Invertebrate Interactions with Red Grouse (*Lagopus lagopus scoticus*)

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Author's Declaration

This thesis and the data presented in it are the results of my own original work, except where due acknowledgement has been made. No part of this work has been submitted in any previous application for a higher degree. The views expressed in this thesis are mine and not those of the University.

Alan Kirby

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Chapter 1

General Introduction: Factors Affecting Red Grouse Production

1.1 Managing wildlife populations

The management of wildlife populations is a widespread practice across the world. There are many reasons why management takes place and these include food production, pest control, conservation and sport. Due to the number of species targeted many different forms of management exist, for example fish stocks are managed for food by setting quotas (Begon *et al.* 1990), many deer species are controlled by culling or habitat management (Prior 1987) and barnacle geese *Branta leucopsis* are conserved by establishing reserves and management agreements with local farmers (Cope *et al.* 2003).

To effectively manage a population it is important to understand the major factors that affect it, such as predation, disease or resource scarcity, and the impact any proposed management solutions may have on the related community. Unfortunately many management schemes are implemented widely without their benefits/costs being evaluated (Whitby 2000).

Many species are managed in the UK indirectly, mainly as beneficiaries of agri-environment schemes (Ovenden *et al.* 1998), however, many wildlife populations are directly managed for the purposes of conservation or economics or both. One of these species is the red grouse *Lagopus lagopus scoticus*.

1.2 The importance of red grouse

The red grouse is a gamebird of economic and conservation value in upland areas of Scotland and Northern England (Hudson 1992). The economic value of red grouse increased in the 19th century, as driven shooting became popular. The management needed in order to produce the density of birds necessary for such sport led to a number of management practices, such as muirburn, that have shaped much of upland Britain. The result is moorland dominated by heather *Calluna vulgaris,* a habitat internationally recognised as being of high conservation value (Thompson *et al.* 1995). The red grouse was moved from the UK green list of wild birds to the amber list in 2002 due to a population decline of between 25 and 49% in the last 25 years (Gregory *et al.* 2002). The main declines have occurred in areas such as Southwest England, Northern Ireland and Wales; however, numbers remain plentiful enough for many viable commercial shoots in Northern England and Scotland to persist (Aebischer 2002 from Game Conservancy Trust 2002).

1.3 Aspects of Red grouse biology

Adult red grouse feed predominately on heather, and its shoots make up over 90% of the dietary intake (Jenkins *et al.* 1963, Wilson 1911). Despite most moors providing a superabundance of food, greater breeding densities are observed on areas with a high proportion of heather (Miller & Watson 1978, Moss 1967 from Savoury 1978). This relationship is demonstrated by the inverse relationship between heather cover and territory size (Miller & Watson 1978). Territories are established in autumn by males and are maintained until summer. The territories can break down during winter months due to snow cover, but are quickly re-established in spring. Females make nests in late April or early May and begin to lay eggs. Incubation begins when the clutch is complete. Clutch size usually varies between 5 and 15 eggs and incubation lasts for approximately 22 days. The chicks are nidifugous, relying on their mother for brooding only. Family groups begin to break down in the autumn when males move on to set up territories and females go in search of a mate for the coming season.

1.4 Factors affecting red grouse chick survival

Red grouse suffer their highest mortality rates as chicks, with most death occurring by day 15 (Moss *et al.* 1981). Many factors can play a role in grouse chick quality and these include maternal effects, predation, disease, weather and diet.

1.4.1 Maternal effects

Maternal effects can play an important role in governing chick survival. In birds, maternal effects have been shown to influence many measures relating to chick production and their subsequent quality. These measures include clutch size, the immunocompetence of offspring and body mass (Price 1998). An example of the strength of maternal effects comes from the collared flycatcher *Ficedula albicollis* whose clutch size can be affected by up to 25% (Price 1998). In red grouse and the closely related ptarmigan *Lagopus mutus* the weight of eggs has been shown to effect chick survival, which implies that the condition of the hen may be important (Moss *et al.* 1981, Moss & Watson 1984). Furthermore in a cross-fostering experiment Smith (in prep.) demonstrated that hen quality had a large direct effect on chick survival regardless of post hatch conditions.

1.4.2 Predation

Predators of grouse chicks include raptors such as the hen harrier *Circus cyaneus*, merlin *Falco columbarus* and short eared owl *Asio flammeus*, corvids such as ravens *Corvus corax* and carrion crows *Corvus corone corone* and mammals such as the fox *Vulpes vulpes* and stoat *Mustela erminea* (Jenkins *et al.* 1964). Out of this assemblage merlins and short eared owls only have an impact when the chicks are relatively small due to their inability to handle large prey (Jenkins *et al.* 1964) and corvids are known to infrequently take chicks preferring predation at the egg stage (Picozzi 1975).

The most frequently discussed predator is the hen harrier. Redpath (1991) attributed 91% of observed chick losses to hen harriers on a study moor at Langholm in Southern Scotland. Furthermore grouse moors with a breeding pair of hen harriers produced on average 17% fewer young grouse. These statistics highlight the large impact that predation can have locally on red grouse populations (Redpath 1991, Redpath & Thirgood 1997). The breeding density of hen harriers has been shown to be positively associated with the density of meadow pipits on grouse moors (Smith *et al.* 2001). In turn the density of meadow pipits is related to various habitat characteristics (Smith et al. 2001).

Predation risk can also increase independently of predator density due to habitat characteristics. The degree of fragmentation of habitat for woodland grouse, i.e. capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix*, is related to predation risk, as brood habitat is lost the predators gain in search efficiency rises exponentially (Storaas *et al.* 1999).

1.4.3 Disease

The effects of disease on grouse chicks can be both direct and indirect. Louping ill, an arbovirus belonging to the tick-borne encephalitis group (McGuire *et al.* 1998), was first identified in red grouse in 1963 (Watt et al. 1963, Williams et al. 1963). In laboratory studies an average death rate of 80% is observed (Reid 1975), although this proportion can be even higher in the field (Reid *et al.* 1978). The sheep or castor bean tick *Ixodes ricinus* transmits the disease but is not responsible for viral amplification. Sheep tick infestation in the absence of louping ill can also lead to chick fatalities (Chapter 4), the mechanism is most likely due to loss of feeding ability due to eyes becoming swollen shut or the energy loss associated with heavy parasitism.

The parasitic gastro-intestinal nematode *Trichostrongylus tenuis* may indirectly effect chick survival by lowering the amount of maternal input in to the eggs before laying

(Delahay & Moss 1996, Shaw & Moss 1990). Maternal condition has been shown to affect survival of offspring in a number of bird species and this is usually physically apparent as a change in egg size or lay date (Price 1998). These relationships have been shown in grouse and the closely related ptarmigan (Moss *et al.* 1981, Moss & Watson 1984). Delahay & Moss (1996) propose that the larger loss of weight during egg laying of hens with high burdens of *T. tenuis* may cause an increase in chick mortality rate by affecting the quality of brooding and other aspects of maternal care.

1.4.4 Weather

As with disease, weather may have a deleterious affect on chick survival before hatching by way of maternal effects. Although some evidence for this exists in the closely related willow grouse *Lagopus lagopus* (Brittas 1988, Steen *et al.* 1988) the areas in which these birds live are subject to more extremes of climate. In the red grouse the effect may come from warm April temperatures. Moss *et al.* (1981) presented some weak evidence to suggest that increases in April temperatures led to some clutches being laid early and the subsequent survival of early clutches was poor. This suggests that the effect is part maternal effect and part physical environment.

The affect of weather post hatch has two possible routes of influence. The first is that increases in cold or wet weather can lead to a loss of feeding time as chicks must brood more in order to maintain body temperature (Erikstad & Andersen 1983, Erikstad & Spidso 1982). The second is the effect of weather on the invertebrate prey available.

Differences in the type of prey available generally and in the types of habitat suitable for foraging in bad weather are suggested as a reason for poor chick survival in bad weather (Erikstad & Spidso 1982). Furthermore weather conditions can cause temporal differences between the chicks' peak need of invertebrates and the preys' peak availability (see section 1.3.5).

