites within these moors, whereas parasite burdens were determined for the entire moor. It is acknowledged that this may have introduced error, but it was the most accurate way to estimate parasite burden from the data available.

Timing of parasite burden estimation is also important. Most grouse have been collected for this purpose during the grouse-shooting season (August 12th to December 10th). Although parasite burdens have been estimated accurately, they do not necessarily reflect what the parasite burden would have been in the spring as parasite burdens will change throughout the year due to recruitment of parasites during the summer and autumn months (Hudson 1992). Spring is the time when parasites are most important in terms of breeding production, but parasite burden estimations were only available from grouse shot during the grouse season.

2.4.2. Food quality and weather

Food quality, in terms of nitrogen and phosphorus concentration in heather, was found to be higher on English moors than on Scottish moors. This was probably due to the negative association of rain and the positive association of July temperature with nitrogen and phosphorus concentration in heather. Food quality in Scotland is probably lower because it is colder and wetter than England. Another reason for this could be underlying rock type (Jenkins *et al* 1967, Picozzi 1968, Moss *et al* 1975) with England having more 'rich' moors with high nutrient content and Scotland having more nutrient 'poor' moors.

The food quality estimation in this study was obtained from data collected in one year, (1997). This has been related to other data from over 15 years. Data on breeding production and parasite burdens were averaged to allow for this. Various other factors may affect the nutrient content of the heather. These factors include weather and possibly other environmental factors, muirburn and grazing pressure.

2.4.3. Food-parasite interaction and the effect on breeding production

Breeding production was lower in grouse populations in Scotland than in England. As population cycles are longer in Scotland, we would expect this to be the case, with lower overall production meaning lower population growth rate.

There was a three-way interaction of area, parasites and food quality which had a very small but significant association with breeding production both in terms of young to old ratio and young per female grouse.

Previous studies have examined parasites and food quality in relation to breeding production. Parasites have been shown to have a negative effect on breeding production in grouse (Hudson 1986, Hudson *et al* 1992), and food quality has also been shown to be associated with breeding production (Moss *et al* 1975). The interaction between parasites and food quality and the effect on breeding production has not previously been examined.

Breeding production estimates for this study were taken from data collected during annual grouse counts, and although this is a recognised way of measuring grouse density (Hudson & Newborn 1995), the estimates of breeding production probably suffer from a degree of

inaccuracy. However, with the data available, young-to-old ratio and number of young per hen were the best estimates of breeding production that could be obtained. Clutch size, hatching success and chick survival would have helped identify which components of breeding success may have been influenced, but this information was not available.

However, the most important interaction taking place was a three-way interaction between food, parasites and area (Scotland/England). This interaction had a negative association with breeding production in both Scotland and England. This negative association was greater in Scotland, suggesting that the interaction between food quality and parasites has a greater effect on breeding production of grouse in Scotland than in England. This interaction between food, parasites and area could give rise to different population cycles between Scotland and England. The interaction has a greater negative influence on breeding production in Scotland, which means that overall production would be lower, and so the growth rate of the population would also be low. The population would take a relatively long time to reach a level where factors causing a crash would act, hence generating long population cycles in Scotland. This is examined in more detail in Chapters 4 and 6. In England, the interaction has a lesser negative influence on breeding production, meaning that overall production is higher, the population growth rate is higher, and so the period of cycles is shorter than those in Scotland.

2.4.4. Future work

In this study I have shown that a three-way interaction between food, parasites and area can influence the variation in population cycles between different areas. Future work could look at this interaction in more detail, looking more closely at different areas to find other factors that may also influence variation in population cycles, such as parasite transmission rate (Hudson *et al* 1985). This has implications for grouse moor managers, as different approaches to maximising grouse numbers may be required in different areas. The effect of a food-parasite interaction on the breeding production of grouse is examined experimentally in Chapter 4 of this thesis.

In summary, the difference in population cycles between areas is due to a three-way interaction between food, parasites and area influencing population growth rate and therefore influencing the period of the cycles.

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CHAPTER 3

VARIATIONS IN RED GROUSE POPULATION DYNAMICS: FOOD-PARASITE INTERACTION AND BODY CONDITION

3.1. Introduction

Parasitism can directly influence the nutritional status of an animal by affecting both the physiology and feeding behaviour of the host (Hall 1985, Scott 1988). Parasites may reduce the amount of energy or specific resources available to the host animal, depending on first, the nutrients taken from the host, and secondly damage to the host. When the plane of nutrition is high the parasite may have little effect but when parasites have substantial energetic or damage costs, these will be reflected by a reduction in the body condition and reproductive success of the animal host (Hudson 1986a, Moller 1993, Richner *et al* 1993). However, the extent to which these costs affect the host may depend on the level of nutrition attained by the host.

In red grouse *Lagopus lagopus scoticus,* the intestinal parasitic nematode *Trichostrongylus tenuis* has such an effect on breeding production. *T. tenuis* probably affects body condition through the damage it causes to the caeca of the grouse. The adult worms burrows into the caecal mucosa causing disruption to the plicae and internal bleeding, which probably reduces digestive capability and affects the normal functioning of the caeca (Watson *et al* 1987). *T. tenuis* reduces both body condition estimated as relative mass and mass gain of grouse (Wilson & Wilson 1978, Hudson 1986a & b). Experiments on captive grouse also show that individuals infected with high numbers of *T. tenuis* produce fewer eggs, eat less, gain less weight, have lower energy consumption and expenditure than those with little or no infection (Shaw & Moss 1990, Delahay *et al* 1995, Delahay & Moss 1996).

Previous independent field studies have shown that both nutrition (Moss *et al* 1975, Watson *et al* 1984) and parasites (Hudson 1986a) can influence the reproductive success of red grouse, and that breeding production is increased when parasite infections are reduced through treatment with anthelmintic (Hudson 1986a, Hudson *et al* 1992).

Modelling of the grouse system has shown that *T. tenuis* reduces breeding success and this is sufficient and necessary in combination with other factors to generate population cycles as observed in grouse populations (Anderson & May 1978, May & Anderson 1978, Dobson & Hudson 1992, Hudson *et al* 1998).

Red grouse feed predominantly on a nutrient-poor diet of young shoots of heather, *Calluna vulgaris*. They feed selectively on heather that is high in nutrient content, choosing to feed on plants with high nitrogen and phosphorus content (Moss *et al* 1975, Savory 1983). Nutrient content of heather also differs between grouse moors, with 'rich' moors, lying on base-rich rocks such as limestone, having heather of higher nutritive value (greater nitrogen and phosphorus content) than 'poor' moors with underlying acidic rocks such as granite (Jenkins *et al* 1967, Picozzi 1968, Moss *et al* 1975).

Grouse population cycles differ between areas. Moors in Scotland typically have cycles of 6-12 years, whereas moors in Northern England exhibit population cycles of 4-5 years (Potts *et al* 1984, Hudson 1992). The period of a population cycle will be influenced by the balance between the intrinsic growth rate of the grouse population and time delays in the density-dependent processes influencing population growth (May 1981). The variation in the period of grouse population cycles could be a result of lower growth rates in populations with long cycle periods. One hypothesis is that this would be influenced by an interaction between food and parasites influencing the production by grouse, and therefore having an effect on population growth rate and the period of cycles.

Lack (1954) suggested that food availability had a dominating role in limiting the numbers of an animal but would interact with parasites when these were abundant. Numerous studies have been undertaken on the role of animal nutrition, as reviewed by Boutin (1990) but few have examined the potential interactive effects of food and parasites.

This chapter examines the hypothesis that food and parasites interact and have an effect on the body condition of red grouse, which could explain the variation in grouse population cycles between different areas.

This hypothesis is examined by using long-term data to look at the effect of parasites on body condition, and the effect of any interaction between nutrition (heather quality) and parasites on body condition.

3.2. Methodology

3.2.1. Long-term data

Data on red grouse have been collected by the Game Conservancy Trust (GCT) and Peter Hudson over twenty years, from grouse moors in both Scotland and England, to form a large database containing long term data. This study used data taken from this database, concerning worm burdens and biometrics of grouse.

3.2.2. Data collection

This database was added to during the three years of this study. Between 1996 – 1998 I visited grouse moors to obtain shot birds for assessing worm burdens. These grouse were obtained either on the shoot day or soon after having been kept in a game larder. Body measurements, of mass and wing length, were taken and the guts removed for worm counts.

3.2.3. Worm burdens

T. tenuis infections in shot grouse were estimated by performing worm counts (Hudson 1986a, Hudson & Newborn 1995). Their caeca were removed, cut into five sections, opened out by cutting lengthways and the contents washed with water over a 210 μm gauze. The adult worms were then washed into a solution of 300 ml of water. Four subsamples of 10 ml were taken, and the worms in each were counted. The numbers of worms from these subsamples were added together and then multiplied by 15 to give the total number of worms per grouse.

3.2.4. Heather quality and weather variables

The GCT collected heather samples from grouse moors in 1997. These heather samples were analysed by the GCT for nitrogen and phosphorus concentration to provide an estimate of heather quality (Smith *et al* 1999). These data were used in this study to provide an estimate of grouse food quality. Weather variables were also included in this study. These were temperature, taken as the average in July across a range of years (Hudson 1992), and rainfall taken as the average number of wet days across a range of years (Hudson 1992).

3.2.5. Body condition estimates

Physiological condition of wild birds can depend on the amount of fat they have relative to their body mass (Morton *et al* 1991). Body condition has previously been estimated in a range of different non-invasive ways including fat scoring (Scott *et al* 1995), infra-red interactance (Roby 1991) and visual estimation from body measurements (Lyons & Haig 1995). Body mass is the measurement most often used to assess condition in ecological studies (Brittas & Marcström 1984). In this study body mass was used as a measure of body condition and wing length used to correct for the difference in body size between birds.

An alternative technique for assessing body condition of an animal by measuring the electrical conductivity of body tissues was also used.

3.2.6. Statistical analysis

Data were analysed with Minitab 11. All results of statistical tests were tested for normality using an Anderson Darling normality test. For statistical analysis the long-term data used did not include data from young grouse, as both worm burdens and body condition of young grouse in August are not representative of the population as a whole. As many different people have collected the GCT data over 20 years, some records were incomplete with missing values and zeros entered when values were unknown. For this reason, records with missing values, and records showing worm burdens as zero were not included in the analysis.

Data were only included where mass and wing length of grouse, worm burden and heather quality were available (Moors included in the analysis are listed in Appendix 1B). As heather quality was only estimated in one year (1997) all data were reduced to an average for each moor.

As the distribution of worms within a moor was known not to be normally distributed (Hudson 1992) the mean value of worms would not necessarily describe the data very well, so the median value of worms was used for each moor.

3.3. Total body electrical conductivity (TOBEC)

A non-invasive technique for predicting lean body mass, body fat content and water content of an individual was used to estimate body condition of grouse.

3.3.1. TOBEC methodolgy

Grouse carcasses were scanned with the TOBEC before the guts were removed during visits to estates in Scotland to collect shot grouse in 1997 and 1998. Grouse were individually placed in an EM-SCAN/TOBEC® Model SA-3114 measurement chamber and scanned with an electromagnetic field. This provided a reading that was calibrated and used to estimate body fat content of the grouse. As the positioning of the subject was crucial to obtaining precise results (Walsberg 1988, Scott *et al* 1991, EM-SCAN/TOBEC® 1994) grouse were secured in the same position for each scan by means of elastic bands. One band kept the head bent forward along the sternum and one kept the legs and feet bent towards the body. The grouse were then placed in a curved carrier plate. Each grouse was scanned five times and the readings averaged to obtain a final reading. Temperature was also known to affect the results (Walsberg 1988, Scott *et al* 1991, EM-SCAN/TOBEC® 1994), so the temperature of each bird was recorded before scanning. During data collection, the scanning equipment was set up inside a game larder where possible to minimise the effects of environmental factors on the results.

3.3.2. TOBEC calibration

To estimate fat content, the TOBEC scanning device needs to be calibrated for each species by lipid extraction. Twenty grouse were randomly selected to be used for the calibration. These grouse were scanned at a series of different grouse body temperatures. Birds were heated by placing them in a plastic bag and submerging the carcass in hot water. If birds required cooling they were placed in a fridge. Temperatures in the field ranged from just above 0° C where the bird had been kept in a cold store, to almost 40° C for a freshly shot bird. Birds were scanned at temperatures between these values, at approximately 5°C intervals and five repeat readings were taken for each bird at each temperature, which were later averaged (Table 3.1.). Time constraints meant that only 12 grouse were scanned at a range of temperatures and the other eight were only scanned once.

Table 3.1. Average TOBEC readings (E is reading value obtained) for birds used in the calibration process, taken at different temperatures.

Bird no.	Temp.	Mean E	S.E.
1	4.5	228.2	10.19
2	5.0	163.2	1.77
3	5.0	292.6	8.64
4	5.5	272.2	3.73
5	5.5	283.2	3.65
6	6.0	320.2	4.09
7	5.0	283.6	1.03
8	5.0	309.6	2.11
9	5.0	281.4	2.25
10	6.0	218.2	1.74
11	6.0	272.0	1.67
12	6.0	252.0	2.28
1	12.0	214.6	9.38
2	12.0	175.0	8.59
3	13.0	224.8	23.54
4	10.0	313.6	12.43
5	12.0	295.8	11.37
6	12.0	365.8	25.89
7	11.5	328.6	10.05
8	12.5	298.0	12.96
9	11.0	321.8	17.73
10	11.0	195.6	16.45
11	12.0	185.2	16.56
12	11.0	268.0	13.45
1	24.0	383.0	8.54
2	24.5	304.6	1.40
3	23.5	388.2	2.80
4	24.5	430.2	9.49
5	22.5	432.8	3.32
6	23.0	493.4	3.35
7	24.5	475.8	18.83
8	25.5	514.8	10.70
9	24.5	483.4	1.86
10	24.5	293.0	6.19
11	25.5	401.6	4.19
12	25.0	382.0	2.59
13	5.5	239.8	20.14
14	5.0	294.0	24.47
15	6.5	178.0	8.56
16	6.0	270.4	7.09

Bird. no	Temp.	Mean E	S.E.
1	30.0	467.4	7.17
2	30.5	322.2	4.59
3	27.0	476.6	13.86
4	30.0	471.8	11.73
5	32.0	522.6	8.45
6	27.5	609.8	4.93
7	31.5	571.8	10.05
8	32.0	554.0	2.84
9	31.0	467.6	6.48
10	30.0	338.4	7.16
11	29.0	441.2	9.08
12	30.0	425.6	6.01
1	40.0	533.8	25.26
2	43.0	462.6	30.38
3	40.0	565.2	20.13
4	40.0	615.6	7.49
5	41.0	653.4	8.93
6	42.0	824.8	6.34
7	45.0	757.4	13.72
8	44.0	685.6	19.22
9	43.0	552.4	16.91
10	40.0	373.6	10.00
11	38.0	527.2	23.25
12	40.0	484.0	5.26
1	7.0	247.8	8.69
2	7.0	184.2	9.00
3	7.0	285.6	9.79
4	8.0	277.6	6.98
5	8.0	305.4	6.44
6	8.0	345.8	11.16
7	8.0	286.4	7.02
8	8.0	307.0	13.20
9	8.0	308.2	7.88
10	8.0	219.8	6.01
11	8.0	268.0	3.70
12	8.0	242.2	8.80
17	4.5	277.6	14.06
18	7.0	258.6	13.54
19	7.0	266.6	15.70
20	6.0	284.0	5.55

Lipid content of these grouse was estimated by first removing feathers, recording mass and then chopping into small pieces. The carcass was then minced to produce a finely divided and homogenous mass. Two portions of approximately 200g were weighed into aluminium foil dishes and frozen for 16 hours and the moisture removed in a freeze drier for one week. Dry weight was recorded and the following equation used to estimate the moisture content of the carcass.

Moisture content of carcass (%) = (Loss in weight/original weight) * 100

To determine fat content, two separate 10g samples of the freeze-dried material were weighed into Whatmans extraction thimbles. The tops were closed with cotton wool, two clean extraction flasks were weighed individually and each thimble placed in a Soxhlet extraction apparatus. The fat was then extracted with petroleum spirit over a period of two days into the extraction flasks. Both flasks were weighed, dried to a constant weight at 105 °C, cooled in a desiccator and weighed again. The following equations were used to estimate the fat content of the grouse carcasses.

% fat in dry carcass = [(weight of flask+fat)-weight of flask]/weight of sample * 100

% fat in original carcass = [% fat in dry carcass*(100-M)]/100

where M =moisture content of original carcass

The lean mass of each bird was calculated from the information on the fat content of each bird. Regression analyses were used to predict lean mass from TOBEC readings whilst correcting for temperature differences. Once lean mass was estimated from this equation, the fat content of grouse was predicted (Table 3.3.).

3.4. Results

3.4.1. Differences in worm burdens between areas

Worm burdens were lower on Scottish moors than on English moors (Table 3.3, Figure 3.1.) and this difference was significant (Mann Whitney W = 544.0 Df = 1,38 $P = 0.0001$).

3.4.2. Food quality and weather

Food quality, in terms of nitrogen and phosphorus concentration in heather, was lower on moors in Scotland (Table 3.3, Figure 3.2.) than on moors in England (Table 3.3, Figure 3.2.). This difference in food quality between Scottish and English grouse moors was significant (GLM Nitrogen $F_{1,38} = 30.89$, $P < 0.001$; Phosphorus $F_{1,38} = 6.24$, $P = 0.017$).

On grouse moors involved in this study, mean rainfall is very similar for moors in Scotland and England (Table 3.3.). Average temperature in July is higher in England than in Scotland (Table 3.3.). When rainfall and temperature variables were added to the analysis, the differences between Scotland and England in terms of food quality could be explained.

There was a negative association between rainfall and food quality in terms of both nitrogen (GLM $F_{1,38} = 8.37$, $P = 0.006$) and phosphorus (GLM $F_{1,38} = 11.30$, $P = 0.002$). July temperature showed a positive association with both nitrogen (GLM $F_{1,38} = 46.64$, $P < 0.001$) and phosphorus (GLM $F_{1,38} = 10.06$, $P = 0.003$) concentration in heather.

3.4.3. Differences in body condition between areas

There was little difference in the body condition estimated as mass/wing length^3 between grouse populations on moors in Scotland and England (Table 3.3.). There was no effect of area on body condition when measured by mass/wing length^3 (GLM $F_{1,38} = 0.05$, $P = 0.825$).

Table 3.3. Mean values of variables entered in analysis (± 1 SE) for both Scotland and England. n = 19 for all Scottish variables, n = 20 for all English variables.

Variable	Scotland	England
Median worm	1075 ± 172	3073 ± 387
% P	0.075 ± 0.003	0.085 ± 0.002
% N	1.297 ± 0.038	1.553 ± 0.027
July temperature (°C)	14.16 ± 0.067	15.1 ± 0.046
Rainfall (wet days)	161.84 ± 3.53	161.50 ± 3.02
Mass/wing length^3	0.00008 ± 0.00	0.00008 ± 0.00

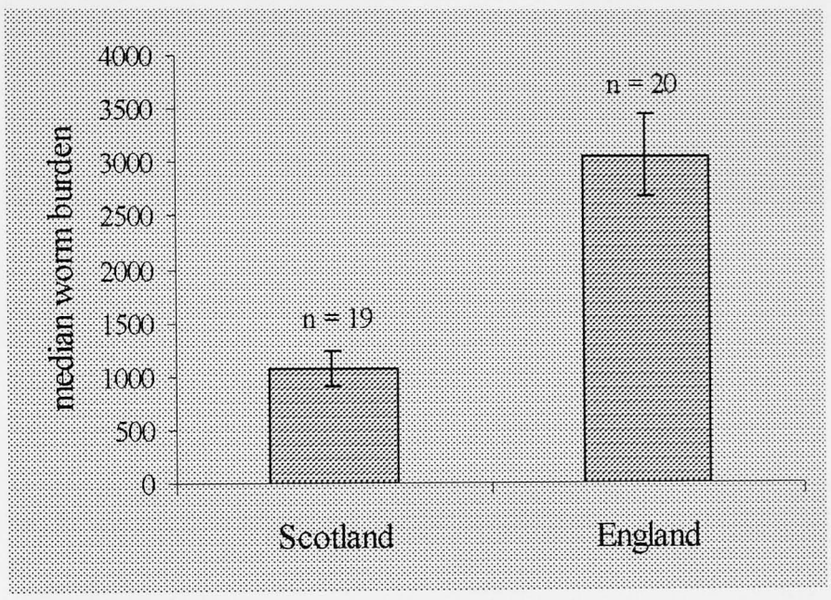
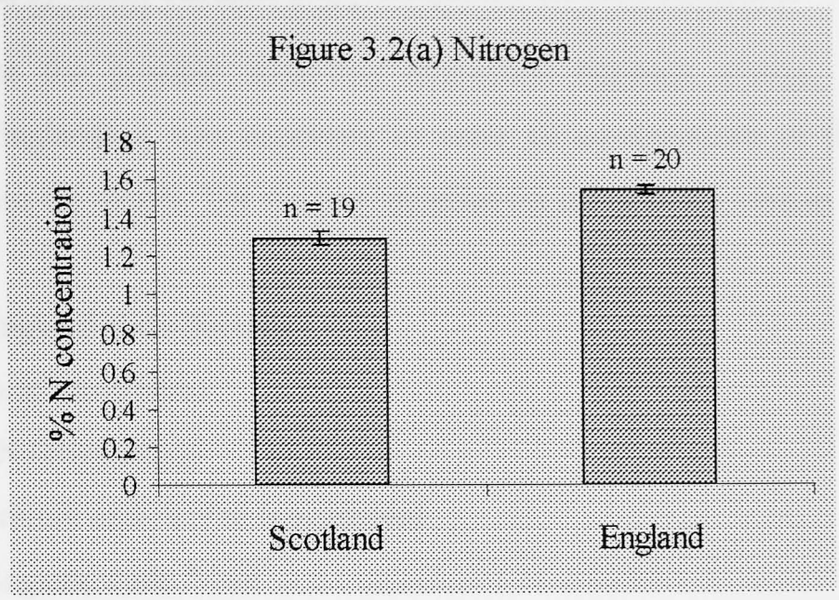


Figure 3.1. Mean median worm burden (± 1 SE) of grouse populations on Scottish and English moors. n = sample size.



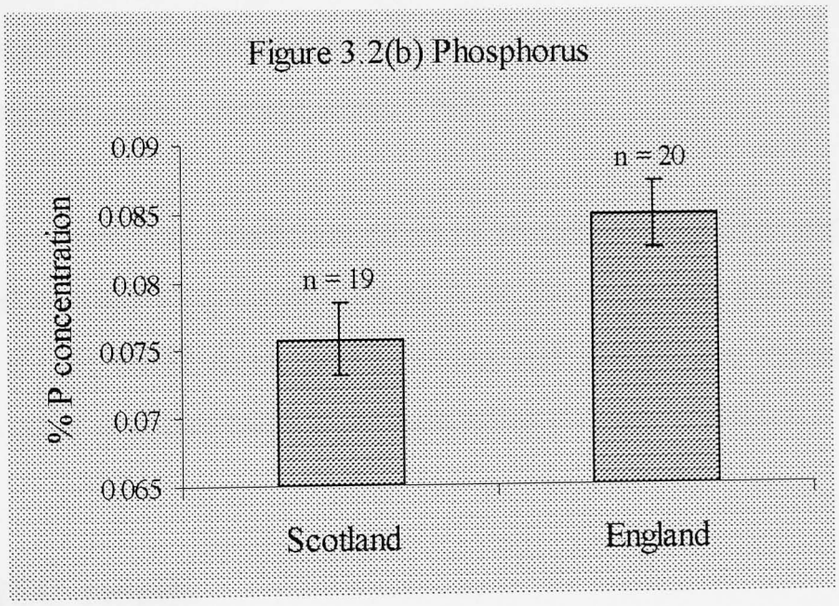


Figure 3.2. Mean nitrogen (Fig. 3.2(a)) and phosphorus (Fig. 3.2(b)) concentration in heather (± 1 SE) on moors in Scotland and England in 1997. n = sample size.

3.4.4. Effect of worm burdens and food quality on body condition

To examine the possible three-way interaction between worms, food quality and area (Scotland/England) it was necessary to enter all combinations of the interactions between variables into the model. The starting variables for the analysis were as follows:

Scotland/England code (factor)
Median worm (covariate)
%P and %N (covariates)
July temperature and rainfall (covariates)
Scotland/England code * %P
Scotland/England code * %N
Median worm * %P
Median worm * %N
Median worm * Scotland/England code
Scotland/England code * median worm * %P
Scotland/England code * median worm * %N

There was no three-way interaction effect of worms, food quality and area on body condition as estimated as mass/wing length^3 (GLM Area, worm burden and nitrogen interaction $F_{1,38}$ = 2.10, P = 0.159; GLM Area, worm burden and phosphorus interaction $F_{1,38}$ = 2.41, P = 0.133). No other variables had a significant effect on body condition.

3.5. TOBEC-results

3.5.1. Calibration of TOBEC

The following regression equation accounted for 99.6% of the variation in lean mass from TOBEC results (r^2 = 0.996, $F_{4,79}$= 4858.84, P < 0.001)

Lean mass = -45.9 + 0.933 mass + 0.243 wing length - 0.119 temp +11.0 log mean E

Where mass is the mass of the individual grouse, wing length is measurement of each grouse, temp is body temperature at time of reading, and log mean E is log 10 transformed mean of 5 TOBEC scans.

Table 3.3. Variables from grouse used in TOBEC calibration procedure, including biometrics, moisture content, fat content and lean mass.

Bird no.	Mass (g)	Wing length (mm)	% Moisture	% Fat	Actual fat content	Lean mass (g)
1	660	217	67.95	2.16	14.26	645.74
2	545	201	67.68	1.93	10.52	534.48
3	680	214	66.55	2.55	17.34	662.66
4	630	212	68.64	1.92	12.10	617.90
5	660	216	67.74	2.29	15.11	644.89
6	680	220	67.66	1.50	10.20	669.80
7	650	214	71.91	0.99	6.44	643.56
8	715	221	69.22	2.19	15.66	699.34
9	575	210	70.22	1.49	8.57	566.43
10	550	219	69.56	1.43	7.87	542.13
11	640	217	70.61	0.91	5.82	634.18
12	610	210	69.42	1.12	6.83	603.17
13	670	209	70.65	1.25	8.38	661.62
14	700	231	70.43	1.02	7.14	692.86
15	550	206	70.34	1.12	6.16	543.84
16	650	214	70.32	1.51	9.82	640.18
17	650	217	70.31	1.84	11.96	638.04
18	635	202	67.90	3.11	19.75	615.25
19	590	206	70.59	1.69	9.97	580.03
20	690	200	66.65	2.68	18.49	671.51

This equation was used to estimate the lean mass of individual grouse, and by subtracting lean mass from actual mass, the fat content of individual grouse (Table 3.3.).

As TOBEC is sometimes unreliable under field conditions (EM-SCAN/TOBEC® 1994) this r^2 value seemed very high. Therefore the regression model was run without TOBEC readings included, and without temperature also.

With just mass and wing length entered into the regression model the following equation accounted for 99.6% of the variation in lean mass ($r^2 = 0.996$, $F_{2, 79} = 9469.86$, $P < 0.001$).

Lean mass = -28.9 + 0.944 mass + 0.249 wing length

From these results it is apparent that the addition of data obtained from TOBEC in this case does not change the accuracy of estimating fat content of grouse, which simply can be estimated from the body measurements of mass and wing length alone.

3.5.2. TOBEC-food-parasite interaction

Although results gained from TOBEC may not be of much use, they were used to look at the effect of any interaction between worms and food quality on body condition of grouse measured in this way in Scotland in 1996 and 1997. Grouse from the following Scottish grouse moors were used:

Aberarder; Balmoral; Burncastle; Clune; Corrybrough; Crubenmore; Edinglassie; Garrogie; Glenbanchor; Glenturret; Invermark; Lochearnside.

There was a difference in body condition between male and female grouse in terms of fat content (GLM $F_{1,208} = 24.56$, $P < 0.001$) with female grouse having lower fat content than male grouse. July temperature showed a negative association with fat content of grouse (GLM $F_{1,208} = 11.73$, $P = 0.001$). There was no interaction effect of worms and food quality on the fat content of grouse (GLM worm burden * %P $F_{1,208} = 0.56$, $P = 0.497$, GLM worm burden * %N $F_{1,208} = 1.92$, $P = 0.167$).

3.6. Discussion

This study investigated the hypothesis that an interaction between food and parasites may have an effect on the body condition of red grouse, which could help to explain the variation in grouse population cycles between areas. This section summarises the results of this study and discusses them in detail in relation to this hypothesis.

The results of this study show that worm burdens are lower in Scottish grouse populations than in English grouse populations. Food quality, in terms of nitrogen and phosphorus content in heather is lower in Scotland than in England, although this can be explained by weather conditions. Analysis of long-term data showed no difference in relative body condition as estimated by mass/wing length^3 between Scotland and England. There is no evidence to show that a food-parasite interaction is taking place and influencing body condition. The use of TOBEC to estimate body condition proved to be of little value. Data obtained from TOBEC showed that female grouse had higher fat content than male grouse, but failed to show a food-parasite interaction effect on body condition in terms of fat content.

The results show that there is a difference between areas in terms of worms burdens and food quality, although it would appear from the results that food and parasites do not interact to influence body condition.

3.6.1. Worm burdens

The long-term data showed worm burdens to be lower in Scotland than in England. This is expected, as grouse densities are generally lower in Scotland than in England (Hudson 1992, Smith *et al* 1999) and so we would expect lower worm burdens in Scotland.

3.6.2. Food quality and weather

Food quality was lower in Scotland than in England, with lower levels of nitrogen and phosphorus in heather collected from Scottish moors. This supports the hypothesis that food quality may be having an effect on production and causing population cycles to differ between areas. The difference between Scotland and England was probably due to the negative association of rain and the positive association of July temperature with nitrogen and

phosphorus in heather. Food quality in Scotland is probably lower because the weather is colder and wetter than in England. Another reason for the difference in food quality between areas may well be underlying rock type (Jenkins *et al* 1967, Picozzi 1968, Moss *et al* 1975) with England having more 'rich' moors with high nutrient content, and Scotland showing more 'poor' moors with lower nutrients.

The food quality estimation in this study was obtained from data collected by GCT in only one year (1997). This has been related to other data from over 15 years. Data on worm burdens and body condition estimates were averaged to allow for this. Other factors may also influence nutrient content of heather, such as other environmental factors, soil type, muirburn and grazing pressure.

3.6.3. Body condition

There was no difference in body condition between Scotland and England. The data were averaged for this analysis, and so perhaps if the data were looked at for individual years we would see a difference between areas in body condition. There may be a difference within specific years, and this may depend on what stage of the cycle different populations are at. This would support the hypothesis that lower body condition and therefore lower production could influence population growth rate and the period of cycles, leading to longer population cycles in Scotland than in England. This cannot be supported from this study.

The time of collection of grouse is important as worm burdens estimated from grouse shot in August are likely to differ from the worm burden that influenced body condition earlier in the year, when condition is more important for breeding success. Body condition estimates taken from grouse in August are also likely to be different from actual body condition at the time of breeding.

3.6.4. Food-parasite interaction and the effect on body condition

There was no three-way interaction between area (Scotland/England), worm burdens and food quality found to be having an effect on body condition. No other variables had any effect on body condition of grouse.

Although there was no visible interaction of food and parasites, there may have been effects on other measures of body condition that were not examined in this study. Only body mass was considered in this study. There may be other effects on condition that have not been measured or are not clearly visible, and are more important in terms of grouse production. The absence of a food-parasite interaction does not mean the hypothesis that such an interaction is taking place should be refuted. In fluctuating grouse populations, worm burdens will be highest just after the population is at its greatest density, when there is also competition for territories and therefore food. It is at this time that a food-parasite interaction is most likely to occur.

Another reason why no interaction between food and parasites was found is that grouse may compensate for poor quality food by eating greater amounts, or selecting food of higher nutrient content (Savory 1983).

3.6.5. Effects at population level

Although no food-parasite interaction was found to have an effect on body condition in this study, it is possible that an interaction could occur in high-density grouse populations, where worm burdens were high and food more limited, similar to what occurs in snowshoe hare populations (Murray *et al* 1998). Longer population cycles in Scotland could be due to poor food quality alone, with an interaction occurring when worm burdens get really high. Poor food quality may just reduce production enough to increase the period of population cycles, by reducing not only visible body condition but condition in relation to reproductive success, which is probably more important in terms of population cycles. Grouse in Scotland are generally at lower densities than grouse in England, and so it will take longer for worms to increase to a level where they have a possible interaction with food quality and start to influence production.

3.6.6. TOBEC

Although this technique for estimating body condition worked well during the calibration process, its use in the field may have introduced variation in the results. The machine was sensitive to environmental changes such as wind and temperature, as found in Roby (1991), and was therefore difficult to use in the field. Any future work concerning TOBEC would have to be performed in more suitable surroundings to ensure reliable results.

However reliable the calibration process was, the results gained from use of TOBEC did not increase the predictability of fat content of grouse from the already high predictive value from using just body measurements of mass and wing length. In terms of measuring body condition, TOBEC proved to be of little use in this case.

Female grouse were shown to have lower fat content than male grouse. Despite the probability that TOBEC did not predict the fat content of these grouse very accurately, the overall picture that female grouse are of poorer body condition than male grouse is probably correct. It is reasonable to expect female grouse to be of lower body condition than male grouse, as most data were collected during August and September when female grouse have spent the previous few months laying and incubating eggs, and then rearing chicks. It is widely accepted that this breeding effort will result in females being in poorer condition than males.

July temperature had a negative association with fat content of grouse. This suggests that as average July temperature is lower in Scotland than in England, that fat content would be lower in grouse on English moors. Grouse in Scotland should have higher fat content because they live in a colder, wetter climate and will require more fat to survive colder winters.

There was no interaction of food and parasites having an effect on the fat content of grouse. This is expected as no effect on body condition of such an interaction was found previously.

In summary, although both food quality and worm burdens are lower on Scottish moors than on English moors, no food-parasite interaction was found that could influence body condition and lead to lower production and lower population growth rates in Scotland. This does not mean that the hypothesis should be refuted, as within certain circumstances a food-parasite interaction may occur.

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CHAPTER 4

THE INTERACTION BETWEEN PARASITES AND FOOD QUALITY: EFFECT ON THE BREEDING PRODUCTION OF FEMALE RED GROUSE

4.1. Introduction

To maximise their fitness, animals must find the optimal trade-off between survival and reproductive success. In bird species with low survival rates, maximising reproductive success consists of maximising clutch size relative to brood survival (Charnov & Krebs 1974). In nidicolous bird species, such as the great tit *Parus major*, the ability to feed and rear a brood places a constraint on the optimal clutch size (Lack 1966). However, this constraint is removed for nidifugous bird species, such as red grouse, where brood sizes above a certain threshold will not increase the mortality of the parents. As such, clutch size and the factors that determine clutch size are likely to be important determinants of fitness and clutch size is probably influenced by female condition.

Both food and parasites are thought to have a major influence on the reproductive success of animals (Lack 1954). Independent field studies on red grouse have established that both food (Moss *et al* 1975) and parasites (Hudson 1986) can influence reproductive success. In his book *The Natural Regulation of Animal Numbers*, Lack (1954) examined some of the early data on food and parasites of red grouse and proposed that the two would interact and cause fluctuations in red grouse populations.

Previous population studies on red grouse *Lagopus lagopus scoticus* have found that poor breeding success can be associated with high numbers of the gut parasite *Trichostrongylus tenuis* (Potts *et al* 1984). Experiments conducted on a grouse population in Northern England demonstrated experimentally that breeding production of red grouse can be significantly increased when parasite burdens are reduced by dosing with an anthelmintic (Hudson 1986, Hudson *et al* 1992).

Modelling of host-parasite systems has shown that parasite-induced reduction in fecundity will destabilise host numbers and, within limits set by the tension of other parameters, generate population cycles (Anderson & May 1978, May & Anderson 1978). These models have been developed and applied specifically to the red grouse - *T. tenuis* system, and the level of parasite-induced reduction in breeding success has proved sufficient and necessary to generate cyclic fluctuations similar to those observed in grouse populations (Dobson & Hudson 1992, Hudson *et al* 1998).

Food is also known to have an important impact on the breeding production of red grouse. They feed predominantly on the young shoots of heather *Calluna vulgaris* which is a high-fibre, low-protein food. Jenkins *et al* (1967) proposed that food may influence the breeding success of red grouse in three different ways: (1) heather growth in summer, which determines the amount of green heather in winter and is correlated with breeding success; (2) heather browning in winter, which reduces available green heather in spring and is correlated with breeding success and (3) timing of heather growth starting in spring, influences available food for females in spring. Grouse selectively feed on heather that is high in nutritive value, choosing plants that have high nitrogen and phosphorus content (Moss *et al* 1975, Savory 1983).

Maternal nutrition of female red grouse both before and during egg-laying is related to breeding production and could be an important factor in determining breeding success (Moss *et al* 1975). Manipulation of food quality by application of nitrate fertiliser has experimentally demonstrated that an increase in nitrogen increases heather growth and nitrogen content and in some cases increased breeding production, although the effect was not sufficient to account for population cycles (Watson *et al* 1984).

As both food quality and parasites influence the breeding production of grouse one could postulate that the two interact to have a combined effect. After experimental studies on captive grouse Delahay & Moss (1996) suggested that wild grouse eating low-quality food may suffer a greater impact of *T. tenuis* on breeding production. If this is the case then a reduction in food quality would increase the slope of the relationship between parasites and breeding production.

Grouse population fluctuations differ between areas. Moors in Scotland generally have longer cycles, of 6-12 years, than moors in Northern England where population cycles are around 4-5 years (Potts *et al* 1984, Hudson 1992). The period of a population cycle will be influenced by the intrinsic growth rate of the grouse population and by environmental effects that cause time delays in population growth (May 1981). The difference in grouse population cycles between areas could be due to variation in food quality, giving rise to *T. tenuis* having a variable effect on the breeding production of grouse, and therefore influencing the grouse population growth rate and so the period of population cycles.

This study examines the hypothesis that an interaction between food and parasites and the effects on breeding production could explain variations in cycle pattern between different grouse populations. This hypothesis is examined by manipulating both food quality and parasite burdens in a factorial experiment, and looking at whether this interaction is sufficient to account for differences in population fluctuations between areas.

4.2. Study sites

Two study sites were used, located on Ralia Estates, Inverness-shire. South Drumochter was a managed grouse moor of 2023 hectares covering NN6479 and the surrounding area (O.S. 1:50 000 Sheet 42) in the southern Cairngorms. The altitude varied between 375 and 936 metres, and the habitat was predominantly mire. The grouse population was managed for driven grouse shooting, with both predator control and heather burning taking place. The vegetation was grazed by hares, sheep during the summer, and red deer in the winter.

The second study site was at Crubenmore, which covered an area of 1214 hectares (NN6487 O.S. 1:50 000 Sheet 42). The altitude varied between 315 and 544 metres. This grouse population was also managed for driven grouse shooting, with predator control and heather burning taking place. The vegetation was grazed by sheep during the winter, and by roe deer, hares and rabbits all year round.

4.3. Methodology

4.3.1. Radio tagging grouse

I caught female red grouse at night during February and March 1996, 1997 and 1998. Birds were dazzled at night using a quartz halogen lamp and caught in a large net (Hudson 1986). Necklace radio transmitters were fitted around their necks. The radio transmitters' (supplied by Biotrak Ltd) mass was approximately 15g, and have been shown to have no effect on grouse behaviour (Thirgood *et al* 1995). Each female had a radio of different frequency so that individuals could be easily followed. Body measurements from each female were recorded, including mass and wing length.