1.4.5 The diet of red grouse chicks

Gallinaceous gamebird chicks are nidifugous and begin to feed themselves an omnivorous diet soon after hatching. Of the twenty-one species of Galliformes included in a review by Savoury (1989), sixteen were recorded as having a diet consisting of over 90% invertebrate prey in the first 2 weeks of life. Only 2 species, which includes the red grouse, made up less than 10% of their diet with invertebrate food (Savoury 1989). Despite the small amount of invertebrate food taken in by red grouse it is still believed to be extremely important for grouse chick growth and survival (Park *et al.* 2001, Savoury 1977, 1989). Many bird species are thought to be sensitive to changes in the abundance of invertebrate food. This is most keenly demonstrated by the strong correlation between the falls in invertebrate numbers on farmland and the decline of many farmland birds that specialise on feeding their broods insects (Benton *et al.* 2002)

The type, as well as the quantity, of invertebrate food is important for growth rates and, in turn, survival. This has been shown in many gamebirds by providing chicks with both simulated diets and a restricted range of invertebrate prey (Borg & Toft 1999, Erikstad &

Spidso 1982, Liukkonen *et al.* 1996, Potts 1986, Richard *et al.* 2002, Southwood & Cross 1969, Warner *et al.* 1982). Willow grouse foraging patterns in cold wet summers differ markedly in habitat use from warm dry ones, this is presumably due to avoidance of vegetation types that will lead to chicks becoming wet and chilled. The change in foraging patterns alters the dietary intake and leads to changes in survival (Erikstad & Spidso 1982).

Red grouse utilise invertebrate food for approximately three weeks post hatch. Park *et al.* (2001) demonstrated that when invertebrate consumption increased chick growth rates increase, which, in turn, is correlated with better survival. Invertebrate food has a higher digestible protein content than plant material and higher concentrations of the two sulphur based amino acids, methionine and cystine, which are essential for feather synthesis (Bolton & Blair 1974, Savoury 1989). An example of the nutrient benefit of invertebrate food is shown by *Tipula subnidicornis*, a usual prey item. This crane-fly contains nine times the nitrogen and seven times more phosphorous than heather, which is the main food source of both adults and chicks (Leslie 1911, Butterfield & Coulson 1975, Savoury 1977).

Though the invertebrate food taken by red grouse chicks is varied, Diptera make up a large percentage of the diet. Of these the tipulid family makes up the majority of invertebrate food consumed (Grimshaw 1911, Hudson 1986, Savoury 1977, 1989, Park *et al.* 2001). Tipulids may be preferred, as many species are relatively sedentary making them vulnerable to predation (Butterfield & Coulson 1975).

The intake of invertebrate prey by grouse chicks can be influenced by the availability both spatially and temporally. The abundance of invertebrates spatially is governed by habitat type, with factors such as substrate type and vegetation characteristics playing a role (Coulson & Whittaker 1978, Sanderson *et al.* 1995). Park *et al.* (2001) demonstrated that more invertebrates were eaten in areas where more were present and this led to better growth rates and survival. The size of an average prey item, as well as the abundance of invertebrates, may also play a role. Picozzi *et al.* (1999) showed that capercaillie *Tetrao urogallus* chick survival was correlated with the size rather than abundance of invertebrate prey items in mid-June. The size of prey items and not just the number have also been shown to be important in nestling weight and fledging success of Great tits *Parus major* and blue tits *Parus caeruleus* (Naef-Daenzer & Keller 1999). Larger prey items may increase overall intake of invertebrate food or lead to greater foraging efficiency allowing chicks to minimise energy expenditure due to feeding.

The main prey species that red grouse chicks prey upon are targeted in their adult stage. The periods in which these invertebrates are present in the environment are relatively short. For example *Tipula subnodicornis* emerges from the substrate over a period of about 3 weeks (Coulson 1962), with *Molophilus ater,* another tipulid, emerging for approximately 11 days (Hadley 1969), both these species have been identified as important prey items of grouse (Coulson & Whittaker 1978, Grimshaw 1911). Furthermore, these two species along with an annelid worm *Cognettia sphagnetorum* form 75% of the invertebrate biomass on areas of blanket bog on a moorland reserve in the north of England (Coulson & Whittaker 1978). Over 80% of the invertebrate biomass is gained and lost in the 6 weeks from mid May until the end of June. Therefore, the main source of chick food insects is transient and so it is assumed that chick hatch is timed to correspond with the emergence of the peak in invertebrate food. There is some evidence that the date of chick hatch is earlier in years when April temperature is high (Moss *et al.* 1981) the same cue that causes earlier invertebrate pupation and therefore, emergence (Coulson & Whittaker 1978). However, in the great tit/blue tit system the same temperature cues are used by both birds and invertebrates but do not guarantee synchronisation between peak invertebrate biomass and the chick's window of major reliance on their caterpillar food. This is because the caterpillars' hatch and development is much more flexible than that of the birds (Van Noordwijk *et al.* 1995). Although the tits hatch earlier in warm years and later in cold years (Van Balen 1973) a time lag of just 2-3 days from the peak of caterpillar availability can have a marked effect on great tit fledging success (Van Noordwijk *et al.* 1995). The larger the time lag observed, the lower the nestling weight and fledging success (Dias & Blondell 1996). Perrins (1991) showed that the temporal relationship between the tits and the caterpillars was more important to fledging success than sheer abundance of food.

In the grouse/crane fly system the emergence times fluctuate between years, habitats and altitude. Hadley (1969) showed that *M. ater* emergence fluctuated between the years of study by up to 8 days. The type of substrate the larval stages inhabit can also affect the emergence by up to a week. Each graduation of 300 ft (approximately 100m) can lead to differences in emergence of 7-9 days. With upland areas suffering large increases in temperature and acidification due to global warming and pollution (SNH 2002) any affect on synchronisation may cause a marked affect on chick growth rate and/or survival.

1.5 The aims of study and thesis outline

This study focuses on identifying the spatial and temporal patterns that exist between invertebrate availability as chick food and red grouse production. Experimental manipulations of aspects of the moorland system are evaluated for their benefits to both grouse production and invertebrate abundance.

Biotic and abiotic factors governing invertebrate availability are investigated in chapter 2, as are the effects of small-scale experimental treatments of grazer exclusion, nutrient addition and pH status manipulation. Chapters 3 and 4 focus on a large-scale fertilisation experiment with attention being given to the broad-scale results of grouse production, invertebrate availability and vegetation changes (Chapter 3) and also the mechanisms that may affect grouse production (Chapter 4). The affects of temporal synchronicity between grouse chicks and the invertebrate food supply are investigated in chapter 5.

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Chapter 2

Manipulation of Invertebrate Numbers and Vegetation Characteristics on Grouse Moors: A Small Scale Experiment

2.1 Abstract

The factors that affect the distribution and abundance of invertebrate groups important in the diet of red grouse chicks were studied on moors in the central Scottish highlands. The pH status of these generally acidic moors was shown to be important with the higher the pH reading the greater the number of invertebrates trapped. This was true both generally and for the sub-order Nematocera that is arguably the most important grouse chick food group.

During the investigation three experimental treatments were applied in a factorial design in order to manipulate invertebrate numbers. The treatments were; grazer exclusion, N,P,K fertilisation and application of lime. Excluding grazers did not show a detectable effect on the number of invertebrates entering the traps. When combined with fertiliser as a treatment, grazer exclusion led to an increase in the amount of grasses and sedges present in the experimental plots. The addition of fertiliser was broadly successful in increasing the numbers of miscellaneous invertebrates and Nematocera. Counter-intuitively the application of fertiliser and lime simultaneously led to a decrease in sward height. The pH status of the experimental plots was raised by adding lime. Despite this manipulation of pH status no effect on invertebrate numbers was detected. However, liming led to a decrease in various minority plant species.

2.2 Introduction

2.2.1 The importance of moorland and its management

Heather *Calluna vulgaris* dominated moorland in the UK is a dwarf shrub community recognised internationally as a habitat of high conservation value (Thompson *et al.* 1995). The system retains its structure due to management practices employed to benefit the production of red grouse *Lagopus lagopus scoticus* a gamebird of economic and conservation importance (Hudson 1992). Vegetation structure is maintained by many physical factors but is kept in its successional stage by muirburn, a rotational burning regime giving rise to a number of different aged stands of heather and preventing birch and pine establishment, and grazing.