4.3.2. Manipulation of parasite levels

Female red grouse were alternately allocated to treatment groups. Grouse were dosed orally using a syringe with a narrow tube attached so the contents of the syringe could be delivered into the crop. Grouse were dosed with either 2ml of water as a control treatment, 2ml of anthelmintic (Bionem containing 7.5% levamisole hydrochloride) to remove parasites, or 2ml of solution containing *T. tenuis* larvae to increase parasite numbers. I carried out the latter under a Home Office licence.

4.3.3. Cultivation of T. tenuis *larvae*

Caecal faeces were obtained from grouse populations in the north of England (by GCT staff) known to have high worm burdens, during January 1998 . These caecal faeces were cultured at 22°C for 7 days to allow *T. tenuis* eggs to hatch and develop into third stage infective larvae (Wilson 1979) which were collected and concentrated into solution using Baermann apparatus (MAFF 1978). The larval solution was then mixed to give a homogenous suspension, and the number of larvae per ml estimated using the modified McMaster technique (MAFF 1978). The solution was centrifuged at 1500rpm for 2 minutes to reduce the volume of the solution. The larval solution was then diluted with water and divided into individual volumes of 2ml containing approximately 10,000 infective larvae. According to data in Wilson (1979) this should lead to an adult worm burden of approximately 3500 worms.

4.3.4. Radio tracking

Once tagged, I tracked females weekly to find their location and to determine survival. When required, intensive radio tracking, in the form of triangulation was carried out. Bearings were taken of each bird's location from a series of fixed points, the location of which were determined from the median of multiple readings taken with a global positioning system. Tests showed that this method was an accurate way of establishing single locations of individual grouse, and could be used to gather several locations in order to estimate home range location and size. This was also undertaken in the third year of study to check for differences between years and moors with respect to home range location and size, and for allocation of birds in the third year into fertilised and not fertilised groups.

4.3.5. Breeding production data collection

I tracked female grouse at the beginning of May to find the location of their nests. Once found, each nest was marked with a cane placed ten paces north of the nest. Clutch size was recorded, and checked after ten days, so females were only disturbed twice during the incubation period. The nests were checked every two to three days by radio tracking from the cane, without disturbing the females, until the eggs hatched. Shells and eggs left in the nest were counted and hatching success estimated. Hatch date was estimated from the condition of the shells and the time since the nest was last checked. The female grouse were tracked again when the chicks were 4 days (3 - 6) and 10 days (9 - 12) of age to get an estimate of chick survival. Timing of sampling varied slightly due to weather conditions, since chicks were not disturbed in cold or wet conditions. Chicks were located by a pointing dog, caught, and body measurements recorded. A final flush of females and their brood took place in the first week of August, to get a final count of brood size and an estimate of chick survival.

4.3.6. Intensity of **Trichostrongylus tenuis** *infections*

Biometrics were taken from all radio tagged females that were shot during the grouse shooting season (12th August to 10th December) and their caeca removed for worm counts (Hudson 1986, Hudson & Newborn 1995). The caeca were cut into sections, opened and their contents washed with water over a 210μm gauze. The adult worms were washed into a solution of 300 ml of water and four subsamples of 10 ml taken. The worms in these were counted, added together and multiplied by 15 to give an estimated number of worms per bird.

A sample of shot grouse with natural infections were also collected for estimating worm burdens in the rest of the grouse population, and for comparison with all experimentally treated birds.

4.3.7. Faecal egg counts - The McMaster technique

The McMaster egg counting technique was used to count the number of *T. tenuis* eggs in a sample of caecal faeces (MAFF 1978). Samples were collected by either radio tracking female grouse at night without disturbing them, marking the roost location, and returning the next day to collect the sample, or by collecting a sample from the nest site. A solution was made containing 0.5g caecal faeces and 10ml saturated salt solution. Five 0.1ml samples were taken for egg counting using a McMaster slide. The total numbers of eggs in each of the five samples were then used to estimate the number of eggs per gram of caecal faeces.

4.3.8. Fertiliser treatment

I manipulated heather quality by adding NPK 21-8-11 fertiliser to heather plots. Trials were carried out during 1996 to assess the effects of the fertiliser on heather, and the appropriate concentration to use (Watson *et al* 1984). Fifteen plots of $1m^2$ within a uniform stand of heather were randomly allocated to each of three treatment groups: control with no fertiliser; 50g of fertiliser (10.5g of nitrogen); 100g of fertiliser (21g of nitrogen). Heather growth and nutrient content were then measured throughout the growing season. Heather growth was measured by recording new shoot growth in millimetres from 9 different shoots on the 15^{th} of the month throughout the growing season, and small samples of heather shoots were collected at the same time for nutrient analysis.

Based on the results from this trial, fertiliser was applied to eighteen areas of 20 m^2 within individual grouse home ranges on South Drumochter during early April 1997 at a concentration of 21g nitrogen per m^2. Eighteen areas of 20 m^2 were also marked in grouse territories classed as unfertilised. Fertiliser was also applied to six $2m^2$ plots which were used for monitoring growth and nutrient content. Forty plots of $20m^2$ were randomly selected on Crubenmore for use in the 1998 experiment and fertiliser was applied to half of these during August 1997, the rest were considered as control areas.

Heather biomass was measured on each of these areas on Crubenmore in August 1998 (for technique see Chapter 5). Grazing pressure by herbivores was assessed indirectly by counting the proportion of heather tips grazed at twenty points within the areas in August 1998 (the same points at which measurements were taken for estimating biomass). A ruler was laid in the heather, and the number of grazed tips of heather lying within a 10 cm by 2 cm strip were counted. A measure of the use of these areas by grouse was obtained indirectly by collecting all fibrous grouse faeces on the areas in August 1998. These were subsequently oven dried at 60 °C for 5 days and weighed to find their dry weight.

4.3.9. Nutrient analysis

Heather samples collected from experimental areas during 1996, 1997 and 1998 were all frozen until further analysis could take place. They were then oven dried at 60 °C for 5 days to remove moisture, then ground to a fine powder. Nitrogen content was estimated by taking approximately 0.2g of heather sample, which was placed in a Leco Protein/Nitrogen Analyser Model FP-328 and the result expressed as % nitrogen or protein content (pers. comm. Roslin Institute).

Phosphorus was estimated by taking 1g of heather sample, which was ashed for 16 hours at 550 °C. 6M HCl was added to dissolve the sample, and water added to make it up to 50ml. The sample then went through a TRAACS machine for phosphorus analysis, with the result displayed as % phosphorus content (pers. comm. Roslin Institute).

4.3.10. Experimental design

In the first year of study, 37 female grouse were caught and tagged on South Drumochter, 18 were anthelmintic treated and 19 were given water as a control. In the second year of study, 52 female grouse were caught and tagged on South Drumochter, 26 were anthelmintic treated and 26 given water as controls. No grouse from the previous year were included.

Twenty of these birds were intensively radio tracked to establish the location of their home ranges, the remaining birds were tracked less intensively. Once a mean location for each grouse had been established, birds were randomly allocated to fertiliser treatment group, and fertiliser was applied to areas within the home range of half the birds. The rest were considered controls. This gave a factorial experimental design, with four experimental groups:

1. anthelmintic treated, with fertiliser
2. anthelmintic treated, no fertiliser
3. control, with fertiliser
4. control, no fertiliser

In the last year of study, 63 female grouse were caught and tagged on Crubenmore, of which 34 were anthelmintic treated and 23 were given infective *T. tenuis* larvae. Another 6 grouse received no treatment, and these were not included in the analysis. Fertiliser was applied to areas on the moor the previous autumn and birds were allocated to the fertiliser treatment groups using the distance from their nest to the nearest experimental plot. There were four experimental groups:

1. anthelmintic treated, with fertiliser
2. anthelmintic treated, no fertiliser
3. infective larvae treated, with fertiliser
4. infective larvae treated, no fertiliser

4.3.11. Statistical Analysis

Data were analysed with Minitab 11 and Statistica 5.0. All results of statistical tests were tested for normality using an Anderson Darling normality test. Breeding production data from 1996 were analysed separately as only one manipulation (of parasites) took place in 1996. Data from 1997 and 1998 were combined for analysis of breeding production to give larger sample sizes, with parasite manipulations treated as worms (controls in 1997, larvae dosed in 1998) or no worms (anthelmintic dosed in 1997 and 1998).

4.4. Results

4.4.1. Did treatment influence worm burdens?

Dosing with anthelmintic significantly decreased the worm burdens of grouse compared to controls and non-experimental grouse shot in 1996 (GLM $F_{2,19} = 8.82$, $P = 0.002$, Figure 4.1.).

No such comparison could be made for either 1997 or 1998 since no control birds were shot during the 1997 grouse shooting season, and only one dosed bird and one wormed bird were shot during the 1998 season. However, worm egg counts performed on caecal faeces collected from experimentally treated grouse in June 1998 showed no difference in number of eggs per gram with treatment groups (GLM $F_{1,13} = 0.10$, $P = 0.763$), although this technique is considered unreliable for the accurate quantification of *T. tenuis* burdens (Hudson & Dobson 1997).

4.4.2. The effect of fertiliser treatment on growth and nutrient content of heather

There was no difference in the mean number of heather shoots grown between the three treatment groups throughout the growing season (two way repeated measures ANOVA $F_{2,12} = 0.977$, $P = 0.404$, Table 4.1.). The number of shoots varied significantly with time ($F_{3,36} = 17.485$, $P < 0.001$) but there was no interaction between time and treatment ($F_{6,36} = 0.528$, $P = 0.783$). There was a significant effect of fertiliser treatment on growth increment (in mm) during the growing season (two way repeated measures ANOVA $F_{2,11} = 7.2$, $P = 0.008$, Table 4.2.). This effect also varied significantly with time ($F_{5,60} = 6.6$, $P < 0.001$), and there was only a weak interaction between the effects ($F_{10,60} =$, $P = 0.100$). These effects were greater during the earlier part of the growing season (Figure 4.2.).

A Tukey HSD test showed that treatment effects were due to both 50g and 100g fertiliser treatment ($P = 0.038$ and $P = 0.004$ respectively). Both treatment groups of 50g (10.5g nitrogen) and 100g (21g nitrogen) significantly increased the protein content of the heather on those sites by October 1996 ($F_{2,13} = 8.99$, $P = 0.005$, Table 4.3.). A significant difference in protein content between heather of the three treatment groups could still be found by May 1997, with these treatment groups again increasing protein content ($F_{2,14} = 6.73$, $P = 0.011$, Table 4.3.).

Table 4.1. Mean values of number of heather shoots grown (± 1 SE) in experimental plots on marked plants in 1996, for three experimental groups.

Date of count	Control	50 g Fertiliser	100 g Fertiliser
23 May 1996	0.98 ± 0.418	3.27 ± 1.60	5.51 ± 2.15
4 June 1996	3.91± 1.23	5.33 ± 1.52	6.51 ± 2.22
18 June 1996	4.78 ± 1.10	6.39 ± 1.96	8.09 ± 2.34
4 July 1996	4.82 ± 1.34	6.22 ± 1.95	7.62 ± 2.16

Table 4.2. Mean values of heather shoot height in millimetres (± 1 SE) measured on plots in 1996 for three experimental groups. All groups n = 9. The difference between means at each measurement is growth increment.

Date measured	Control	50g Fertiliser	100g Fertiliser
15th March (last years growth)	24.16 ± 4.75	33.82 ± 7.37	36.20 ± 3.59
15th April	26.08 ± 4.22	41.64 ± 9.82	45.32 ± 3.73
15th May	28.24 ± 4.17	49.8 ± 10.90	50.46 ± 4.02
15th June	29.36 ± 4.33	53.3 ± 11.60	55.43 ± 5.06
15th July	30.22 ± 4.63	55.40 ± 11.80	58.74 ± 5.53
15th August	31.86 ± 5.42	57.20 ± 12.50	65.40 ± 6.27
15th September	31.98 ± 5.41	58.40 ± 12.00	68.02 ± 7.38

Table 4.3. Mean values of protein concentration in heather (± 1 SE) collected from plots in three experimental groups from 1996.

Date measured	Control	50g Fertiliser	100g fertiliser
October 1996	6.780 ± 0.255	7.597 ± 0.278	8.262 ± 0.238
May 1997	7.334 ± 0.185	8.288 ± 0.363	8.724 ± 0.244

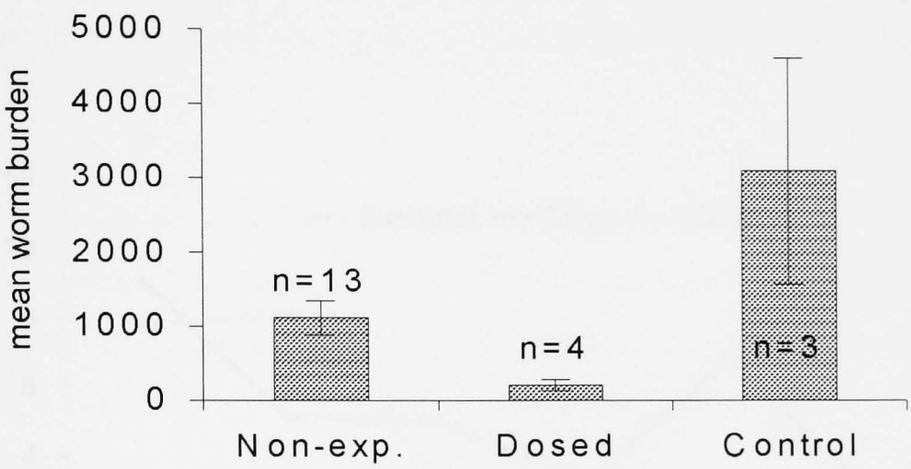

Figure 4.1. Mean worm burdens (±1SE) for three treatment groups of red grouse shot in 1996.

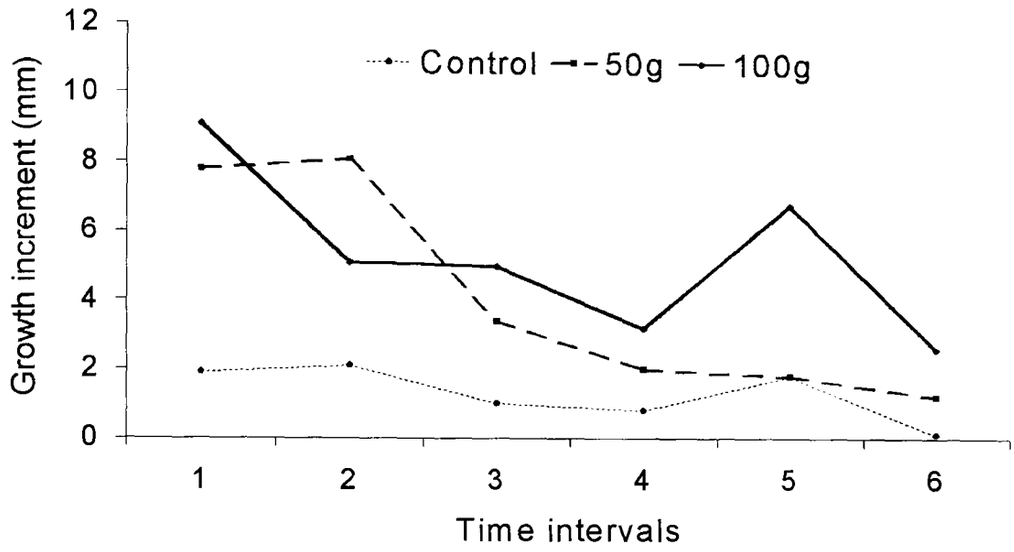

Figure 4.2. Effect of fertiliser on growth of heather for three treatment groups in 1996. Time intervals are as follows: 1. 15 March – 15 April; 2. 15 April – 15 May; 3. 15 May – 15 June; 4. 15 June – 15 July; 5. 15 July – 15 August; 6. 15 August – 15 September.

In 1997, fertilised plots on South Drumochter showed a tendency to have grown more in height by the end of the growing season with the mean height on fertilised plots at 43.83 mm (± 2.05 n = 3) and 25.55 mm (± 7.01 n = 3) on control plots (GLM $F_{1,5} = 6.26$, $P = 0.067$). Protein content was increased by fertiliser treatment throughout the growing season (two way repeated measures ANOVA $F_{1,4} = 15.247$, $P = 0.017$) and although this did not vary with time ($F_{3,12} = 2.566$, $P = 0.103$) there was an interaction between time and treatment ($F_{3,12} = 6.192$, $P = 0.008$).

In 1998 on Crubenmore, fertilised areas were visibly greener in appearance than control areas by May 1998. There was also more visible evidence of grazing having taken place on fertilised areas. There was a significantly greater biomass of young heather on fertilised than control areas (GLM $F_{1,39} = 4.19$, $P = 0.048$, Table 4.4.), and protein content was higher in fertilised heather throughout the spring and summer of 1998 (GLM March $F_{1,10} = 153.86$, $P < 0.001$; May $F_{1,8} = 40.66$, $P < 0.001$; July $F_{1,29} = 45.48$, $P < 0.001$, Table 4.4, Figure 4.3.).

The amount of grazing by sheep and other herbivores (including grouse) was greater on sites that had been fertilised, than on control areas (GLM on square-root transformed data $F_{1,39} = 100.05$, $P < 0.001$, Table 4.4.). Grouse usage of the sites was higher on fertilised than control areas, as the dry weight of grouse faeces (fibrous) collected was significantly greater from fertilised areas (GLM on square root transformed data with biomass of young heather as a covariate $F_{1,39} = 6.86$, $P = 0.013$, Table 4.4, Figure 4.4.).

Table 4.4. Mean values (± 1 SE) of variables measured on Crubenmore in 1998. n = 20 unless stated otherwise.

Variable measured	Fertilised	Control
Biomass of young heather (g)	143.70 ± 11.80	104.30 ± 15.20
Protein content – March	9.54 ± 0.22 n = 5	6.32 ± 0.15 n = 6
Protein content – May	10.87 ± 0.46 n = 4	6.98 ± 0.41 n = 5
Protein content – July	11.10 ± 0.23 n = 17	8.84 ± 0.25 n = 13
Grazed heather tips	82.55 ± 9.07	12.00 ± 1.71
Fibrous faeces (g)	40.71 ± 7.28	23.35 ± 7.45

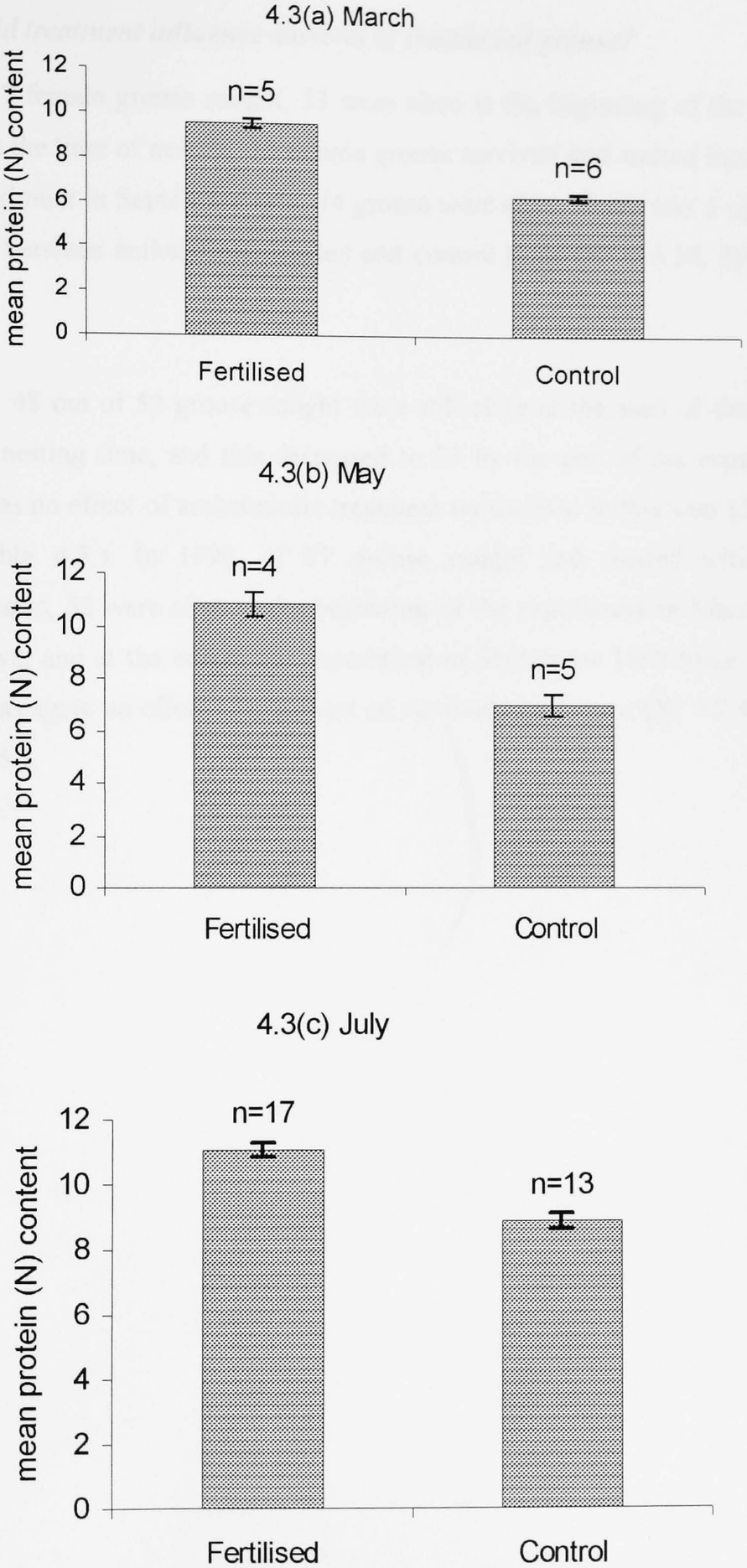

Figure 4.3. Protein (N) concentration in heather (±1SE) on fertilised and control areas, during (a) March, (b) May and (c) July 1998. n = sample size.

4.4.3. Did treatment influence survival of female red grouse?

Of the 37 female grouse caught, 33 were alive at the beginning of the experiment in March 1996. At the time of nesting, 30 female grouse survived and started incubating. By the end of the experiment in September 1996 14 grouse were alive. There was a significant difference in survival between anthelmintic treated and control birds ($X^2 = 5.34$, $Df = 1$, $P = 0.05$, Table 4.5.).

In 1997, 48 out of 52 grouse caught were still alive at the start of the experiment, 36 were alive at nesting time, and this decreased to 25 by the end of the experiment in September. There was no effect of anthelmintic treatment on survival in this year ($X^2 = 0.01$, $Df = 1$, $P > 0.05$, table 4.5.). In 1998, of 57 grouse caught and treated with infective larvae or anthelmintic, 52 were alive at the beginning of the experiment in March. At nesting time 43 were alive, and at the end of the experiment in September 1998 there were 28 grouse alive. There was again no effect of treatment on survival in this year ($X^2 = 2.44^{-03}$, $Df = 1$, $P > 0.05$, Table 4.5.).

Table 4.5. Number of grouse surviving at the start of the experiment, at nesting time and at the end of the experiment in August before the shooting season, for grouse with worms and without worms.

	Worms	No worms
1996 start	16	17
1996 nest	15	15
1996 end	11	3
1997 start	25	23
1997 nest	18	18
1997 end	13	12
1998 start	21	31
1998 nest	17	26
1998 end	12	16

4.4.4. Did treatment increase breeding production?

There was no effect of treatment with anthelmintic on clutch size (GLM $F_{1,28} = 1.08$, $P = 0.308$, Table 4.6.), hatching date (GLM on Log 10 transformed data $F_{1,24} = 0.61$, $P = 0.444$, Table 4.6.) or hatching success (GLM on Log 10 transformed data $F_{1,28} = 0.05$, $P = 0.833$, Table 4.6.). There was no effect of treatment on the number of chicks surviving at 3-6 days, 9-12 days and at the final count (two way repeated measures ANOVA $F_{1,35} = 0.745$, $P = 0.393$, Table 4.6.), no effect of time ($F_{2,70} = 1.96$, $P = 0.147$) and no interaction between time and treatment ($F_{2,70} = 1.13$, $P = 0.326$).

However there was an effect of treatment on the percentage of chicks surviving from clutch to 3-6 days, 9-12 days, and the final count (two way repeated measures ANOVA $F_{1,35} = 4.89$, $P = 0.033$, Table 4.6., Figure 4.5.) and also an effect of time ($F_{2,70} = 5.57$, $P = 0.005$) but no interaction between time and treatment ($F_{2,70} = 0.25$, $P = 0.773$). A Tukey HSD test showed that chicks of anthelmintic treated female grouse had greater survival to 9-12 days ($P = 0.04$) and at the final count ($P = 0.006$).

With the 1997 and 1998 data combined there was no effect of either treatment on clutch size (GLM on X^2 transformed data Worms $I_{1,76} = 0.19$, $P = 0.662$, Fertiliser $F_{1,76} = 0.18$, $P = 0.669$, Interaction $F_{1,76} = 0.32$, $P = 0.575$, Table 4.7.), hatching date (GLM on Log 10 transformed data Worms $F_{1,65} = 0.00$, $P = 0.980$, Fertiliser $F_{1,65} = 0.59$, $P = 0.447$, Interaction $F_{1,65} = 0.28$, $P = 0.601$, Table 4.7.) or hatching success (GLM on Log 10 transformed data Worms $F_{1,66} = 1.38$, $P = 0.244$, Fertiliser $F_{1,66} = 1.01$, $P = 0.320$, Interaction $F_{1,66} = 0.22$, $P = 0.644$, Table 4.7.).

Table 4.6. Mean values for red grouse breeding production parameters (±1SE) for birds treated with anthelmintic (no worms) and controls (worms) in 1996, Sample sizes given in brackets.

Breeding parameter	Worms (controls)	No worms	Signif.
Clutch	8.53 ± 0.36 (15)	8.07 ± 0.22 (14)	$P = 0.308$
Hatch Date (julien)	157 ± 2.33 (13)	155 ± 0.78 (12)	$P = 0.444$
Hatching Success	76.39 ± 9.90 (15)	84.91 ± 9.7 (14)	$P = 0.833$
Chicks surviving at 3-6 days	5.77 ± 0.82 (13)	6.60 ± 0.47 (10)	$P = 0.393$
Chicks surviving at 9-12 days	4.25 ± 0.69 (12)	5.60 ± 0.51 (10)	$P = 0.393$
Chicks surviving at final count	3.75 ± 0.71 (12)	4.88 ± 0.58 (8)	$P = 0.393$
% survival clutch - 4 days	65.26 ± 8.21 (13)	84.88 ± 6.76 (9)	$P = 0.033$
% survival clutch - 10 days	48.83 ± 7.67 (12)	71.52 ±8.34 (9)	$P = 0.033$
% survival clutch - final	43.37 ± 8.21 (12)	60.83 ± 9.01 97)	$P = 0.033$

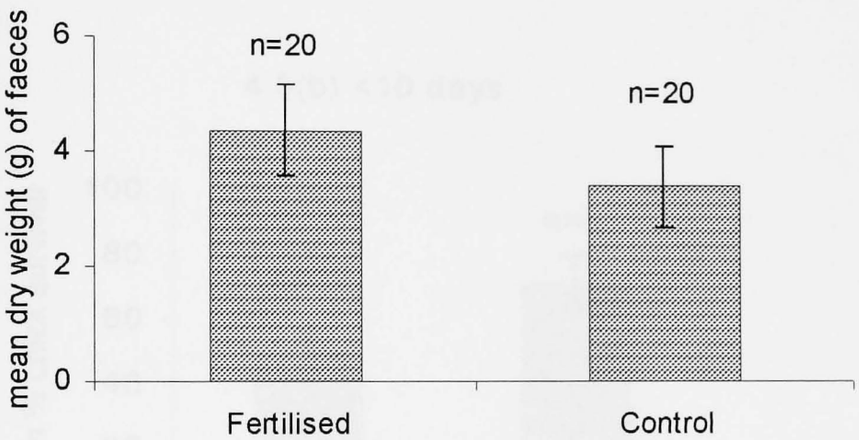

Figure 4.4. Mean dry weight of grouse faeces (±1SE) on fertilised and control areas. n = sample size.

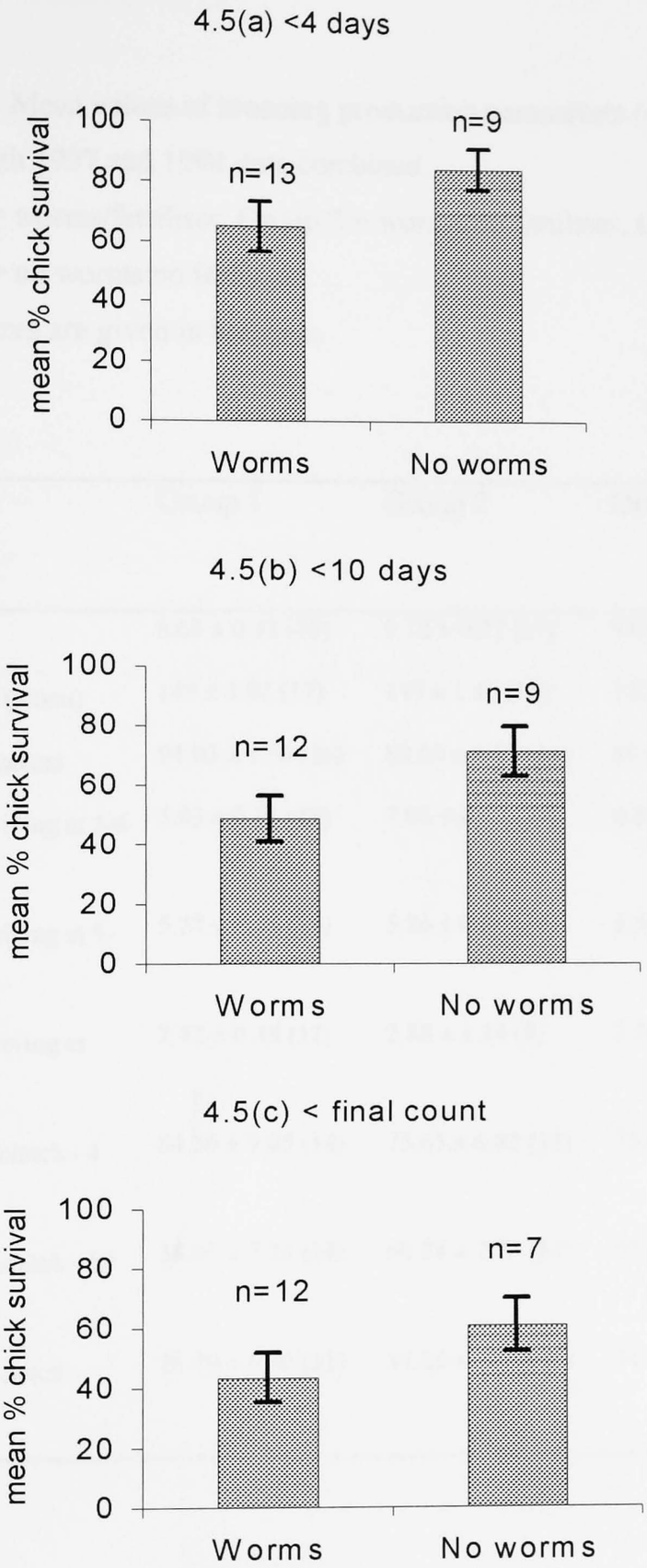

Figure 4.5. Percentage chicks surviving (±1SE) from (a) clutch to 4 days, (b) clutch to ten days and (c) clutch to final count in two treatment groups of female grouse in 1996.
n = sample size.

Table 4.7. Mean values of breeding production parameters (±1SE) for the four experimental groups with 1997 and 1998 data combined.

Group 1 = worms/fertiliser, Group 2 = worms/no fertiliser, Group 3 = no worms/fertiliser, Group 4 = no worms/no fertiliser.

Sample sizes are given in brackets.

Breeding parameter	Group 1	Group 2	Group 3	Group 4
Clutch	8.63 ± 0.42 (16)	9.12 ± 0.27 (17)	9.00 ± 0.21 (17)	8.94 ± 0.29 (17)
Hatch Date (julien)	149 ± 1.82 (17)	149 ± 1.46 (14)	150 ± 1.16 914)	147 ± 2.16 9 (11)
Hatching Success	94.03 ± 1.56 (16)	88.84 ± 5.93 (14)	89.49 ± 5.79 (14)	86.72 ± 7.31 (13)
Chicks surviving at 3-6 days	5.93 ± 0.81 (15)	7.08 ± 0.77 (13)	6.50 ± 0.74 (12)	6.00 ± 1.05 (7)
Chicks surviving at 9-12 days	5.27 ± 0.61 (15)	5.86 ± 0.86 (14)	5.55 ± 0.76 (11)	4.14 ± 0.91 (7)
Chicks surviving at final count	2.42 ± 0.48 (12)	2.88 ± 1.14 (8)	3.70 ± 0.79 (10)	1.80 ± 0.80 (5)
% survival clutch - 4 days	64.36 ± 9.05 (14)	75.65 ± 6.82 (13)	73.42 ± 7.61 (12)	71.23 ± 11.24 (7)
% survival clutch - 10 days	58.63 ± 7.23 (14)	60.88 ± 7.75 (14)	61.90 ± 7.71 (11)	48.73 ± 9.52 (7)
% survival clutch - final	28.59 ± 6.36 (11)	31.25 ± 12.51 (8)	41.56 ± 8.64 (10)	21.11 ± 9.69 (5)

There was a tendency for anthelmintic treated grouse to have a greater number of chicks surviving at 3-6 days, 9-12 days and at the final count (3 way repeated measures ANOVA $F_{1,75} = 3.821$, $P = 0.054$, Table 4.7., Figure 4.6.) but there was no effect of fertiliser treatment ($F_{1,75} = 0.881$, $P = 0.350$). Chick survival varied significantly with time ($F_{2,150} = 5.615$, $P = 0.004$). There was no interaction effect between the two treatments ($F_{1,75} = 0.219$, $P = 0.641$) nor any interaction between time and treatment ($F_{2,150} = 0.243$, $P = 0.783$).

Anthelmintic treatment had no effect on the percentage of chicks surviving from clutch to 4 days, clutch to 10 days, or clutch to final count (3 way repeated measures ANOVA $F_{1,74} = 1.078$, $P = 0.302$) as had fertiliser treatment ($F_{1,74} = 0.093$, $P = 0.760$). There was an effect of time ($F_{2,150} = 5.956$, $P = 0.003$). There was no interaction effect between the two treatments ($F_{1,74} = 1.077$, $P = 0.302$) and no interaction between time and treatment ($F_{2,150} = 0.152$, $P = 0.858$). There was no effect of year or moor in any of the above and so these factors were removed from the model.

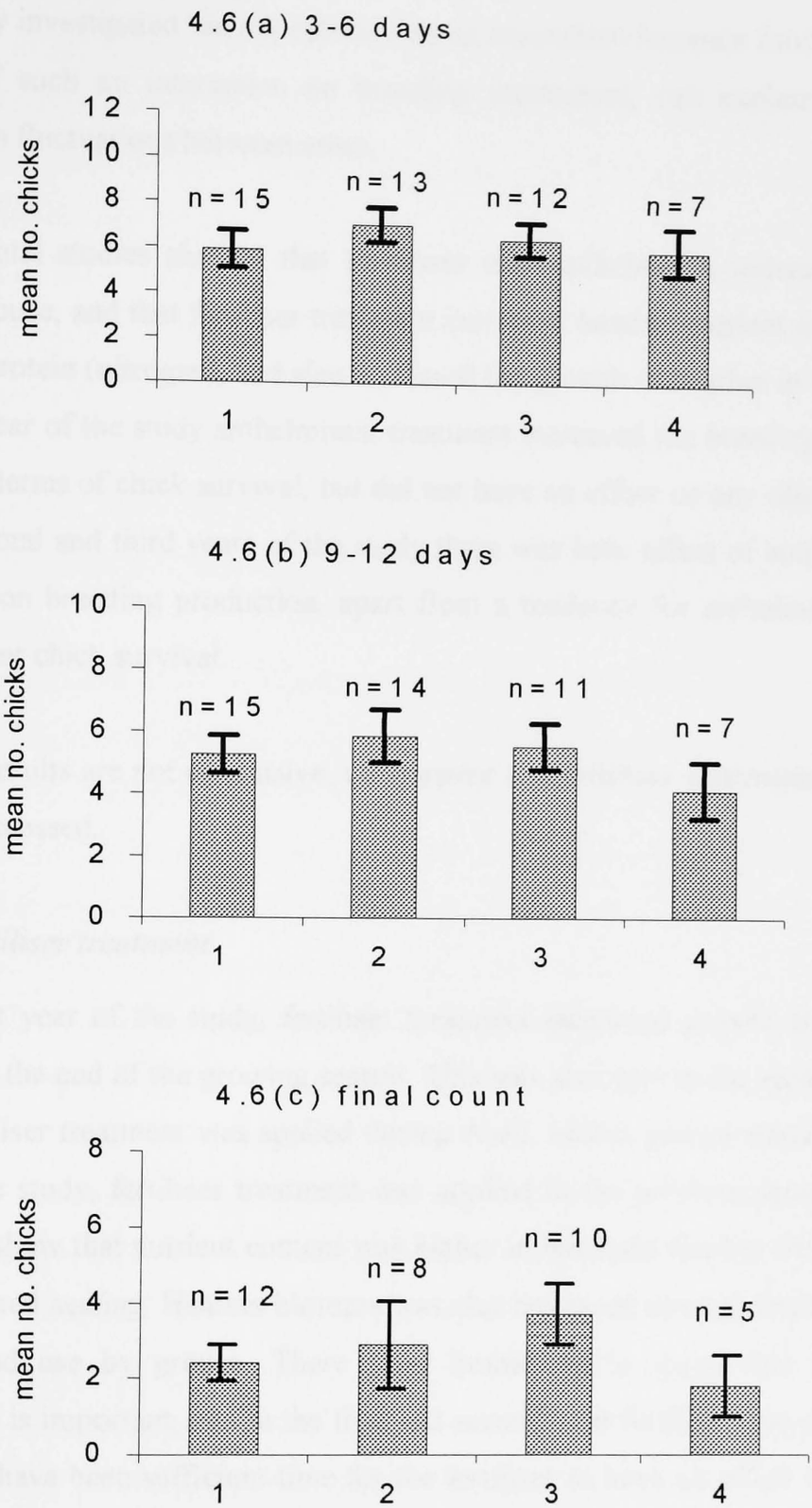

Figure 4.6. Number of chicks surviving (±1SE) at (a) 3-6 days, (b) 9-12 days and (c) final count in 4 experimental groups of female grouse in 1997 and 1998.

n = sample size. Group 1 = worms/fertiliser, Group 2 = worms/no fertiliser, Group 3 = no worms/fertiliser, Group 4 = no worms/no fertiliser

4.5. Discussion

This study investigated the hypothesis that an interaction between food and parasites, and the effects of such an interaction on breeding production, can explain variations in grouse population fluctuations between areas.