2.2.2 The invertebrate community of heather dominated moorland

The invertebrate community on moorland is relatively species poor with approximately 1100 being recorded on the Moorhouse national nature reserve compared to around 4000 from Wytham woods in Oxfordshire (Coulson & Whittaker 1978). Of the species present over 60% are from the order Diptera (Nelson 1965, from Coulson & Whittaker 1978).

The distribution of the invertebrates present is governed by both substrate and vegetation characteristics and these are spatially auto correlated (Sanderson *et al.* 1995). The substrate is the most important factor for many of the major inhabitants of moorland, for example the number of eggs laid and the subsequent survival of eggs and larval stages of *Molophilus ater*, a small crane-fly, is dependent on the substrate type (Hadley 1969, 1971). Other invertebrates, including many hemipterans, respond to the level of food plants available rather than substrate (Richardson *et al.* 2002).

The periods in which these invertebrates are present in their adult forms in the moorland environment are relatively short. For example *Tipula subnodicornis*, a crane fly, emerges over a period of about 3 weeks (Coulson 1962), with *Molophilus ater* emerging over approximately 11 days (Hadley 1969). Furthermore, these two species along with an annelid worm, *Cognettia sphagnetorum*, can form 75% of the invertebrate biomass on areas of blanket bog (Coulson & Whittaker 1978). Over 80% of the above ground invertebrate biomass is gained and lost in the 6 weeks from mid May until the end of June. The transient nature of the majority of the invertebrate community has repercussions for the predators that feed upon them.

2.2.3 Red grouse as predators of invertebrates

To the managers of moorland the most important predators of invertebrates are the chicks of the red grouse. Like many other game birds grouse chicks feed on invertebrates in the first 3-4 weeks of life before commencing a diet equivalent to that of an adult bird (Savoury 1977, 1989). Of particular importance to grouse chicks are members of the Nematocera, a sub-order of dipterans that include the crane flies and the midges (Coulson & Whittaker 1978, Grimshaw 1911, Park *et al.* 2001, Savoury 1977, 1989).

As the role of invertebrates as food is thought to be important in the production of grouse, the factors that affect their distribution and abundance are of interest for management. Furthermore manipulation of invertebrate numbers for the benefit of grouse production could be seen as an important tool for game managers in the future. The manipulation of grazing regimes, nutrient addition and pH status could all play a role in managing the invertebrate community.

2.2.4 The impact of grazing on invertebrate communities

The impact of grazing can have a marked effect on the invertebrate community. For example in the remaining fragments of Scots pine, *Pinus sylvestris*, forest the exclusion of vertebrate grazers leads to a large increase in many invertebrate orders, including the Lepidoptera, Hemiptera and Diptera (Baines *et al.* 1994). This change in invertebrate production could be due to changes in plant community structure due to grazing or direct competition for resources (Baines *et al.* 1994). Heavily grazed fragments of Scots pine woods also support fewer black grouse, *Tetrao tetrix*, and this may be due to a lack of invertebrate food for chicks (Baines 1996).

The increasing height of food plants and therefore, their structural complexity can lead to an increase in the number of species and abundance of invertebrates present (Lawton 1983). With greater heather height the number of lepidopteran larvae recovered from the vegetation increases (Haysom & Coulson 1998), this may have important consequences for red grouse chicks.

2.2.5 Nutrient addition on moorland and its impact on invertebrates

The addition of nutrients to the grouse moor system has been investigated in a series of experiments in the 1960's and 70's (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984). These experiments focused on the effect of fertilisation on grouse density and production and overlooked the impacts on invertebrates. In work on a related dwarf shrub community Richardson *et al.* (2002) showed that the abundance of invertebrates increased with nutrient addition, although the diversity decreased. The effect that fertiliser is most likely to have on invertebrates, is to improve the survival and/or fecundity of species that are herbivorous or feed on organic material. For example the survival rates of heather beetle, *Lochmaea suturalis*, on lowland heath, have been indirectly shown to benefit by addition of nitrogen by increasing the larval growth rate and increasing the average weight of an adult (Power *et al.* 1998).

The increase in heather cover, annual growth rate and flowering has been shown to increase with the addition of fertiliser (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984), as have grasses commonly found on moorland (Alonso & Hartley 1998). In the absence of grazers the addition of fertiliser has also been shown to increase the density of heather canopy (Alonso & Hartley 1998). These measures all indirectly measure vegetation complexity and therefore, may lead to a greater diversity or abundance of invertebrates (Lawton 1983).

2.2.6 pH status and invertebrate production

Acid pollution can have a damaging effect in the uplands despite relatively low levels of deposition occurring. This is because the naturally acidic conditions of moorland and the species of plants and animals that occupy them are more vulnerable to change (SNH 2002). In many fresh water stream, river and pond systems liming has been used as a method to reverse acidification and has resulted in increases in acid sensitive invertebrates (Bradley & Ormerod 2002, Fjellheim & Raddum 2001, Miskimmin *et al.* 1995, Walseng *et al.* 2001) and in some cases fish numbers (Walseng *et al.* 2001). When tried in wetland catchments in Wales the structure of the invertebrate community changed markedly but numbers did not (Buckton & Ormerod 1997), however, only coleopterans, hemipterans and arachnids were considered. If the invertebrate community on grouse moors has been affected by acid deposition an increase in pH may lead to an increase in the invertebrate communities' diversity and/or abundance.

2.2.7 Study aims

The aim of this study is to investigate possible factors concerned with invertebrate distribution and to determine whether the abundance of invertebrates can be manipulated. Grazer exclusion, fertilisation and liming are used as experimental techniques and their effect on invertebrates and habitat investigated.

2.3 Materials and Methods

2.3.1 The study site

The study site is in the Spey Valley in the Scottish Central Highlands. The study used four contiguous moors managed intensively for driven grouse shooting, South Drumochter, Phones, Cuaich and Ralia. All the areas used for experimentation were characterised as either blanket bog or wet heath. The sites were between the altitudes of 350m to 450m.

2.3.2 Random plot assignment

48 areas representative of the main habitat characteristics of the estates were chosen in April 2000. Of these plots, 24 were drawn at random to become the experimental plots. Each experimental site consisted of a pair of 10m X 10m plots, one marked with posts and the other fenced (see treatments). These experimental plots were monitored in the summers from 2000-2002.

2.3.3 Physical variable monitoring

Each site had a number of physical variables measured in order to characterise them. Exposure was estimated by taking 8 measures of the angle to the horizon with a clinometer, each measure being taken at 45° to the proceeding one starting at north. The resulting data was used to calculate a measure of exposure named TOPEX (Forestry

Commission 1991). These measurements were taken once at the beginning of the experiment.

The water table status was monitored in each plot using a sip well. A tube of 5cm diameter with holes drilled along its length was sunk to a depth of 75cm. The measurement taken was the distance between ground level and the surface of the water in the well. The water table status was recorded each time the plot was visited in the season, once every 8 days in 2000 and once every 10 days in 2001-2.

The pH was monitored by taking water samples at the beginning and the end of the monitoring season and testing with a bench pH meter.

2.3.4 Vegetation surveys

In the August of each season the vegetation in each 10m X 10m plot was surveyed. 25 random points were assigned on a 1m grid and located. At each point a number of measurements were taken. Sward height was measured with a marked cane with the record being at the point where the tallest piece of vegetation touched the stick. The amount of heather, including cross-leaf, *Erica tetralix*, and bell heather, *E. cinera,* which were sparse, was classified by counting the number of shoots that touched the cane, as were grass and sedges. Minority species, mainly herbs, were recorded in one miscellaneous category. Ground cover was recorded by allotting the substrate to one of five categories; moss (other than *Sphagnum spp.*), *Sphagnum spp.*, lichen dominated, leaf litter dominated and moss/lichen/litter mix.

2.3.5 Experimental treatments; grazer exclusion

Three experimental treatments were applied to the plots. The first treatment was grazer exclusion. A fence was erected in March 2000 on one plot of each of the 24 experimental sites. Each fence was 1m high with an outward facing lip in order to prevent grazers burrowing under the fence. Despite the fences being low enough for red deer *Cervus elaphas* and roe deer *Capreolus capreolus* to jump it was believed that the small plots would elicit a neophobic response and not be breached. In the second and third years of the study occasional signs of grazing were seen in a small number of plots. The impact was measured by recording the ratio of grazed shoots to ungrazed shoots along two 1m transects. No ratio for the fenced plots ever exceeded 18% of the grazing seen in the corresponding unfenced plot. Due to this small impact the treatment of grazer exclusion was placed in statistical models as a two level factor.