Experimental studies showed that treatment with anthelmintic reduced parasite burdens of female grouse, and that fertiliser treatment increased heather nutrient content significantly, in terms of protein (nitrogen), and also increased the growth of heather in height and biomass. In the first year of the study anthelmintic treatment increased the breeding production of female grouse in terms of chick survival, but did not have an effect on any other breeding parameter. In the second and third years of the study there was little effect of anthelmintic and fertiliser treatment on breeding production, apart from a tendency for anthelmintic treated grouse to have greater chick survival.

As these results are not conclusive, the parasite and fertiliser treatments and their effects will now be discussed.

4.5.1. Fertiliser treatment

In the first year of the study, fertiliser treatment increased growth and nutrient content of heather by the end of the growing season. This was also true in the second year. In both these years fertiliser treatment was applied during April, before grouse started nesting. In the final year of the study, fertiliser treatment was applied in the previous autumn. Results from the final year show that nutrient content was higher in fertilised heather from March, well before grouse started nesting. Heather biomass was also increased through fertiliser treatment, as was grazing and use by grouse. There were limitations in using this treatment. Timing of application is important, and in the first and second year fertiliser was applied in April which would not have been sufficient time for the fertiliser to have an effect on heather growth and nutrient content before grouse started nesting. This problem was overcome in the final year by applying the fertiliser in the previous autumn, so that nutrient content of heather had improved even before the growing season began.

4.5.2. Effects of fertiliser treatment on breeding production of grouse

Fertiliser treatment had no effect on any aspect of breeding production in either the second or final year of the study. This was probably due to a timing effect in the second year, with fertiliser treatment being applied too late to have an effect on the female grouse. The failure of fertiliser treatment to have an effect on breeding production in the final year can presumably be attributed to the location of fertiliser treatment areas. As fertiliser was applied in the previous autumn to ensure improvement of heather quality by the spring of the final year, these areas could not be located within the home range of individual grouse and were randomly placed instead. When grouse were caught and tagged in the final year it was not possible to ensure that they were grouse that would use these areas. In both 1997 and 1998 it was difficult to know if fertilised areas were large enough and utilised enough by female grouse to influence their diet during the breeding season when nutrients are most important.

Although the effect of the fertiliser treatment was to increase protein (nitrogen) content, and growth in height and biomass, these may not be the limiting factors for grouse. Grouse have been shown to feed selectively on heather that is high in nitrogen and phosphorus content (Moss *et al* 1975, Savory 1983), but in this case the fertiliser may not have improved the heather in a suitable manner. An increase in biomass or growth in height is not really important in terms of feeding for grouse, as it is young new shoots they prefer, although an increase in the biomass of young heather may be beneficial to them during winter when the heather is not growing.

Fertilising heather has the effect of improving heather quality in ways that could influence the breeding production of grouse. According to Jenkins *et al* (1967), food may influence the breeding production of grouse in three ways: heather growth in summer which determines the amount of green heather in winter; heather browning in winter; timing of heather growth in spring. Fertiliser treatment has been shown in this study to increase heather growth in summer, therefore increasing the amount of green heather available during the winter. As heather growth in summer is significantly correlated with breeding success of grouse (Jenkins *et al* 1967) fertiliser should also have the effect of improving breeding production. Heather browning in winter has not been estimated in this study, but it can be assumed that if fertiliser treatment leads to more green heather in winter, then heather browning will not be of such a consequence to grouse. Timing of heather growth in spring is brought forward by fertiliser

treatment (Moss *et al* 1975), therefore increasing the amount of food available for female grouse. Whether fertiliser treatment has the effect of improving the nutrient content of heather, or of increasing the amount of heather available in spring, it is beneficial to female grouse for the breeding season after fertiliser application and for 1-2 years subsequent to this (Watson *et al* 1984) although the nutrient content will get lower.

4.5.3. Parasite treatment

In the first year of the study, treatment with anthelmintic reduced the worm burdens of radio tagged female grouse, in agreement with Hudson (1986, Hudson 1992, Hudson *et al* 1992). Treatment with infective *T. tenuis* larvae in the final year did not appear to increase parasite burdens, although treating grouse in this way has previously been carried out successfully on captive grouse (Wilson 1979). That grouse were not found to be infected with *T. tenuis* could be due to sampling error. Samples for faecal analysis were collected from some, but not all, grouse treated with infective larvae and it may be the case that these were not truly representative. The McMaster egg counting technique used to establish levels of *T. tenuis* infection can be unreliable in determining actual levels of parasite infection due to high variation in egg counts. Furthermore, the infective larvae may not have been viable at the time they were used to treat grouse, although this is highly unlikely as they were rigorously checked to ensure they were alive. A trickle dose of infective larvae may have been more successful in establishing an infection in the grouse, rather than one large single dose, but was not feasible in this study.

4.5.4. Effects of parasite treatment on breeding production of grouse

Results show that in the first year of the study, anthelmintic treated grouse had more chicks surviving that control grouse, and in the second and final years this was also true. There was no effect of anthelmintic treatment on clutch size, hatching success or chick survival. Other effects have probably muted these effects. On South Drumochter during the first two years of the study, natural parasite burdens were lower than they had been previously, therefore control grouse that were given water would not have had the expected high levels of *T. tenuis* infection. This would result in there not being a large enough difference in parasite burdens between anthelmintic treated and control grouse to show a significant effect on all breeding production parameters. Parasite burdens estimated from grouse shot in August in the first year of the study may not truly represent the actual level of parasite infection in the population at

the time of nesting. The same argument may relate to *T. tenuis* infections estimated in the final year from faecal samples collected from nest sites after chicks had hatched. The final year remains the most unclear, due to the uncertainty of the success of treatment with infective *T. tenuis* larvae. The procedure performed should have left grouse infected with approximately 3500 adult worms, enough to have a deleterious effect on breeding production. Crubenmore had low levels of natural parasite infection in this year, and although this would not have affected control grouse as they were the ones given anthelmintic, if treatment with infective larvae was not a success then there would be no difference in parasite burdens between the two groups of grouse.

Treatment with anthelmintic to remove parasites has been shown to improve breeding production of female grouse in numerous replicated studies (Hudson 1986, Hudson *et al* 1992). This is also true of captive grouse where infection with parasites reduced breeding production of female grouse (Wilson 1979, Shaw & Moss 1990). Experiments on captive grouse are of interest, but the results cannot be applied directly to wild grouse as they have a different caecal structure from captive grouse (Moss 1972). Although treatment with infective larvae was successful in captive grouse, the fact that wild grouse have a different caecal structure may explain why this procedure was not successful in this study.

4.5.5. Parasite-food interaction

Results from this study show that there was no interaction between anthelmintic treatment and fertiliser treatment on the breeding production of grouse. This is not surprising given that these treatments on their own did not influence most of the breeding production parameters, and even where anthelmintic treatment showed a tendency for increasing the survival of chicks, there was no effect of fertiliser treatment on chick survival. Placement and timing of fertiliser application, low natural parasite burdens and unsuccessful infection with *T. tenuis* are probable reasons for no interaction between food and parasites being found.

4.5.6. Effects at population level

The effects of *T. tenuis* on the breeding production of grouse have previously been shown to be both sufficient and necessary to cause cyclic population fluctuations (Dobson & Hudson 1992, Hudson *et al* 1998). Variation in food quality, although affecting breeding production of grouse, has not been sufficient to explain population declines (Watson *et al* 1984). The aim

of this study was to investigate the interaction between food and parasites, and to use the results to explain variations in grouse population fluctuations.

The results from this study were unable to replicate previous studies so no conclusions could be drawn or comment made on the occurrence of a food-parasite interaction.

4.5.7. Future work

While the experimental design used in this study failed, there could well be an interaction between food and parasites. To test the hypothesis that a food-parasite interaction influences breeding production and can explain variations between grouse population fluctuations a larger-scale experiment is needed. Using a grouse moor with known high parasite burdens and fertilising large areas of moor would reduce the chances of the experiment failing to show a difference between the experimental groups, and ensure that the treatments carried out would be successful. To complete this investigation, the experiment would have to be replicated on several grouse moors.

In summary, although treatment with anthelmintic reduced parasite burdens and fertiliser treatment improved the quality of heather, these treatments did not influence breeding production of grouse. This was considered a consequence of limitations in the experimental design. As the experimental results of this study are inconclusive, it is not possible to say if this interaction is sufficient to account for the differences in red grouse population fluctuations, or to refute the null hypothesis.

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CHAPTER 5

ESTIMATING HEATHER BIOMASS - A SIMPLE TECHNIQUE

5.1. Introduction

Grouse moors cover approximately 1.5 million hectares of Britain, and are an important land use in many upland areas. The majority of this area is heather moorland, dominated by heather *Calluna vulgaris* (Hudson & Watson 1985). Heather moorland supports a wide range of flora and fauna and is considered to be a diverse and important habitat. As well as red grouse, heather moorland provides grazing for sheep, red deer, mountain hares and in some places cattle. These herbivores feed to varying degrees on the current year's growth of heather (Miller 1979).

Maintaining heather moorland requires regular and careful muirburn balanced with optimal grazing, and the maintenance of this heather sward is central to the management of red grouse (Thompson *et al* 1995). The aim of grouse moor management is to produce heather stands of mixed age which provide food (young shoots) and cover (young and old shoots) for red grouse (Hudson & Newborn 1995).

Many varied techniques for estimating the biomass of vegetation have been used in ecological research to examine several different variables such as fire behaviour, crop productivity, grazing potential, regeneration and site productivity (Catchpole & Wheeler 1992).

Determining the relative proportions of young and old heather biomass should provide a measure of the productivity of an area through biomass gain and also give an indication of grazing pressure (Moss 1969). Obviously grouse will be directly influenced by the complete removal of heather since it is their main food plant and essential for grouse persistence (Hudson 1992), but they may also be influenced by more moderate levels of grazing.

Being able to estimate biomass of heather would be a useful tool in grouse moor management, for determining stocking rates and intensity of muirburn. Biomass of heather may also prove useful in partly explaining density and breeding success of red grouse (Moss *et al* 1975). The aim of this study was to provide a simple technique for estimating the biomass of heather in the field.

5.2. Methodology

5.2.1. Study areas

Samples were measured and collected from three different moors within Ralia Estates in the Scottish highlands. These were Crubenmore (NN6487 O.S. 1:50 000 Sheet 42), South Drumochter (NN6479 O.S. 1:50 000 Sheet 42), and Ralia (NN7397 O.S. 1:50 000 Sheet 35).

5.2.2. Measuring technique

Heather was measured on thirty areas of 1 m^2, chosen at random and included a variety of heather of different height, age and cover. A 1 m^2 grid, with string forming gridlines crossing at forty five points within a bamboo frame, was placed on the vegetation and measurements recorded at the points where gridlines crossed within the quadrat. Measurements were taken with the assistance of a bamboo cane marked with lines at 5cm intervals and with a 1 cm white band at the base. The measurements recorded at each point were height of heather, number of young (last year's growth) shoots touching the cane, number of old (previous years' growth and woody stems) shoots touching the cane, and visibility of the white band at the base of the cane (when holding the cane at arms length). When all measurements had been recorded, vegetation within the quadrat was cut down to moss level and collected.

5.2.3. Heather biomass

Vegetation collected from each of the thirty quadrats was weighed to give a measure of total biomass. The vegetation from each quadrat was then subsampled, with subsamples representing between 2 and 30% of the total biomass in each case. The variation in size of subsample was due to the differing amounts of vegetation collected, which were very large in some cases.

These subsamples were then sorted into categories of young and old (including woody) heather, and other plant species. These were weighed to give the biomass of young and old heather and other plants in each subsample, and then to work out the biomass of these in the whole of each sample.

5.2.4. Statistical analysis

Data were analysed using Minitab 11. All results of statistical tests were tested for normality using an Anderson Darling normality test. Regression analyses were performed on the data to produce regression equations for predicting biomass of heather from the measurements taken.

5.3. Results

Samples of vegetation collected ranged from 265g to 2570g in biomass. Multiple regression analyses were undertaken using the variables listed in Table. 5.1.

Variables which were not significant within the regression analyses were removed and the following regression equation explained 80.3 % of the variation in total biomass of heather ($r^2 = 80.3$, $F_{4,29} = 30.46$, $P < 0.001$).

Total biomass = -1179 - 1339 log % touch + 480 log young + 1116 log old + 1407 log ht

Where log % touch = log 10 % touches (% of cases where heather touched the cane)

log young = log 10 number of young touches

log old = log 10 number of old touches

log ht = log 10 mean height

The biomass of young heather alone could be predicted by the regression equation below, which has an R^2 value of 51.2 % ($r^2 = 51.2$, $F_{1,29} = 31.42$, $P < 0.001$).

Biomass of young heather = - 9.6 + 2.02(number of young touches)

Similarly the biomass of old heather (including woody stems) could be predicted. This regression equation explains 95.8 % of the variation in the biomass of old heather ($r^2 = 95.8$, $F_{3,29} = 220.55$, $P < 0.001$).

Biomass of old heather = -449 + 5.37 % touch - 2.40 young + 0.945 total biomass

Where % touch = % touches (% of cases where heather touched the cane)

young = number of young touches

Table 5.1. Variables of heather measured in the field and their description

Variable	Description
height	mean height of heather within the quadrat
old touches	total number of old shoots touching the cane
young touches	total number of young shoots touching the cane
% touches	% of cases where heather touched the cane
% tip visible	% of cases where the cane base was visible

5.4. Discussion

The aim of this study was to provide a simple technique for estimating biomass of heather in the field. Regression analyses performed on data collected in the field provided regression equations for predicting the total biomass of heather in an area, the biomass of young heather and the biomass of old heather. These equations may prove helpful in assessing productivity of heather on grouse moors, and maybe to the management of grouse moors in terms of the frequency of muirburn and/or the level of grazing pressure that should be undertaken to maintain the heather sward.

One limitation of the technique is that although the methodology was developed using small areas of heather, in practice heather biomass will be estimated over large areas of moorland. This will introduce some error into the estimation of a moor's heather productivity but may allow grouse managers to focus grazing and muirburn practices on specific areas. Indeed, this technique has already been used by the Game Conservancy Trust to provide data on heather productivity, cover and grazing pressure (Smith *et al* 1999) and for calibration of remotely sensed data (Egan *et al* 2000). The technique is also used in Chapter 4 of this thesis to investigate whether fertiliser treatment increases biomass of heather.

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CHAPTER 6

FOOD-PARASITE INTERACTION: - MODELLING THE POPULATION DYNAMICS

6.1. Introduction

Previous studies have shown that the caecal nematode *Trichostrongylus tenuis* can be negatively associated with breeding production of red grouse *Lagopus lagopus scoticus* (Hudson 1986, Hudson *et al* 1992). There is also evidence to suggest that parasites interact with food (and area) to have an effect on breeding production (Chapter 2). The ideal way to examine how these two factors interact is through a series of experimental studies although greater insight into the system may be obtained through a modelling approach.

To explore how this interaction could influence the population dynamics of red grouse and in particular how these interactions would influence population cycle period between areas (Hudson 1992), a dynamic population model approach was applied.

The fundamental model that captured the population dynamics of helminth parasites and their hosts was derived initially by Anderson and May (Anderson & May 1978, May & Anderson 1978). In essence this is a Lotka-Volterra based model (summarised in Begon *et al* 1996) that has specifically been designed to incorporate the features of the parasite-host system, in particular the parasite-induced reduction in host fecundity and the aggregated nature of parasites within their host population.

Dobson and Hudson (1992) refined this model to make it more applicable to the grouse-*T. tenuis* system by incorporating an equation which described the dynamics of the free-living stages and the role of arrested larval development. Figure 6.1. and Table 6.1. illustrate the various birth and death rates of both the grouse and *T. tenuis* populations and the flow rates between the different stages of the life cycle of the parasite.

Dobson & Hudson (1992) found from using their model that population cycles are generated when there is a relatively large impact of parasites on the breeding production of the grouse relative to the effects on survival. In such circumstances parasite burdens build up, reduce fecundity and destabilise the parasite-host interaction.

I postulate that if food quality is going to interact with the parasites then as the food quality gets worse so the effects of the parasite will increase the relative impact of the parasites although at the same time the natural fecundity rate will be related to food quality and be reduced as food quality gets worse. This was explored in the model by running a series of simulations where these two variables were altered.

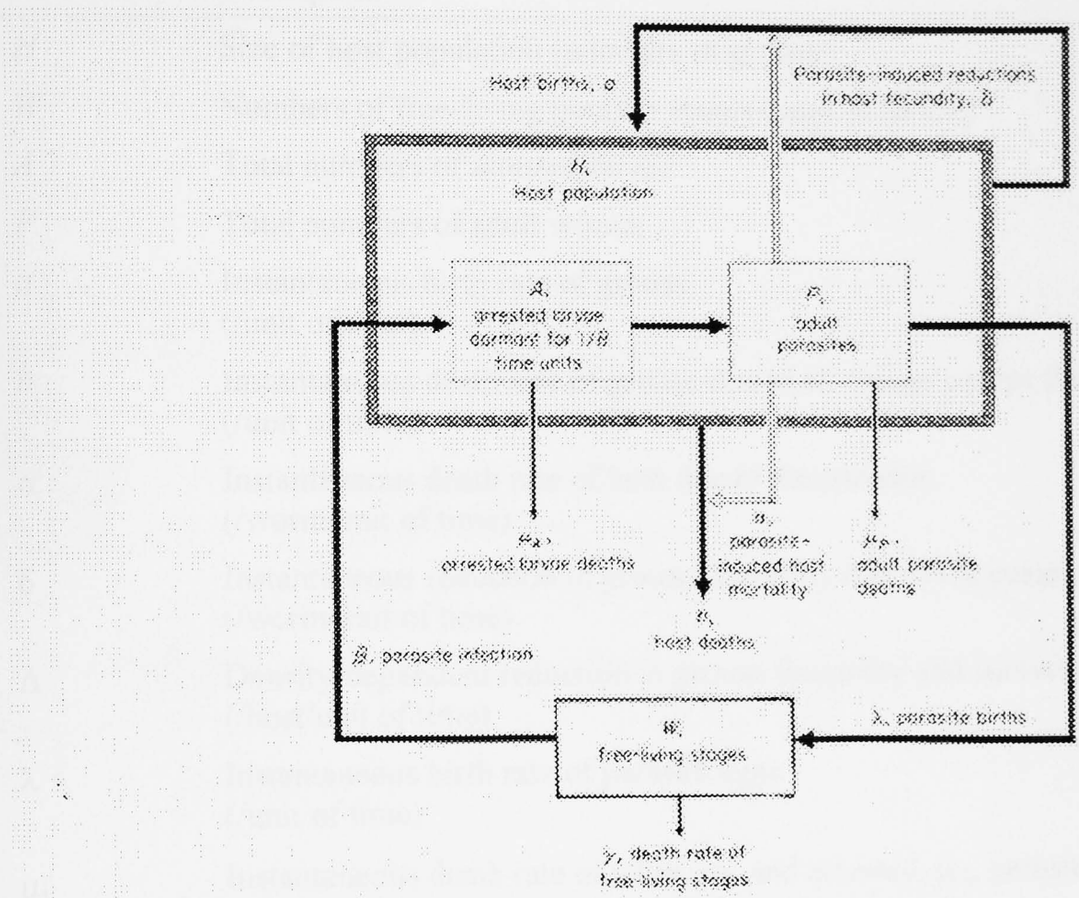

Figure 6.1. Schematic representation of the life cycle of *T. tenuis* in red grouse illustrating the different birth, death and transmission rates occurring in the life cycle and the notation used to denote each process. Note that parasites can affect both host survival and breeding production (Figure from Dobson and Hudson 1992).

Table 6.1. Notation used to denote various population parameters (Table from Dobson and Hudson 1992).