2.3.6 Experimental treatments; the application of fertiliser and lime

Treatments of fertiliser and lime were used in the seasons of 2001 and 2002. The treatments were applied in a 2 X 2 factorial design. Agricultural grade hydrated lime was applied to 12 pairs of plots in late August 2000 and again in late August 2001 at a rate of 300gm^{-1}, an amount estimated to be enough to change the pH by approximately 1 (North Eastern Farmers Agricultural Merchant Pers. comm. 2000). 7,7,7 N,P,K fertiliser was applied in Late August of both years as well as in early April of 2001 and 2002. The application rate was at 100gm^{-1}. This application rate is in the range used in past fertilisation experiments in dwarf shrub communities (Alonso & Hartley 1998, Miller *et al.* 1970, Power *et al.* 1998, Richardson et al. 2002, Watson & O'Hare 1979, Watson *et al.* 1984).

2.3.7 Invertebrate monitoring

Invertebrates were monitored with yellow water traps measuring 40cm X 20cm X 10cm. The colour was chosen due to its attractiveness to the majority of invertebrate groups represented on moorland (Southwood 1978). The traps were emptied once every 8 days in 2000, with traps being set from 1st May to 7th July and once every 10 days in each of the two following seasons (1st May to 1st July in 2001, 3rd May to 24th June 2002).

The samples were sorted into orders or sub-orders in the laboratory. The Nematocera were differentiated from the other dipterans due to their importance as chick food insects (Grimshaw 1911, Hudson 1986, Park *et al.* 2001, Savoury 1977, 1989). The main nematocerans trapped on the study areas were Tipulidae (crane flies) and Chironomidae (non-biting midges), the two major groups identified in faecal samples of chicks in the area by Park *et al.* (2001). The invertebrate measures used in the analysis were the nematoceran count and the sum of the other groups of invertebrates counted. From the latter group the Nematocera were excluded as were individuals of the Hymenoptera and Coleoptera judged to be too large for a grouse chick to feed on. The Acari were also discounted as the samples were heavily biased by mites brought in to the traps by

Bombus spp. This measure of invertebrates will henceforth be referred to as other invertebrates.

2.3.8 Data analysis

The effect of physical variables on the year 1 Nematocera and other invertebrates counts were investigated with generalised linear models (GLM) with negative binomial errors. The minimal model was ascertained by a process of stepwise deletion and addition due to the number of explanatory variables considered, including all 2 way interactions. For this process the single terms in the model were considered as a platform in which to try different combinations of interaction terms. These models were compared after a process of stepwise deletion. The important elements of each of these models was combined and compared before a minimal model was reached. For each site the average number trapped in each period was used. Table 2.1 shows the terms in the maximal model.

Table 2.1. The terms in the maximal model investigating the effect of physical effects on the invertebrate community.

Fixed Terms
Water Table
pH
Grass/Sedge Contacts
Heather Shoot Contacts
Sward Height
Other Plant Species Contacts
TOPEX (exposure)
Ground Cover
Grazer Exclusion
NB: all 2 way interactions considered

The effect of the treatments in years 2 and 3 were investigated with GLMs with negative binomial errors. The models contained the treatments and measures of water table and exposure. These physical variables were included, as they were the ones measured that could not be affected by the treatments. All GLMs were carried out in S-Plus 6 Professional release 1.

The effect of treatment on invertebrate numbers over the entire study was investigated with a repeated measures analysis of variance (repeated ANOVA) after the data were log transformed to achieve normality. The effects on the vegetation characteristics and pH were also investigated this way. These analyses were carried out in GenStat 6th edition.

2.4 Results

2.4.1 Physical factors affecting nematoceran abundance in year 1

The number of Nematocera trapped in the first season increased as pH levels became more alkaline ($\chi^2_{1,46} = 4.54$, $P = 0.033$, Figure 2.1). The derived minimal model contained no other explanatory variables (Table 2.2).

Figure 2.1. The average number of Nematocera trapped at different pH levels. From the minimal model Average Nematocera ~ pH

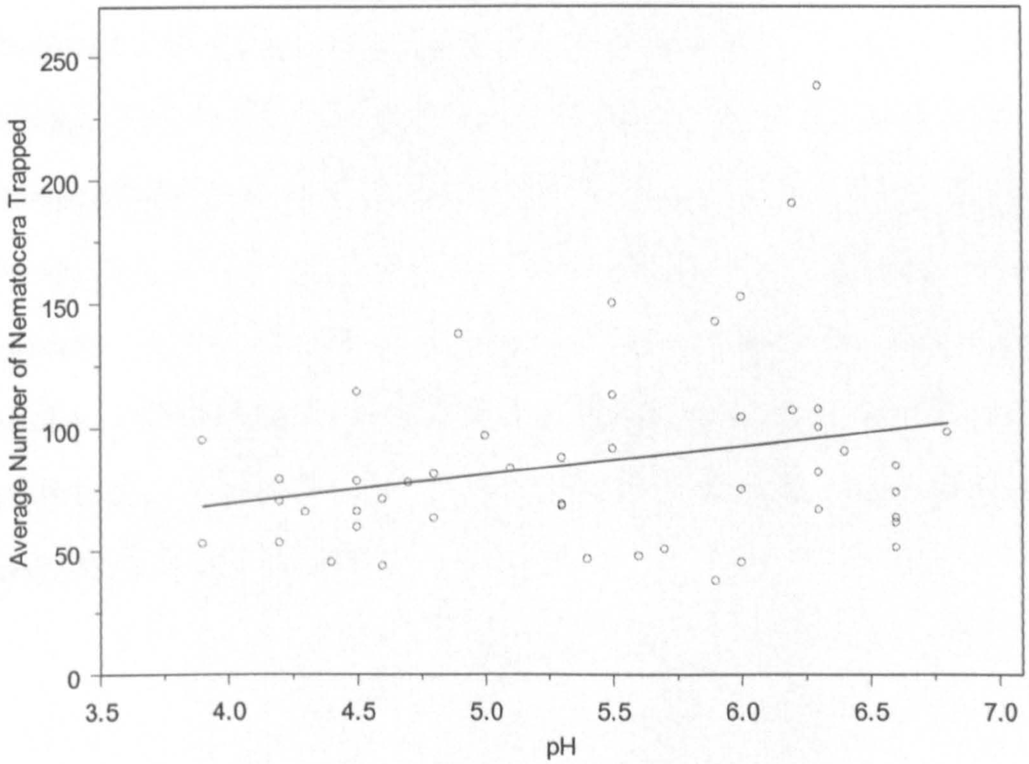


Table 2.2. The χ^2 and probability values for the single terms when stepwise deleted from the model.

Term	χ^2	P-Value
Misc. Species	3.509	0.062
Water Table	2.823	0.093
Ground Cover	3.876	0.423
Sward Height	0.608	0.440
Grass/Sedge	0.342	0.558
Exposure	0.189	0.664
Heather	0.011	0.918
Grazer Exclusion	0.002	0.965

2.4.2 Physical factors affecting other invertebrates abundance in year 1

The number of invertebrates trapped was significantly related to three physical factors, although none of these terms interacted with each other. As the level of exposure decreased the number of invertebrates increased ($\chi^2_{1,44} = 21.99$, $P < 0.001$, Figure 2.2). As the alkalinity of the substrate increased the number of invertebrates counted also increased, like the nematocerans ($\chi^2_{1,46} = 19.37$, $P < 0.001$). The sward height of the vegetation in the experimental areas significantly influenced the numbers of invertebrates trapped ($\chi^2_{1,45} = 9.31$, $P < 0.001$, Figure 2.3), with canopies of greater height producing greater numbers of invertebrates.

Figure 2.2. The average number of other invertebrates trapped at different levels of exposure.