Parameter	Description
H	Size of host population (numbers of grouse)
W	Numbers of free-living parasite stages (eggs & larvae)
A	Total numbers of arrested larvae
P	Total numbers of adult worms
a	Instantaneous birth rate of grouse (/unit of time)
b	Instantaneous death rate of grouse due to all causes except the parasite (/unit of time)
α	Instantaneous death rate of host due to the parasite (/worm/unit of time)
δ	Instantaneous reduction in grouse fecundity due to the parasite (/worm/unit of time)
Δ	Density-dependent reduction in grouse fecundity and survival (/host/unit of time)
λ	Instantaneous birth rate of parasite eggs (/unit of time)
μ_i	Instantaneous death rate of adult, μ_P, and arrested, μ_A, parasite stages in grouse (/unit of time)
γ	Instantaneous death rate of the free-living egg and larval stages (/unit of time)
β	Instantaneous rate of ingestion of parasite infective stages (/host/unit of time)
k	Parameter of the negative binomial distribution which measures inversely the degree of aggregation of parasites within the host population
Θ	The rate at which arrested larvae develop into adult worms (/unit of time)

6.2. The Model

The population dynamics of a host-parasite interaction, including free-living infective larvae can be described by the following set of three coupled differential equations. The first equation describes changes in the size of the host population (H) by considering the gains of the relative growth rate of the host population (a=birth rate, b=death rate) minus the losses in terms of survival (α) and reduced fecundity (δ) determined by the parasite (P).

Equation 1 $$dH/dt = (a - b)H - (\alpha + \delta)P$$

Changes in the free living worm population (W) are determined by balance between the additions from worm egg production (λ) and the losses due to mortality (γ) and the parasites recruited into the adult worm population (βWH)

Equation 2 $$dW/dt = \lambda P - \gamma W - \beta WH$$

The third equation captures the changes in the adult parasite population (P) where parasites are gained from infection (βWH) and then lost through parasite mortality (μ_P), natural host mortality (b) and parasite induced mortality (α) and influenced by the pattern of aggregation of worms within the host population ($P^2/H\ [(k + 1)/k]$)

Equation 3 $$dP/dt = \beta WH - (\mu_P + b + \alpha)P - P^2/H\ [(k + 1)/k]$$

The definition of the parameters used in the model is shown in Table 6.1 and the derivation of the values in Table 6.2. Further details about the derivation can be found in Dobson & Hudson (1992).

The methodology was to run a series of simulations where the relative impact of the parasites on the fecundity of the grouse was altered in relation to change the value of parasite induced reduction in fecundity (δ) and the natural fecundity of the grouse. This in effect was altering first the slope of the relationship between parasites and their reduction in host fecundity and second reducing the intercept of the relationship. The effect of these perturbations were examined on the pattern of population cycles after 20, 50 and 100 years of simulations. If sustained cycles were still observed after 100 years then the cycle period was estimated as simply the mean time interval between peak numbers.

Table 6.2. Population parameters for red grouse and *T. tenuis* (Table from Dobson and Hudson 1992).

Parameter	Symbol	Estimated value (range)
Grouse fecundity	a	1.8 (0-2) year $^{-1}$
Grouse mortality	b	1.05 year $^{-1}$
Parasite fecundity	λ	11 (9.2-11.5) year $^{-1}$
Adult worm mortality	μ_P	1.0 (0.8-1.2) year
Arrested larvae mortality	μ_A	0.5 year $^{-1}$
Mortality of free-living parasite stages	γ	6.5-13 year $^{-1}$
Duration of arrestment	$1/\Theta$	2-6 months
Parasite pathogenicity	α	3 * 10 $^{-4}$ worm $^{-1}$ year $^{-1}$
Parasite reduction in host fecundity	δ	5*10 $^{-4}$ worm $^{-1}$ year $^{-1}$
Aggregation of parasites in hosts	k	1.0 (0.5-1.8)
Transmission rates	β	0.1 (0.6-1.6 * 10 $^{-1}$) host $^{-1}$ year $^{-1}$

6.3. Results

The results from the population model are presented in Fig. 6.2. This shows the relationship between natural breeding rate, the parasite-induced impact on fecundity and the length of population cycles. Where either natural breeding rate or parasite-induced impact on fecundity is low the model shows that population cycles will become damped until the population is no longer after 100 years. At the other end of the scale, where both parameters are very high, and population cycle period is very long, the model predicts populations will move towards extinction with divergent oscillations.

6.4. Discussion

Some important conclusions can be drawn from these results. The model is intrinsically unstable, and for population cycles to occur, the impact of the parasite on grouse fecundity (δ) has to be greater than the impact of the parasite on grouse survival (α). If this is not the case, the parasites will cause death rather than affect breeding production and so cycles will not be present. Indeed, in such circumstances this is stabilising.

When we consider the interaction between food quality and parasites that reduces fecundity then cycle period increases as food quality falls. Even where parasite induced impact on fecundity is low, if low food quality causes a reduction in natural breeding rate then cycle length will increase. This is quite simply a consequence of a reduction in the intrinsic growth rate of the population. The impact of the parasites increases this effect further also influencing cycle period. The results from this model exploration provide one explanation for the variation in population cycle period observed (Figure 6.3.and 6.4.) between Scotland and England (Hudson 1992). While other factors may play a role, this interaction provides a clear testable hypothesis.

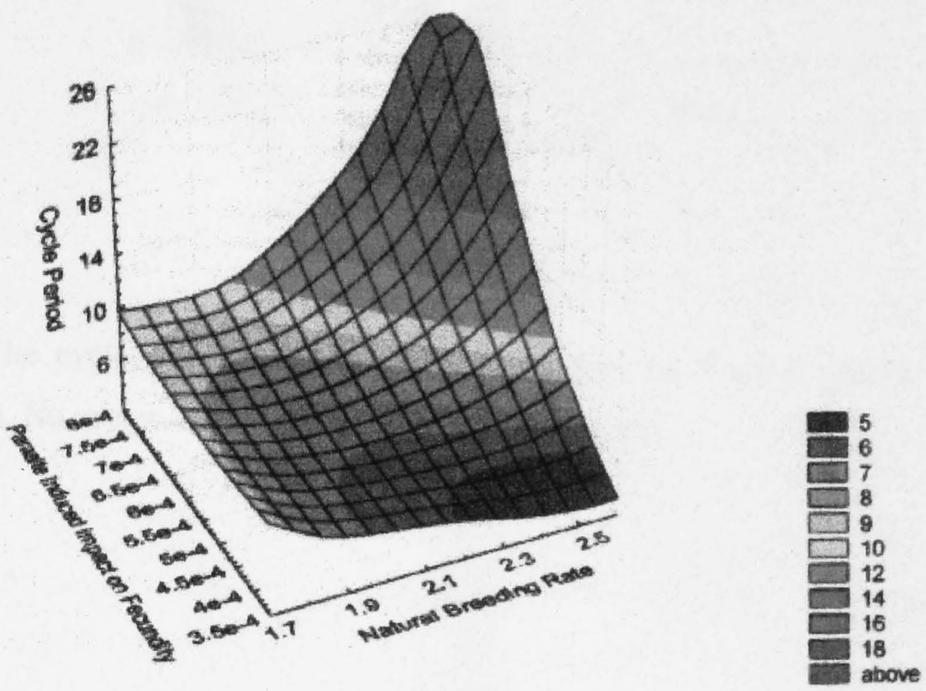

Figure 6.2. Population model results showing the relationship between natural breeding rate, parasite induced impact on fecundity and the length of population cycles.

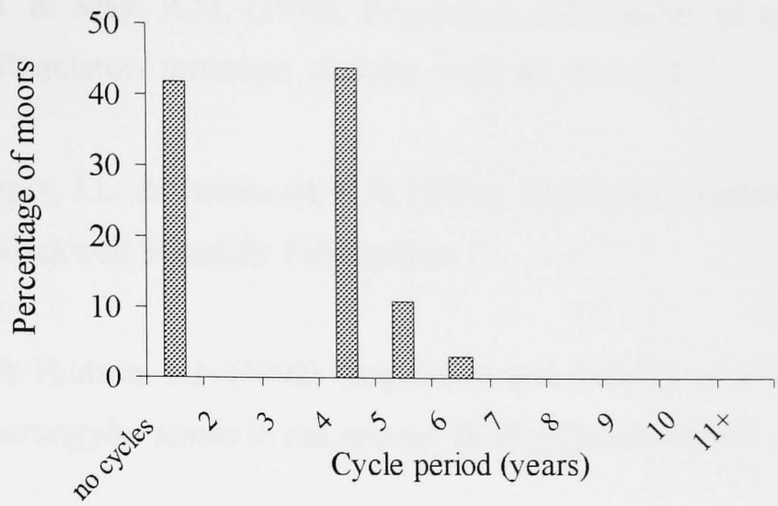

Figure 6.3. The cycle period of red grouse populations on English moors. (Figure from Hudson 1992). No cycles – where populations are non-cyclic.

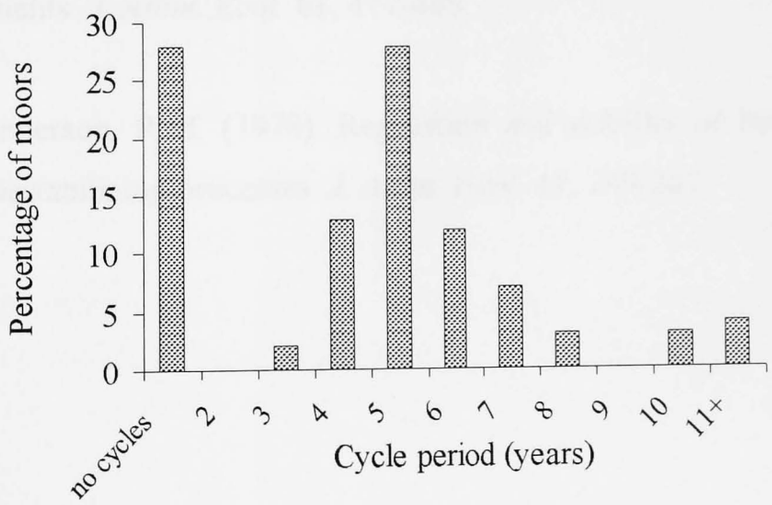

Figure 6.4. The cycle period of red grouse populations on Scottish moors. (Figure from Hudson 1992). No cycles – where populations are non-cyclic.

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CHAPTER 7

GENERAL DISCUSSION

The aim of this study was to investigate the interaction between food and parasites in red grouse *Lagopus lagopus scoticus* to determine the mechanisms and potential causes of the variation in population cycles between different areas. The previous chapters have examined this hypothesis by means of analysis of long-term data, experimental testing of the hypothesis, and by population modelling. This chapter will give a brief overview of the findings of this study and address questions arising from it.

7.1. Main findings and conclusions

Parasite burdens of *T. tenuis* in red grouse were found to be lower in grouse populations in Scotland than in England. Food quality, in terms of nutrient content of heather, was also found to be lower on Scottish moors than on English moors, which could be explained by weather. When considering long-term data, there was a three-way interaction between food, parasites and area that had such an effect on breeding production of grouse that it could explain the variation in population cycle period between different areas. There was no interaction of food and parasites acting on body condition of grouse. Exploring the food-parasite interaction experimentally did not permit the refutation of the null hypothesis that there was no interaction, but this was probably a consequence of limitations in experimental design. Finally, modelling the effects of a food-parasite interaction on grouse populations showed that such an interaction could explain the variations in cycle period between areas.

7.2. The effects of parasites and food on red grouse population cycles

Both food (Moss *et al* 1975) and parasites (Hudson 1986) have previously been shown to influence the breeding production of grouse. Modelling of the grouse-*T. tenuis* system has shown that the effect of *T. tenuis* on grouse breeding production is sufficient and necessary, in combination with other factors to generate the population fluctuations observed in grouse populations in northern England (Dobson & Hudson 1992, Hudson *et al* 1998).

This study has shown that food and parasites and area (Scotland/England), interact to influence the breeding production of grouse, and can explain variations in population cycle period between areas, as shown by population modelling. Most of the variation in population cycle period between Scotland and England (Hudson 1992) could be accounted for by the effect of food and parasites on breeding production. However, this is probably not the case for population cycles lasting longer than eleven years in Scotland. These cycles are more likely to be the product of other factors. Most of these long cycles occur in north-east Scotland, where detailed studies have been carried out on red grouse looking at the hypothesis that intrinsic mechanisms acting through spacing behaviour can explain population fluctuations in red grouse (Watson *et al* 1984).

Although spacing behaviour and kin selection influencing aggression (Watson *et al* 1994) may indeed be part of the cause of population fluctuations in grouse, this would not refute the role that parasites may also be playing in generating the cycles. *T. tenuis* may well influence the spatial structuring of kin quite simply by impacting on breeding production. Low levels of *T. tenuis* will mean higher breeding production, more kin, less aggressiveness and therefore an increase in grouse population density while high levels may do the opposite. Food may also play some role in influencing population density.

7.3. Are grouse the exception?

Many species of animals have regular population fluctuations. Lemmings (Elton 1924), voles (Boonstra 1994), showshoe hares (Erickson 1944) and Canadian Lynx (Stenseth *et al* 1997) and red grouse are amongst those that have been studied in great detail. Most population fluctuations are caused by extrinsic factors, such as food and predators; fewer are caused by parasites.

There is little evidence to suggest that parasites play a role in the population fluctuations of small mammals, and although snowshoe hares have various parasites, these have not been investigated in detail.

On the one hand, work by Stenseth *et al* (1997) indicates that this is a tritrophic interaction which involves predator (lynx), prey (snowshoe hares) and probably vegetation, although the role of food is assumed and there could be a parasite-host interaction or even a parasite-food interaction influencing the dynamics. On the other hand, hares have very low levels of infection (Keith *et al* 1986).

Red grouse have been extensively studied, and the parasite *T. tenuis* has been shown to be the cause of population fluctuations (Hudson *et al* 1998) and in this study has been shown to interact with food to cause variations in population fluctuations. There is some evidence to suggest that parasites may have a similar effect on the population fluctuations of rock partridge in Italy (Cattadori *et al* 1999).

Population fluctuations in Soay sheep *Ovis aries* have also been studied in detail, and Gulland (1992) suggested that both parasites and food contribute to their mortality. Experiments showed that there was little effect of parasites when their sheep hosts were well-fed, but that food shortage resulted in immunosuppression that would allow parasite burdens to increase faster and lead to increased mortality. Therefore, food and parasites could be said to interact to affect population fluctuations in Soay sheep. Red grouse exhibit little or no immune response to infection with *T. tenuis* and so are presumably open to the threat from parasites regardless of food quality.

From this evidence it would seem that parasites may have some role to play in the dynamics of other vertebrate population cycles.

7.4. Why aren't all populations cyclic?

Most animal species have parasites of some description, whether it be microparasites (viruses and bacteria), internal macroparasites (helminths) or ectoparasites (flies, mites, ticks). Any parasite that affects reproduction or survival has the potential to influence population levels. Parasites can affect animal populations in several ways (Newton 1998), with either no effect on population numbers, a permanent reduction in numbers, regular fluctuations in numbers, irregular fluctuations in numbers or declines to extinction.

Cyclic populations, with regular fluctuations in animal numbers, are most likely to occur where there is a simple one host-one parasite system, where the parasite causes population cycles through acting in a delayed density-dependent manner. Red grouse are the best example of this.

One reason why some animal populations with parasites do not undergo cyclic population fluctuations is because they do not have a simple host-parasite system, and instead parasites are shared between hosts (such as ticks and the louping ill virus in red grouse, where sheep are also a primary host). When parasites are shared between hosts then levels of infection are not dependent on the density of the host population alone. The other host species, rates of interspecific transmission and immune responses will all influence parasite burdens and the effects on population change.

7.5. Parasite-host trophic interactions

Parasite-host interactions, such as that of the red grouse-*T. tenuis* system, are in many ways analogous to a predator-prey trophic interaction, with the parasite as the predator and the host species as the prey. Cyclic fluctuations are characteristic of a predator-prey interaction (Lack 1954), where the numbers of predators will fluctuate with the numbers of prey in a density-dependent manner. For example, coyote and lynx numbers fluctuate with numbers of snowshoe hares (O'Donoghue *et al* 1997), and arctic fox numbers fluctuate with numbers of lemmings (Elton 1924).

Some predators are generalist predators, taking a wide variety of prey, and others are more specialist, concentrating on only one prey type. Generalist predators (such as peregrine falcons which prey on grouse, passerines and pigeons) are not likely to cause a density-dependent response in numbers of their prey, because they have several different types of prey. However, a specialist predator (such as Gyr falcons which specialise on ptarmigan over much of the Arctic, Newton 1998) could cause a density-dependent response in their prey species.

A parasite such as *T. tenuis* in red grouse can be considered to be a specialist predator, with an intimate relationship between predator and prey, or parasite and host, since the parasite does not infect other avian hosts within the moorland environment. Such a relationship will have a large impact on the host or prey, and will be more likely to lead to population cycles than a relationship between a generalist predator, or parasite with more than one host, and its prey.

In summary, this study investigated the role of a food-parasite interaction in variations in population cycles between areas. Such an interaction could be the cause of most of the variation in population cycle period between different areas, although other factors may be more important in some cases. Red grouse are not the exception in having population cycles driven by parasites and food. Many species that have parasites do not show cyclic fluctuations, probably because their parasites are shared and they exhibit a strong immune response. The relationship between *T. tenuis* and red grouse can be looked at as a specialist predator-prey relationship.

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The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks

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Running Head: Red grouse chick growth and survival

Keywords: red grouse, chick, invertebrate, diet, survival

ABSTRACT

The role of diet on the growth, survival and movement of red grouse chicks was examined. We compared two areas of moorland in Scotland; a dry heath with a low density of red grouse and poor chick survival and a wetter heath/bog with relatively higher red grouse numbers and higher rates of chick survival. There were no differences in clutch size, or the proportion of eggs hatching between the two moors but brood survival was significantly lower on the dry heath. Radiotagged hens with broods were monitored during the first 12 days following hatching, the chicks captured, weighed and faecal samples collected. Invertebrate samples were collected within brood feeding ranges. Analysis of chick faeces was used to identify dietary components. Heather comprised the major dietary component on both moors. Invertebrates formed a higher component of diet on the wet moor, and this was positively correlated with growth rates, which in turn were positively correlated with chick survival. We present data from an experiment carried out in 1982, in which chicks showed higher growth rates with increasing insect availability. We also show that broods in which all the chicks survived (4-10 days) had smaller home range areas than broods in which some of the chicks died during this period. We suggest that the differences in chick survival between the two populations was due to variations in the abundance of invertebrates, particularly Tipulids. The protein provided by a high invertebrate component in the diet is, therefore, an important determinant of young red grouse chick growth and survival in some areas.

INTRODUCTION

Red grouse (*Lagopus lagopus scoticus*) are restricted to the heather *Calluna vulgaris* uplands of Britain, an internationally scarce and valuable habitat type (Thompson *et al.*, 1995). It is a bird of economic importance as a quarry species and has been the subject of several long-term studies investigating their ecology, population dynamics and behaviour (Jenkins, Watson & Miller, 1963, 1967; Watson & Moss, 1979; Moss & Watson, 1985; Hudson, 1986a; Hudson *et al.*, 1992; Hudson, 1992; Watson *et al.*, 1994). Some of these studies have suggested that variations in chick survival between sites influences productivity, and others that chick survival within a site may play a role in year to year changes in red grouse numbers.