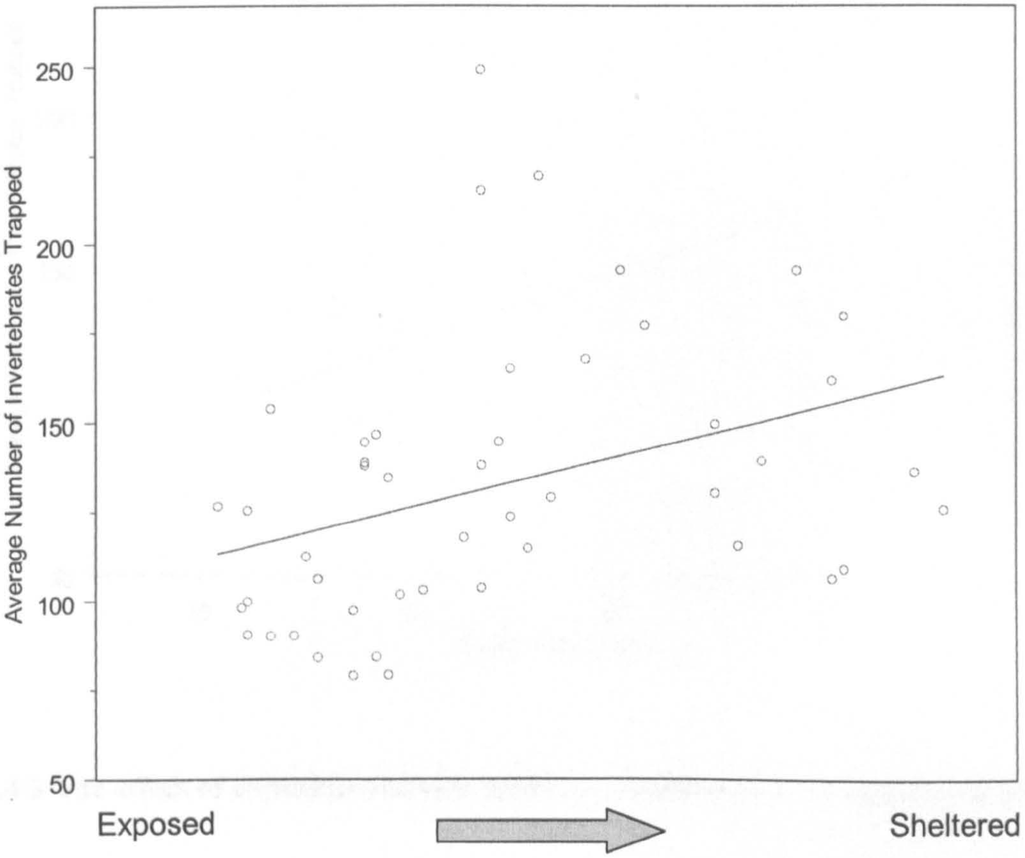
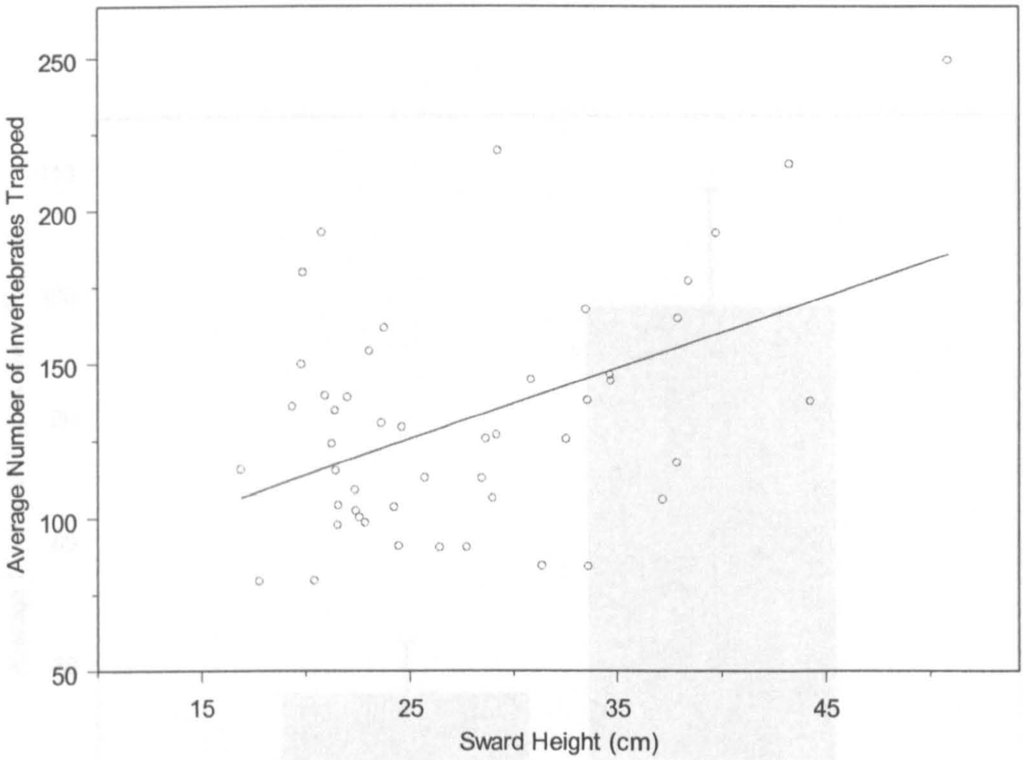


Figure 2.3. The average number of other invertebrates trapped at different sward heights.



2.4.3 The effect of experimental treatments on nematoceran abundance in year 2

The application of fertiliser was significantly related to an increase in the number of Nematocera trapped in the first season of treatment ($\chi^2_{1,46} = 13.12$, $P < 0.001$, figure 2.4). The height of the water table was also of importance to the number of Nematocera trapped ($\chi^2_{1,46} = 3.66$, $P = 0.055$, figure 2.5) with the number trapped declining as the average distance of water from the surface became smaller.

Figure 2.4. The number of Nematocera trapped in areas with and without an application of fertiliser.

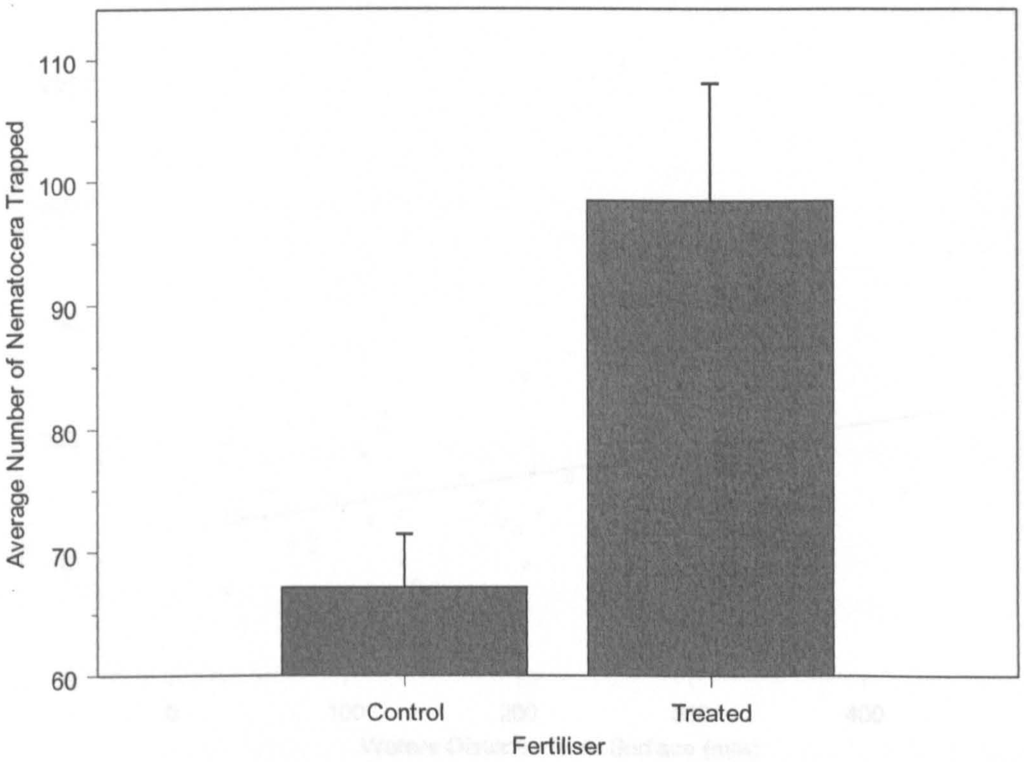
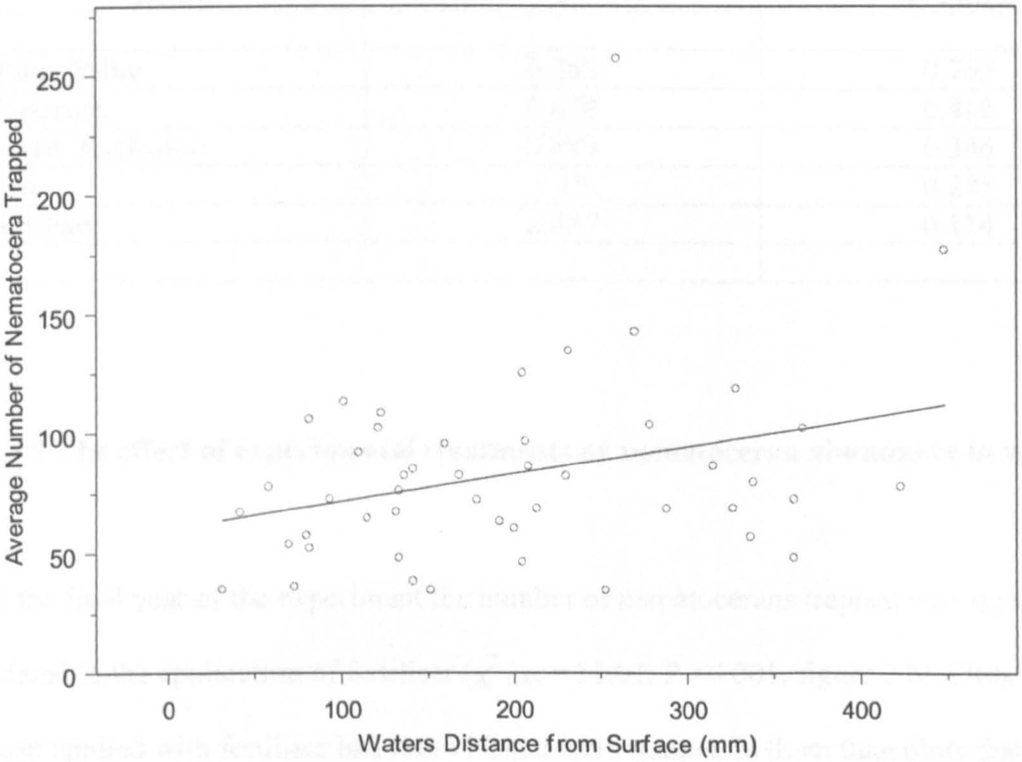


Figure 2.5. The number of nematocerans trapped in relation to the distance of the water table from the ground surface.



2.4.4 The effect of experimental treatments on the abundance of other invertebrates in year 2

The experimental treatments had no detectable effects on the number of other invertebrates trapped in the season following application (table 2.3).

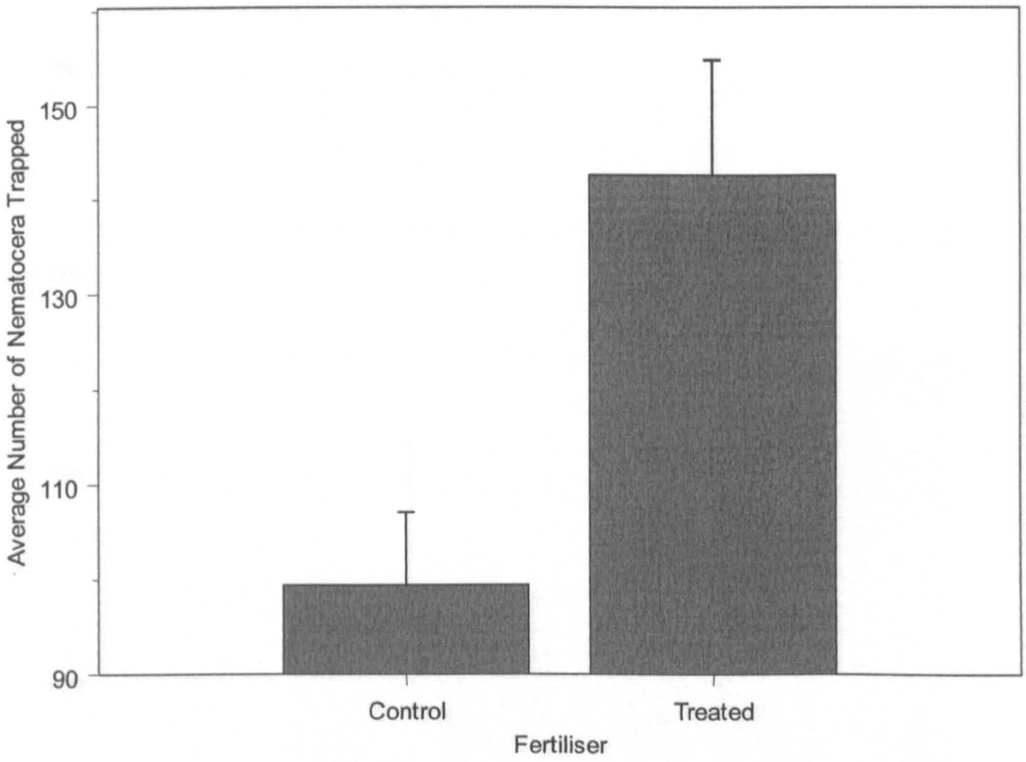
Table 2.3. The χ^2 and probability values of the single terms in the model at the time of stepwise deletion.

Term	X^2	P-Value
Water Table	0.088	0.765
Exposure	0.678	0.410
Grazer Exclusion	0.889	0.346
Lime	1.19	0.275
Fertiliser	2.487	0.114

2.4.5 The effect of experimental treatments on nematoceran abundance in year 3

In the final year of the experiment the number of nematocerans trapped was significantly related to the application of fertiliser ($\chi^2_{1,46} = 11.01$, $P < 0.001$, figure 2.6). Plots that had been applied with fertiliser had more Nematocera trapped in them than plots that had not been treated.

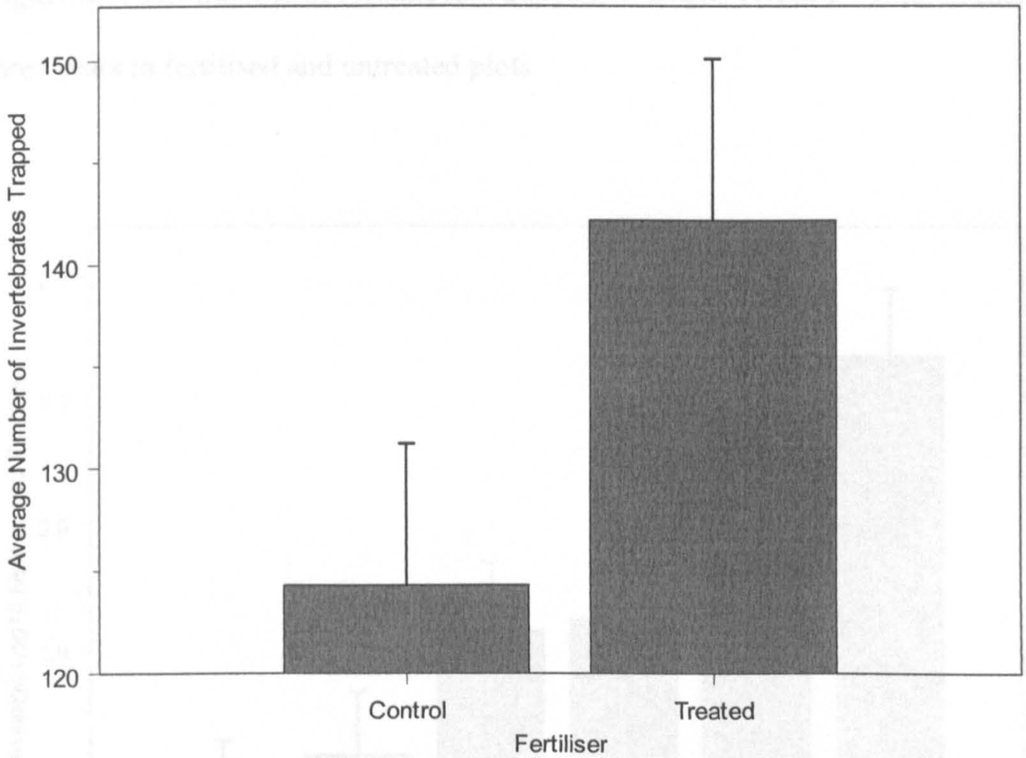
Figure 2.6. The number of Nematocera trapped in plots treated with fertiliser compared to those that received no application.