There is evidence suggesting that chick survival is influenced by the intrinsic quality of the hen together with food availability and weather experienced before laying (Jenkins *et al.*, 1963, 1967; Moss, Watson & Parr, 1975; Moss *et al.*, 1981). Chick survival can also be influenced by the intensity of maternal infection with the caecal nematode *Trichostrongylus tenuis* (Hudson, 1986b). Diseases

such as louping ill can cause direct chick mortality at three to four weeks of age, although this has a limited distribution within this species' range (Hudson *et al.*, 1997). In some areas predation, by species such as the hen harrier (*Circus cyanus*), can also reduce chick survival rates (Redpath, 1991, Redpath & Thirgood, 1997). A protein-rich diet has been shown to influence the early survival prospects of other gamebirds and these proteins are typically obtained through invertebrates (Southwood & Cross, 1969; Hill, 1985; Rands, 1985; Potts, 1986; Hill & Robertson, 1988). Although young red grouse are known to include invertebrates in their diet (Grimshaw, 1911, Butterfield & Coulson, 1975; Hudson, 1986a), heather shoots make up a high proportion of diet by volume. There has been much debate in the past over the importance of invertebrates in red grouse chick diet. Previous studies have found that insects formed only a small proportion by weight of the red grouse chick diet (Savory, 1977) and that there is a high vegetative component in the chick diet of both red grouse and the closely related willow grouse (*Lagopus lagopus*) (Pullianen & Eskonen, 1982), suggesting that invertebrates are relatively unimportant for growth and survival (Savory, 1977). More recently, however, there has been increasing evidence that, particularly in summer, invertebrates are important for some granivorous birds, for whom the bulk of the diet consists of seeds and plant material (Potts, 1986; Wilson *et al.*, 1999).

Despite the large volume of research published on this species there is no evidence from free living red grouse on which to assess the effects of diet, including its invertebrate component, on chick survival. Hudson (1986a) followed the movements and habitat selection of broods in Yorkshire. He found that they concentrated their activity in bog flushes which were particularly rich in those insects identified from the droppings. He also found that chick survival was associated with abundance of insect remains in the droppings of these chicks, although this relationship varied between years. Wet, boggy moorland has been shown to contain higher densities of certain invertebrates sampled by pitfall traps, particularly Tipulids, than dry heaths (Butterfield & Coulson, 1975; Savory, 1977). Tipulids are poor fliers and are usually found resting on vegetation, which presumably makes them more vulnerable to predation by red grouse (Butterfield & Coulson, 1975). In this paper we compare red grouse chick growth, survival and diet during the first 10 days after hatching between two moors; a dry heath and a wetter area of blanket bog. We examine differences in insect availability between the two moors, and present data from an experiment carried out in 1982 which directly tests the effect of invertebrates in the diet upon chick growth and survival. Management options to increase chick survival rates on heather moorland are suggested.

MATERIALS AND METHODS

Study areas and long-term monitoring

Two moors were used for this study, South Drumochter and Ralia, both in Southern Inverness-shire in the Scottish highlands. These moors provide contrasting habitats and red grouse densities. Ralia is a relatively flat, dry heath of 280 m altitude at its central point, South Drumochter (henceforth referred to as Drumochter) is a higher (central point altitude, 480m), wet heath with patches of blanket bog. Red grouse counts have been conducted on both moors since 1985 (Drumochter) and 1986 (Ralia). On each moor red grouse in two $1km^2$ blocks were counted in April and again in July with pointing dogs to obtain estimates of pre-breeding and post-breeding populations (Jenkins *et al.*, 1963). Repeated-measures ANOVAs were used to analyse grouse count data (1986 – 1997). Mean numbers of birds from the two counts were used for the purpose of analysis. These data were used to calculate mean July brood size (when chicks are approximately six to eight weeks old) per estate against which to compare Ralia and Drumochter. Similar counts were conducted on 33 other managed red grouse moors in Scotland for at least five years per site over the period 1985-1996. Nests were also located on Ralia and Drumochter each year through a combination of searches with pointing dogs and following adult hens fitted with radio-transmitters. A sample of adult females shot after the breeding season (August to December) between 1988 and 1996 on both moors were inspected for infections of *T. tenuis* and for the presence of the louping ill antibody.

Radiotelemetry of broods

Females were captured by night lamping during the winter and early spring on each moor (Hudson & Newborn, 1995). Hens were fitted with small necklace radio transmitters similar to those used by Thirgood *et al.* (1995) who found they had no effect on survival or breeding success. Chick growth and survival was monitored in broods produced by 87 hens between 1994 and 1997. Each hen was located weekly during from between late autumn to late winter (October to February) until nesting. Absence of the hen during incubation allowed clutch size to be determined, and the incubating hens were then located every two days to determine hatch date. Hatch success was assessed by examining the nests for shells, unhatched eggs and dead chicks. The intensity with which each brood was then monitored varied depending on accessibility and the number of broods active at any one time. We attempted to capture broods twice during the first 12 days after hatching; once at 4 days (range 3-6), and again at 10 days (range 9-12) using pointing dogs. The range of catch dates was due to weather conditions (chicks were not disturbed during adverse conditions). For the purposes of analysis these

are referred to as 4 day and 10 day captures. Body mass and wing length were recorded for each chick, and averaged per brood. Individual chicks were down clipped at first catch so that they could be identified upon re-capture, and once large enough (> 30 g) were fitted with patagial tags. Diet was assessed via faecal samples obtained from chicks during handling. Invertebrate occurrence in the faeces (dietary invertebrates) was corrected for the number of heather bracts found in the same sample, and is quoted as the number of invertebrates per 100 heather bracts (Hudson, 1986a). Between late May and early July standardised sweep net samples for invertebrates were taken in the area occupied by the brood if the vegetation was not waterlogged.

Home range analysis

Home range area for broods with more than 15 radio locations (fixes), was calculated during the first 12 days after hatching. The number of fixes varied from 17 to 30 with a median value of 23.5. All home range estimates are sensitive to sample size (Robertson *et al.*, 1998), so home ranges here were standardised to 17 fixes by use of a bootstrapping procedure. For broods with more than 17 fixes the bivariate normal ellipse was recalculated (Jennrich & Turner, 1969) for random selections of 17 fixes (for the calculation of mean values 30 replicates was considered sufficient), and the mean value calculated. This allows home range areas to be corrected for differences in the number of fixes between broods.

Chick growth and survival experiment

In addition to data collected in the field, we present data from an experiment carried out in 1982 which directly tests the effect of invertebrate availability on red grouse chick growth and survival (Hudson, 1986a). Three aviaries were erected in a draught free room with brooder lamps. A total of 16 eggs were removed from nests of red grouse on managed grouse moors and hatched in an incubator. Chicks from the same broods were split between the three treatments ensuring that there were no differences in the genetic constitution or quality of chicks between the groups. One group of chicks had access to water and young heather, which was replaced daily and sprayed regularly with water to keep it fresh. The heather provided was not inspected for invertebrates, so chicks in this group may have had access to a very small supply of invertebrates. The other two groups were maintained under identical conditions, but in addition one was given a limited supply of invertebrates (mostly Tipulids) collected from a nearby red grouse moor, and the other provided with invertebrates *ad lib*. Chicks were weighed daily until ten days after hatching. A further three chicks were added to

treatment groups two (one chick) and three (two chicks) on day three; consequently the analysis is confined to data collected between days three and ten.

Data were transformed to achieve normality and homoscedasity and were analysed using MINITAB release 12.1 and STATISTICA release 5.5. Where the assumptions of normality were violated, non-parametric methods were used. Unless otherwise stated General Linear Models were used for analyses, and data are presented as means ± s.e. or medians and interquartile ranges (Q1-Q3).

RESULTS

Comparison of study areas

We tested for differences between the two moors in red grouse density in April (1986-1997) and in July (1986-1996), number of broods produced, and the size of clutches and broods (Table 1). Year was included in this analysis and had no significant relationship with density in April, although there were differences between years in density for July. Drumochter contained significantly more adults per km^2 in April (32.5 ± 2.3) than Ralia (12.9 ± 1.4), and higher numbers of young and adults per km^2 in July (101.5, Q1-Q3: 58.5 - 201.0) than Ralia (20.2, Q1-Q3: 15.3 - 42.6). Significantly more broods were produced on Drumochter (13.0, Q1-Q3: 7.5 - 20.0) than on Ralia (4.2, Q1-Q3: 2.6 - 5.9). A total of 206 nests (Drumochter n=105, Ralia n=101) were located from 1986 to 1996. There were no significant differences between size of clutches on Drumochter (8.2 ± 0.1) and those on Ralia (8.7 ± 0.1), although there were significant differences between years (Table 1). There was also no difference between the proportion of eggs hatching (Mann-Whitney $W_{128,114}$ = 14841.0, NS) on the two moors, excluding those clutches where no eggs hatched. In July, however, when the chicks are approximately six to eight weeks old, mean brood sizes were significantly lower on Ralia (3.5, Q1-Q3: 3.0 - 4.7) than on Drumochter (5.6, Q1-Q3: 4.6 - 6.2; Table 1), indicating that brood survival was lower on Ralia. Comparing these July brood sizes to those obtained from a sample of 33 other managed red grouse moors in Scotland (Fig. 1) identified Ralia as producing amongst the smallest broods and Drumochter amongst the largest.

Table 1 here

Fig. 1 here

Post-mortem assessment of *Trichostrongylus tenuis* numbers in shot adult females showed that median worm burdens were significantly higher in birds on Drumochter (520.0, Q1-Q3: 75.0 - 1508.0) than birds on Ralia (19.0, Q1-Q3: 0.0 - 85.5) (Mann-Whitney $W_{105,34} = 8457.5$, $P < 0.0001$). Median body mass of shot adult females on Drumochter was 600g (Q1-Q3: 556.3 - 648.8) and on Ralia was 575g (Q1-Q3: 550.0 - 626.3). There was no significant difference in female body mass between the two moors (Mann-Whitney $W_{104,34} = 7465.0$, NS). Examination of sera from young birds found no evidence that birds had developed immunity to louping ill on either moor.

Diet analysis

A total of 62 faecal samples (Drumochter n=40, Ralia n=22) were collected from different broods. The occurrence of invertebrates and plant matter are presented in Table 2. Of 155 invertebrates identified from samples on Ralia, weevils (Curculionidae) were the most frequent items (48% by number), followed by crane flies (Tipulidae) 20%, Staphalinidae sp. (8%) and larval Symphyta (6%). On Drumochter, of 1,971 invertebrates identified, Tipulidae were numerically dominant (73%), followed by Chironomidae (24%). No other group comprised more than 1% of the total. With the exception of two Drumochter samples which contained large quantities of unidentified leaf material, the majority of vegetation in the diet comprised heather, its seeds and flowers, sundew heads and moss capsules. There were 44 faecal samples from 1996 (Drumochter n=37, Ralia n=7) for which the exact age of the chicks (between 3 and 12 days) was known. Chick faeces from Drumochter contained a significantly higher proportion of invertebrates per 100 bracts (5.0, Q1-Q3: 2.3 - 12.3) than did chicks from Ralia (2.4, Q1-Q3: 0.6 - 5.6) ($F_{1,41} = 5.11$, $P < 0.05$). There were no significant differences between years, and effect of chick age ($F_{1,41} = 0.26$, NS) was controlled for by including exact age in the model.

Table 2 here

Invertebrate availability

Drumochter sweep samples (1995 and 1996) contained a significantly higher number of insects per sample (35.5, Q1-Q3: 17.0 - 138.3) than did samples from Ralia (9.5, Q1-Q3: 1.8 - 21.3) ($F_{1,36} = 14.26$, $P = 0.001$). A significant interaction between moor and year showed that there was a decrease in the number of insects sampled on Ralia but not on Drumochter in 1996 ($F_{1,36} = 5.31$, $P < 0.05$). The difference between the two moors was largely due to differences in the numbers of Diptera

(Drumochter 30.0, Q1-Q3: 13.0 - 127.0 per sample; Ralia 4.0, Q1-Q3: 0.0 - 6.3). Although relatively few Tipulidae were sampled by sweep netting on either moor they were seven times as abundant on Drumochter (Drumochter 0.0, Q1-Q3: 0.0 - 1.0) per sample; Ralia 0.0, Q1-Q3: 0.0 - 0.0), other Diptera were 22 times as abundant. Excluding Diptera there were no significant differences in invertebrate numbers per sweep between the moors ($F_{1,36}$ = 0.01, NS), although again a significant interaction between moor and year showed that there was a decrease in the number of insects (excluding Diptera) sampled on Ralia but not on Drumochter in 1996 ($F_{1,36}$ = 5.31, $P < 0.01$).

Chick Growth Rates

A total of 40 broods (Drumochter n=31, Ralia n=9) provided data on mean brood body mass and wing length. Exact age of the broods was included in the model as a covariate to correct for any differences in age between the moors. The distribution of exact ages within the 4 day and 10 day old broods did not differ systematically between the moors. Mean brood body mass at 4 days and 10 days was significantly higher on Drumochter than on Ralia (Table 3). Analyses of both mean brood body mass and wing length at 10 days (but not at 4 days) showed significant interactions between exact age and moor, suggesting different growth rates on the two moors. After correcting for exact age, broods on Drumochter weighed on average 3.9g more than those on Ralia at 4 days old and 5.7g more than those on Ralia at 10 days old. Mean wing length showed a similar pattern (Table 3), with broods on Drumochter having an average wing length approximately 6.1mm longer at 4 days, and 5.6mm longer at 10 days than those on Ralia.

Table 3 here

For 15 broods (Drumochter n=7, Ralia n=8) the relationship between dietary invertebrates and mean brood body mass at 4 days and 10 days was investigated. Moor, and a moor-dietary invertebrate interaction were also included in this analysis. At both 4 days and 10 days mean brood body mass increased significantly with invertebrate numbers (4 days: $F_{1,13}$ = 10.52, $P < 0.01$, R^2 = 44.7%, Fig. 2; 10 days: $F_{1,13}$ = 5.59, $P < 0.05$, R^2 = 30.1%;).

Fig. 2 here

Chick survival and invertebrate abundance

A total of 42 broods (Drumochter n=22, Ralia n=20) provided data on diet at around 10 days of age together with the proportion of each brood surviving from hatching to 10 days. Moor, and a moor-dietary invertebrate interaction were also included in this analysis. A significantly higher percentage of chicks survived from broods on Drumochter (median: 71%, Q1-Q3: 50 - 88) than those on Ralia (57%, Q1-Q3: 43 - 71) ($F_{1,40} = 5.98$, $P < 0.05$). Neither invertebrate numbers or the interaction between moor and invertebrate numbers had a significant relationship with brood survival. However, an analysis to investigate the relationship between body mass and survival showed that mean brood body mass at 4 days had a significant positive relationship with the proportion of the brood surviving from hatching to 4 days ($F_{1,31} = 5.11$, $P < 0.01$). In this analysis 22.7% of the variance in proportion of brood surviving was due to mean brood body mass. An outlier with a standardised residual of 2.69 was removed for this analysis, although there was still a significant effect of weight on survival with the outlier included. Moor was included in the starting model but was not significant. There was a similar relationship between body mass and survival at 10 days ($F_{1,32} = 4.59$, $P < 0.05$; $R^2 = 12.5$). Again, moor was not significant in this analysis.

There was a positive correlation between the numbers of invertebrates in the faeces (per 100 heather bracts) and those sampled by sweep netting ($F_{1,16} = 5.31$, $P < 0.05$). Neither moor or the interaction between moor and invertebrate availability were significant.

Home range and survival

Home range area and brood survival was calculated for 17 broods on Drumochter and four on Ralia. Broods in which all the chicks survived between four and days old had home range sizes (0.2 ± 0.02 ha) approximately half that of broods in which some of the chicks died during this period (0.1 ± 0.02 ha) ($T_{16} = 3.93$, $P < 0.01$; Fig. 3). Due to the small sample sizes it was not possible to test for differences in home range area between the two moors.

Fig. 3 here

Chick growth and survival: experimental data

All of the six chicks in the dietary group (one) consisting of only heather progressively lost weight over the duration of the experiment, and none survived past the fifth day after hatching (Fig. 4). Four out of ten of the chicks in the limited invertebrate dietary group (two) died after six to nine days, and all of the three chicks in the unlimited invertebrate dietary group (three) were still alive after ten days. Sample sizes were insufficient to statistically test for differences in survival between the three groups. A repeated-measures ANOVA was used to investigate the effect of invertebrates on chick body mass between day three and ten after hatching: six chicks in group two, and three chicks in group three. Chick age and dietary group had a significant effect on chick body mass ($F_{7,49} = 59.30$, $P < 0.0001$; $F_{1,7} = 7.17$, $P < 0.05$ respectively). There was also a significant interaction between day and dietary group ($F_{7,49} = 3.27$, $P < 0.01$) indicating that the growth rate between the two groups differed, with chicks in the unlimited invertebrate dietary group gaining weight at a faster rate than those in the limited invertebrate group (Fig. 4).

Fig. 4 here

DISCUSSION

The two study sites represented extremes of the observed range of chick survival rates found on managed red grouse moors in Scotland. July counts on Drumochter record the second highest mean brood sizes from a larger sample of 35 moors, Ralia produced the ninth lowest. Although Ralia contained a lower density of birds, clutch size was not significantly different from Drumochter and there were no differences in nest success or egg hatchability. The smaller brood sizes on Ralia observed during July counts appear to be due to poor chick survival. The observed clutch sizes and proportion of eggs hatching together with the observed mean July brood sizes from the counts suggest chick survival rates of 81.3% and 47.3% for Drumochter and Ralia respectively. This compares well to survival in broods of radiotagged females of 71% on Drumochter and 57% on Ralia. Adult birds on Drumochter contained higher numbers of *T. tenuis* than birds on Ralia. However, mean burdens on neither moor approached the level (3000 per bird) that has been identified as being related to a reduction in red grouse condition in populations from northern England (Hudson, 1986a). It is, therefore, unlikely that *T. tenuis* played a significant role in maternal condition or, indirectly, chick survival on these moors, or that this parasite was the cause of chick survival differences between the areas. Ticks were present on Ralia and not found on Drumochter but evidence of louping ill was not recorded. Although hen harriers have been observed on both moors, sightings were infrequent during the main years of this study and it is unlikely that they would have contributed to the difference in chick survival between the two moors. Consequently, we consider it reasonable to exclude *T. tenuis*, louping ill or predation by hen harriers from our considerations. We were not able to compare body mass of hens at capture for radiotelemetry between the moors as birds on Ralia were typically captured in late autumn compared to late winter on Drumochter. However, we compared the body mass of adult females shot on Ralia and Drumochter after the breeding season and found no significant differences. In addition, there were no differences in nest success, clutch size or egg hatchability. These observations do not support the hypothesis that relatively poor maternal nutrition is the cause of poor chick survival on Ralia compared to Drumochter.

Red grouse chick diet

Heather was the dominant food item in this study, occurring in all faecal samples as has been recorded elsewhere (Grimshaw, 1911; Lance & Mahon, 1975; Savory, 1977; Hudson, 1986a). Savory (1977) compared the nutrient content of shoots from chick crops with those collected by hand from the areas where the chicks were feeding. He demonstrated strong selection for tips rich in Nitrogen, Phosphorus and Calcium. The regular occurrence of moss capsules in

this study also conforms with previous work and these items are thought to provide a readily digestible source of protein for young chicks (Savory, 1977). Any analyses of diet using faeces will inevitably be biased towards material which have identifiable, indigestible parts. Plant or animal material that consists of soft, digestible parts or is hard to identify may be overlooked, so percentages of occurrence in faeces should be interpreted with caution. For example, Tipulids are soft bodied and easier to digest than hard bodied invertebrates such as Coleoptera (Green, 1984). It is likely, therefore, that we are underestimating the number of Tipulids eaten by grouse chicks and as a consequence underestimating the importance these invertebrates in grouse chick diet. Since there is no reason that different invertebrate species should differ in digestibility between the two moors our comparisons are valid, although the magnitude of the differences for some groups will be underestimated. The positive correlation between numbers of invertebrates in faeces with numbers sampled by sweep netting indicates that the diet analysis reflects the invertebrate availability (with respect to numbers) on the two moors. Heather flower remains or heather seed, representing the previous years growth, occurred in 50% of the samples. We suspect that heather seed was readily digested by young chicks as broken seed capsules were frequently found in the droppings and that we are likely to have underestimated the occurrence of these items in the diet. It has been suggested that improved heather growth and flowering in the previous season may indirectly influence chick survival through improved maternal nutrition prior to breeding (Jenkins *et al.*, 1963, 1967; Moss *et al.*, 1975, 1981, 1993). Alternatively, it may directly influence chick survival through improved nutrition as heather flowers and seeds were common food items, or it may lead to increased invertebrate densities with similar benefits. There are some limited data on heather quality on the two moors from this study (Game Conservancy Trust, unpublished data) in the form of percentage phosphorous and nitrogen content. These were taken from two sites on each moor in 1997. Heather from Drumochter contained a slightly higher percentage of phosphorous (Drumochter = 0.07%, Ralia = 0.06%) and nitrogen (Drumochter = 1.2%, Ralia = 0.09%) than did samples from Ralia. Whether these differences are of sufficient magnitude to influence chick survival through improved nutrition or differential invertebrate densities is, at present, unclear.