2.4.6 The effect of experimental treatments on the other invertebrates abundance in year 3

The number of other invertebrates trapped in year 3 was related to the fertiliser application, however this relationship was weak and was not quite significant at the 5% level ($\chi^2_{1,46} = 3.17$, P = 0.075, figure 2.7). No other term in the model was close to being significant.

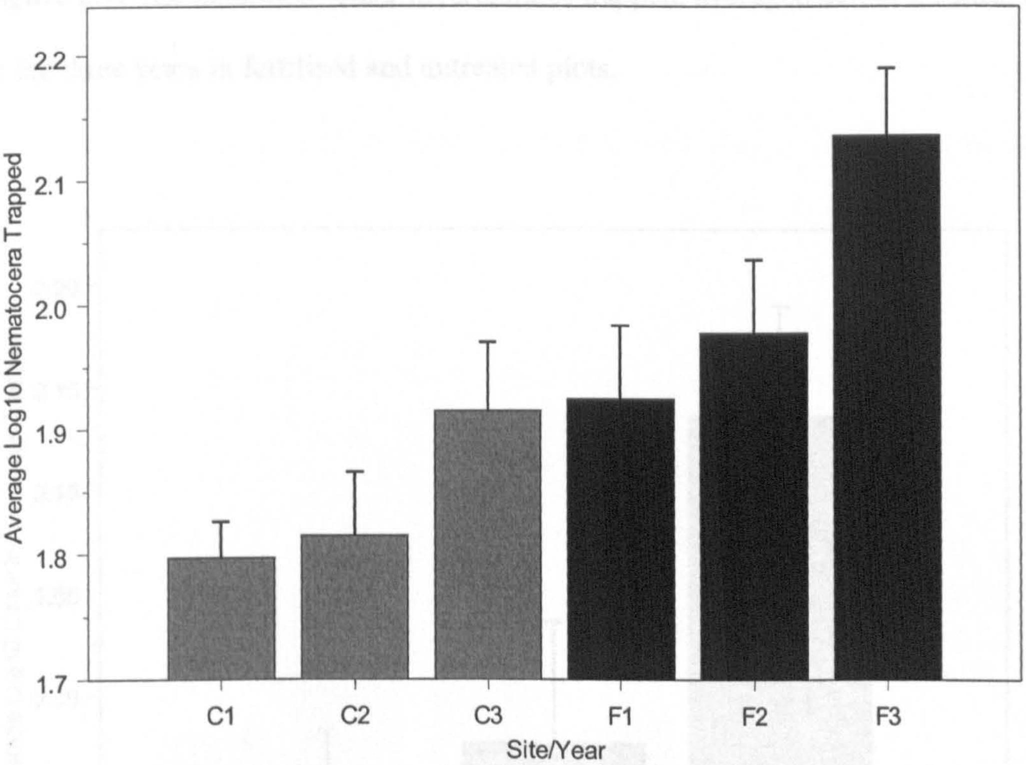
Figure 2.7. The number of other invertebrates trapped in year 3 in plots treated with fertiliser compared to those that received no application.



2.4.7 The effect of experimental treatments on the Nematocera across years

Neither, the exclusion of grazers nor the application of lime were significant in the model (Grazer Exclusion: $F_{1,46} = 0.2$, $P = 0.655$, Lime: $F_{1,46} = 0.73$, $P = 0.398$), nor did they have a significant interaction with time (Time * Grazer Exclusion: $F_{2,80} = 0.28$, $P = 0.750$, Time * Lime: $F_{2,80} = 1.53$, $P = 0.223$). The application of fertiliser had a positive significant effect on the number of Nematocera trapped ($F_{1,46} = 16.19$, $P < 0.001$), although there was no significant interaction with time ($F_{2,92} = 0.7$, $P = 0.5$). The number of nematocerans trapped was effected by year ($F_{2,92} = 16.29$, $P < 0.001$, figure 2.8).

Figure 2.8. The number of Nematocera trapped, averaged across all sites, in each of the three years in fertilised and untreated plots

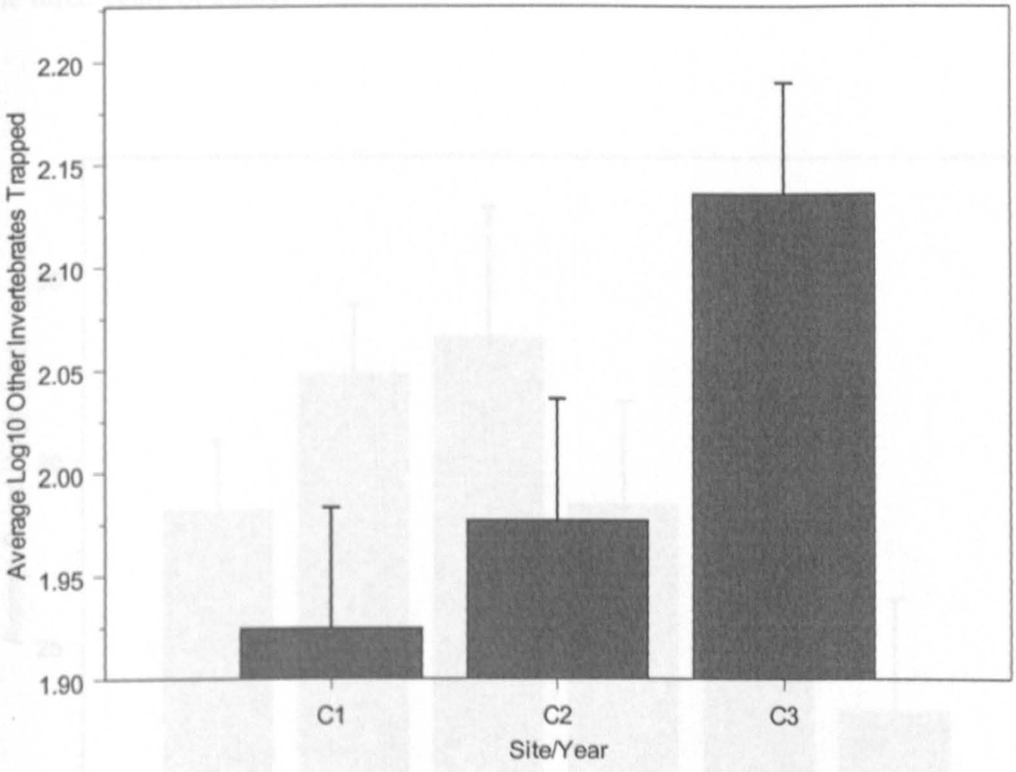


C = Control, F = Treated with fertiliser, Numbers denote year of study

2.4.8 The effect of experimental treatments on the numbers of other invertebrates trapped across years

Time was the only significant term in the model looking at the effects of experimental treatments across years ($F_{2,92} = 3.69$, $P = 0.033$, figure 2.9).

Figure 2.9. The number of other invertebrates trapped, averaged across all sites, in each of the three years in fertilised and untreated plots.