Savory (1977) identified invertebrates obtained from crop samples of 2-3 week old red grouse chicks in N.E Scotland. He found a large predominance (89.1% by number) of Diptera amongst the animal material eaten. Grimshaw (1911) also notes red grouse chicks consuming large numbers of this

species. This is comparable to the results from Drumochter where Diptera again predominated (96.5%), largely comprising Tipulidae (72.9%). On Ralia a wider range of invertebrates were taken and no one group predominated: Tipulids, comprising 20% of the identified invertebrates, Curculionids, Staphylinids and larval Symphyta were the most common. Droppings from Ralia contained significantly fewer invertebrates per 100 heather bracts than did those from Drumochter. Savory (1977) compared the availability of invertebrates and chick diet between topogenous boggy flushes, ombrogenous blanket bog and drier heath. Invertebrate availability and the occurrence of invertebrates in chick diet was highest on the boggy flush areas, intermediate on the blanket bog and lowest on the drier areas, largely due to differences in the numbers of Tipulids. This would support the differences found between Ralia, a dry heath, and Drumochter with its mixture of topogenous and ombrogenous areas.

Chick survival, growth rates and invertebrate abundance

There were significant differences in mean brood body mass and wing lengths at 4 and 10 days of age between the two moors. Chicks on Drumochter appeared to grow faster then those on Ralia. There were positive correlations between mean brood body mass both at 4 and 10 days and the numbers of invertebrates in the diet. There were also positive correlations between mean brood body mass both at 4 and 10 days and the proportion of the brood surviving to these ages. The effect of moor was not significant in these analyses indicating that chick survival is lower on Ralia because of the reduced growth rate. Hudson (1986a) identified a similar relationship from broods in Yorkshire with broods of chicks eating relatively large quantities of invertebrates weighing more than those eating few. By experimentally testing the relationship between chick diet and body mass we have shown that captive red grouse chicks fed only heather lost weight between the ages of 1 and 5 days. Chicks provided with an unlimited supply of invertebrates were significantly heavier and had faster growth rates than those with a smaller component of invertebrates in their diet.

Broods in which all chicks survived (4-10 days) had smaller home ranges than broods in which some chicks died over this period. Similar relationships between home range size, invertebrate abundance and brood survival have been demonstrated for other galliforms (Hill, 1985; Rands, 1985; Potts, 1986; Hill & Robertson, 1988) together with experimental manipulations of invertebrate abundance leading to increased survival and decreased home range size (Rands, 1985).

In this study we have demonstrated that there is a positive correlation between the dietary invertebrate and body mass, and also between body mass and chick survival. Broods on Drumochter had a higher invertebrate component in their diet and a faster growth rate, which in turn results in a higher proportion of chick survival, than those on Ralia. We have also shown experimentally that there is a direct causal effect of dietary invertebrates upon chick body mass and growth rate, and that chicks fed only heather did not survive under controlled conditions. As such we conclude that chick survival and growth rates are related to the invertebrate component of the chick's diet.

Historical changes in red grouse populations

Historically, Ralia has produced large numbers of red grouse. MacPherson (1914) reports it as one of the best shooting moors in the region, producing 4025 birds shot in the 1913 season. Over the period 1979-1994 the average yield was 21 birds per season. It would appear that poor chick survival is one possible cause for the low numbers found on Ralia although it is unlikely that this was a problem in the past. Although a proportion of managed red grouse moors exhibit low rates of chick survival, this is not a universal problem and its role in declining red grouse numbers remains uncertain. In this paper we describe the likely role of invertebrates in relation to low chick survival on one moor; other causes such as predation and disease may be of greater importance in reducing chick survival rates on other moors. That Tipulids occurred in a high proportion of the faecal samples but were relatively scarce in the sweep netting samples may indicate that this sampling method does not accurately reflect Tipulid availability on the two moors. Nevertheless, it would appear that Diptera, particularly Tipulids, do not occur in such large numbers (or percentage frequency) in faecal samples from Ralia as they do in samples from Drumochter and from other studies in Scotland (Grimshaw, 1911; Savory, 1977). There is anecdotal evidence for declines in Tipulid numbers on a neighbouring moor to Ralia which also appears to suffer low chick survival. Although unquantified, Ralia and the neighbouring moor have apparently become drier in recent decades, possibly due to hill drainage or a falling water table; there is anecdotal evidence of bogs drying out and of associated changes in the vegetation over this period. An investigation into Tipulid abundance in relation to soil moisture and experimental manipulations of water levels is needed to determine the direct effects on invertebrate abundance, chick diet and survival.

Management recommendations

There is evidence that increased grazing pressure in upland dwarf shrub communities leads to a reduced invertebrate biomass (Baines, Sage & Baines, 1994; Fuller & Gough, 1999). Little is known,

however, regarding the mechanisms driving such an effect. Similarly, gross differences in invertebrate abundance have been recorded between different vegetation and soil types (Savory, 1977) although again the mechanisms are poorly understood. The abundance of preferred chick food items is known to be high in wet areas of moorland, particularly around bog flushes (Hudson, 1986a). We suggest that decreasing grazing pressure together with the creation of wet areas within drier moorland types, possibly through the blockage of drains, would be beneficial to red grouse chick survival on certain moors (Hudson & Newborn, 1995).

ACKNOWLEDGEMENTS

We would like to thank John and Eira Drysdale and Lord Peel for allowing us access to their land during this study. Financial support was provided by the Scottish Trustees and the Game Conservancy Trust. Thanks to Tim Benton and Kate Buchanan for useful comments on an earlier draft of this manuscript.

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Table 1

General Linear Models for numbers of grouse per km^2 in April and July, numbers of broods, clutch and brood sizes on Drumochter and Ralia. There were insufficient degrees of freedom to include an interaction between year and moor for analyses on the number of grouse in April and July and the number of broods. Year was constrained into these analyses regardless of its significance.

	no. of April adults	**no. of July adults + young**	**no. of broods**	**clutch size**	**July brood size**
moor	$F_{1,11} = 96.59$***	$F_{1,10} = 83.39$***	$F_{1,10} = 43.37$***	-	$F_{1,20} = 13.84$**
year	$F_{11,11} = 2.64$	$F_{10,10} = 4.43$*	$F_{10,10} = 2.59$	$F_{10,185} = 4.96$***	-

Table 2.

Red grouse chick diet on two moors in Scotland ascertained through faecal analysis. The number and percentage of faecal samples containing each item are presented together with the numerical range of individual items per faecal sample where present.

	Overall (n=62)			Ralia (n=22)			Drumochter(n=40)		
Item	**n**	**%**	**range**	**n**	**%**	**range**	**n**	**%**	**range**
Heather Bracts	62	100	23-5600	22	100.0	23-5600	40	100.0	26-4000
Tipulidae	54	87.1	1-142	15	68.2	1-6	39	97.5	1-142
Moss capsule	32	51.6	1-155	8	36.4	1-42	24	60.0	1-155
Sundew Heads	30	48.4	1-146	5	22.7	2-94	25	62.5	1-146
Heather Seed	26	41.9	1-19	6	27.3	1-8	20	50.0	1-19
Chironomidae	22	35.5	1-87	3	13.6	1-3	19	47.5	1-87
Curculionidae	22	35.5	1-37	13	59.1	1-37	9	22.5	1-4
Symphata larvae sp.	15	24.2	1-5	6	27.3	1-5	9	22.5	1-4
Staphylinidae	15	24.2	1-4	9	40.9	1-3	6	15.0	1-4
Heather Hooks	12	19.4	1-10	3	13.6	2	9	22.5	1-10
Elateridae	11	17.7	1-4	6	27.3	1	5	12.5	1-4
Ticks	9	14.5	1-5	3	13.6	1-5	6	15.0	1-3
Opilionidae	8	12.9	1	1	4.5	1	7	17.5	1
Carabidae	7	11.3	1	5	22.7	1	2	5.0	1
Aranaidae sp.	6	9.7	1-2	3	13.6	1-2	3	7.5	1-2
Carabidae larvae	5	8.1	1-2	2	9.1	1	3	7.5	1-2
Symphata sp.	3	4.8	1	1	4.5	1	2	5.0	1
Formicidae	2	3.2	1	1	4.5	1	1	2.5	1
Ichneumonidae	1	1.6	1	1	4.5	1	0	0.0	-
Lepidoptera larvae	1	1.6	2	0	0.0	-	1	2.5	2

Table 3

Mean body mass and winglengths (± s.e.) of broods at 4 days and 10 days, and the results from GLMs testing differences between the two moors. Values presented are corrected for the exact age of the broods. * = $p < 0.05$, ** = $p < 0.01$.

	Drumochter	**Ralia**	**results from GLM**
mean brood body mass (g)			
4 days	25.3 ± 0.6	21.3 ± 0.6	moor: $F_{1,37} = 6.01$*
10 days	42.1 ± 1.5	36.57 ± 2.7	moor: $F_{1,36} = 7.64$*
			age*moor: $F_{1,36} = 8.69$**
mean brood winglength (mm)			
4 days	34.2 ± 0.8	28.1 ± 1.0	moor $F_{1,37} = 6.24$*
10 days	61.2 ± 1.7	55.6 ± 2.1	moor $F_{1,36} = 4.61$*
			age*moor $F_{1,36} = 5.39$*

FIGURE LEGENDS

Fig. 1.

Observed mean brood sizes from 35 managed red grouse moors in Scotland. A 1km^2 area of each moor was counted using pointing dogs in July for at least five years between 1985-1996. The two moors examined in detail in this paper are indicated by black shading (Ralia on the left, Drumochter on the right).

Fig. 2.

The relationship between mean brood body mass at 4 days (range 3-6) and the invertebrate component of the chick diet on Drumochter (?) and Ralia (?).

Fig. 3

Home range area (hectares) of broods in which all chicks survived between four and ten days old (survival =1), and broods in which some chicks died during this period (survival < 1).

Fig. 4

Mean chick body mass in three different dietary treatment groups: heather (•), heather + limited invertebrates (∇), and heather + unlimited invertebrates (■).

Figure 1 (ms 00/53)
Park, Robertson, Campbell, Foster, Russel, Newborn, & Hudson
Red grouse chick growth and survival

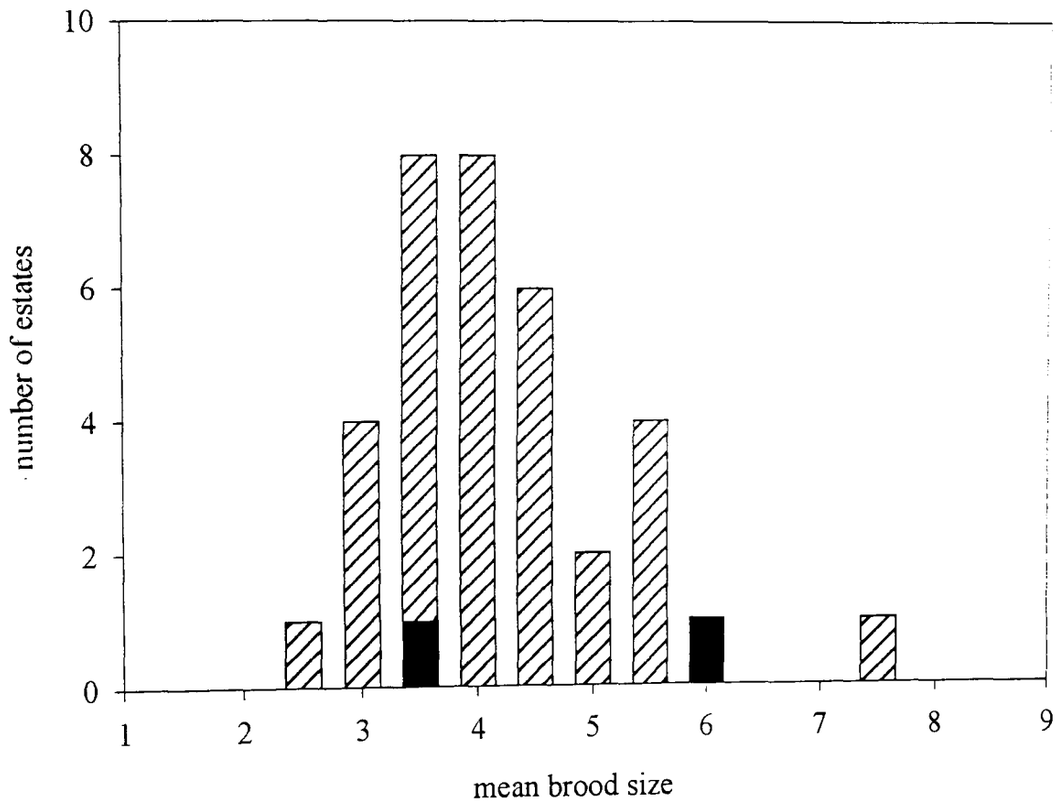

Figure 2 (ms 00/53)
Park, Robertson, Campbell, Foster, Russel, Newborn, & Hudson
Red grouse chick growth and survival

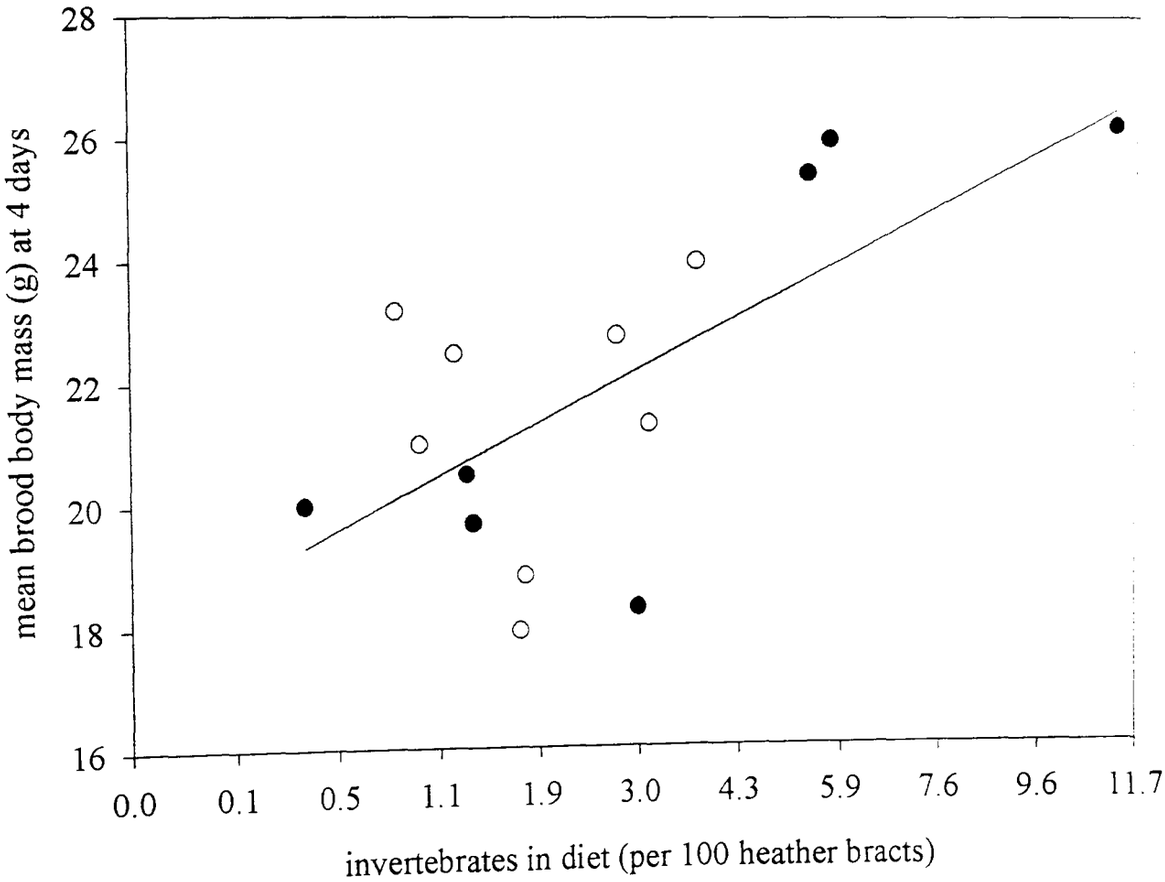

Figure 3 (ms 00/53)
Park, Robertson, Campbell, Foster, Russel, Newborn, & Hudson
Red grouse chick growth and survival

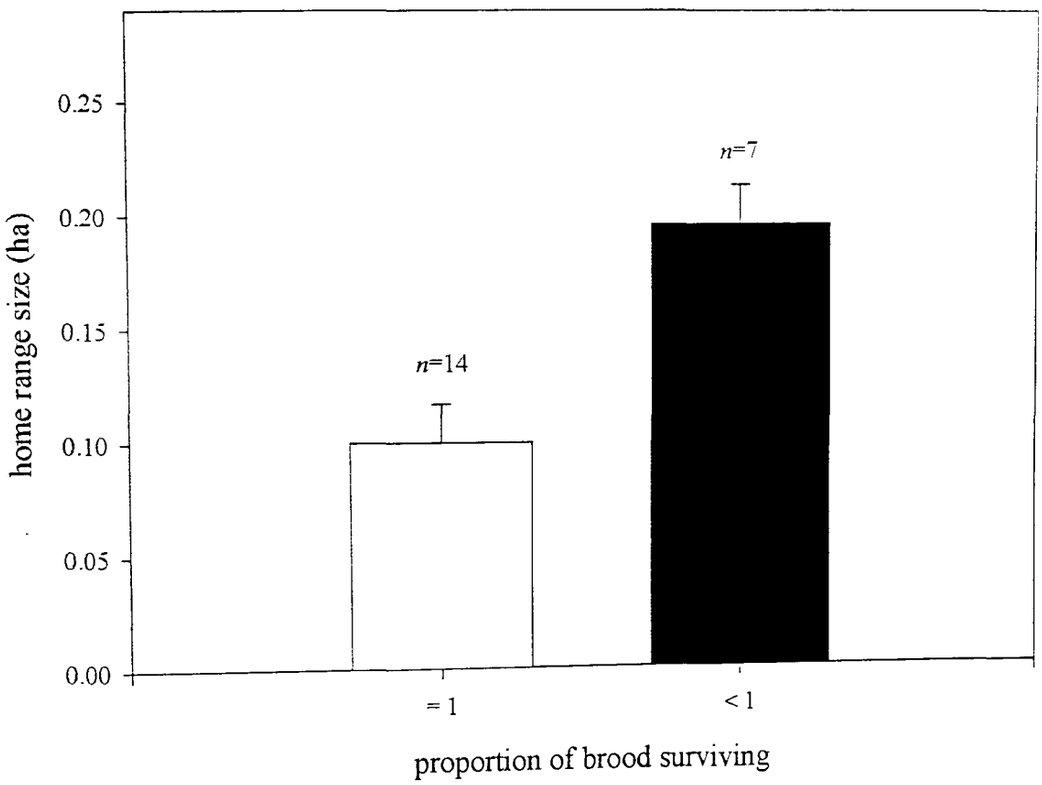

Figure 4 (ms 00/53)
Park, Robertson, Campbell, Foster, Russel, Newborn, & Hudson
Red grouse chick growth and survival