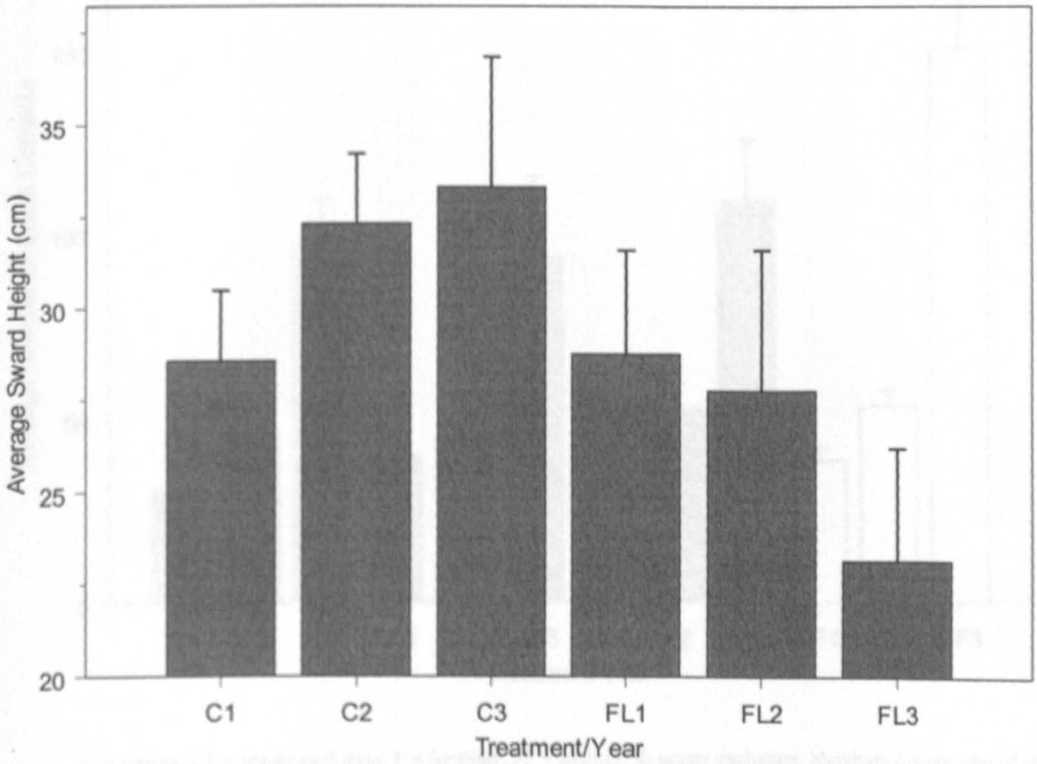
C = Control, Numbers denote year of study

2.4.9 The effect of experimental treatments on vegetation characteristics

2.4.9.1 Sward height

The height of sward became progressively shorter over the three years of study in plots that were treated with fertiliser and lime (Time*Fertiliser*Lime, $F_{2,88} = 3.45$, $P = 0.042$, figure 2.10).

Figure 2.10. The average sward height in plots treated with fertiliser and lime in each of the three years of study.

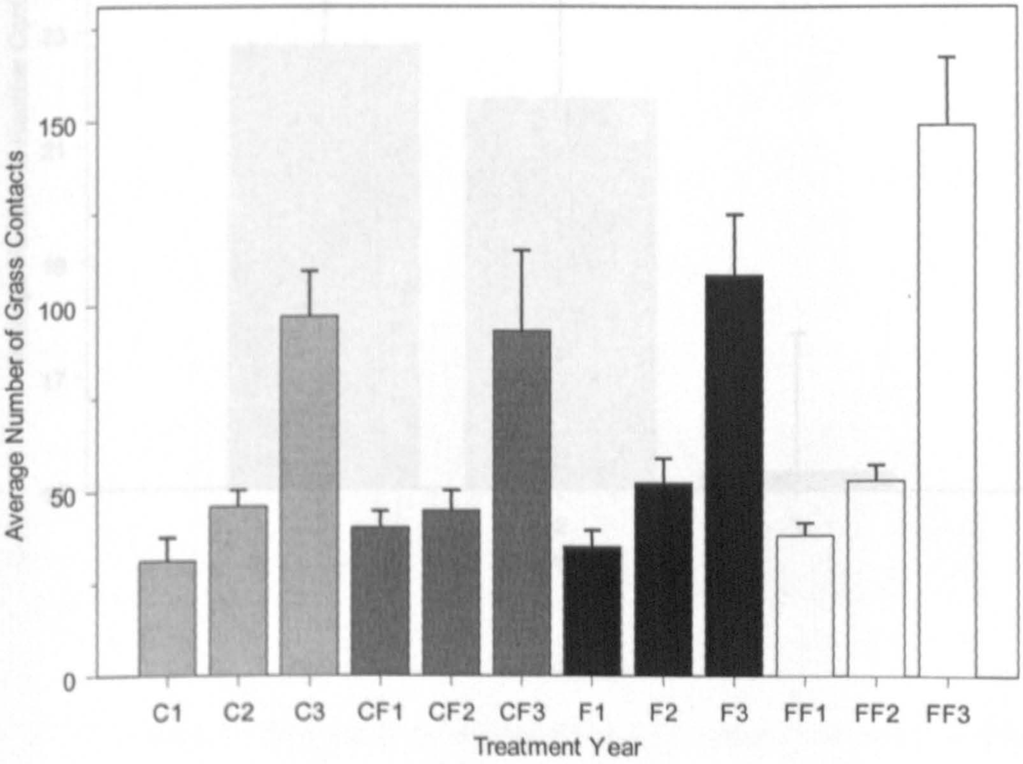


C = Control (untreated), FL = Fertilised and limed

2.4.9.2 Grasses and Sedges

The greatest effect on grass/sedge cover was due to time ($F_{2,47} = 172.91$, $P < 0.001$). The amount of grass/sedge present increased in all treatment categories over time. The interaction term of time*fertiliser*grazer exclusion gave a weak positive result ($F_{2,47} = 3.29$, $P < 0.069$, figure 2.11).

Figure 2.11. The amount of grass present in each of the three years of study in control, grazer excluded and fertilised plots.

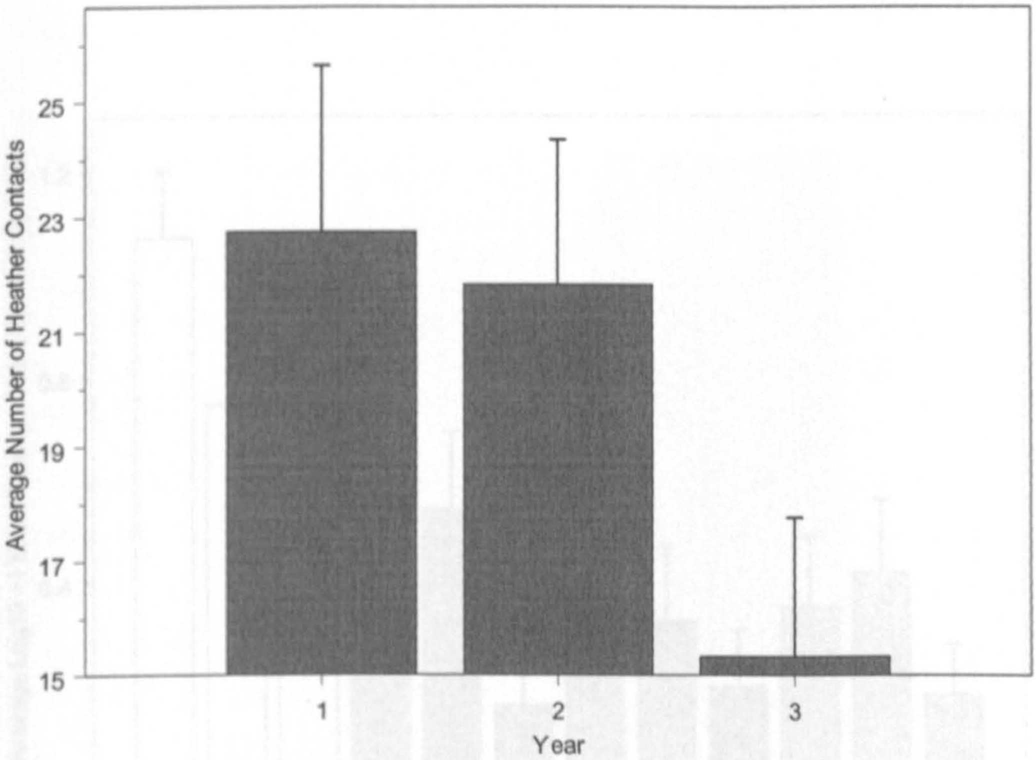


C = control, CF = grazer exclusion, F = fertiliser, FF = fertiliser & grazer exclusion, Numbers denote year of study

2.4.9.3 Heather

The amount of heather does not appear to be affected by the application of fertiliser or lime and the exclusion of grazers. However, the amount of heather recorded did fall over time ($F_{2,47} = 6.58$, $P = 0.004$, figure 2.12).

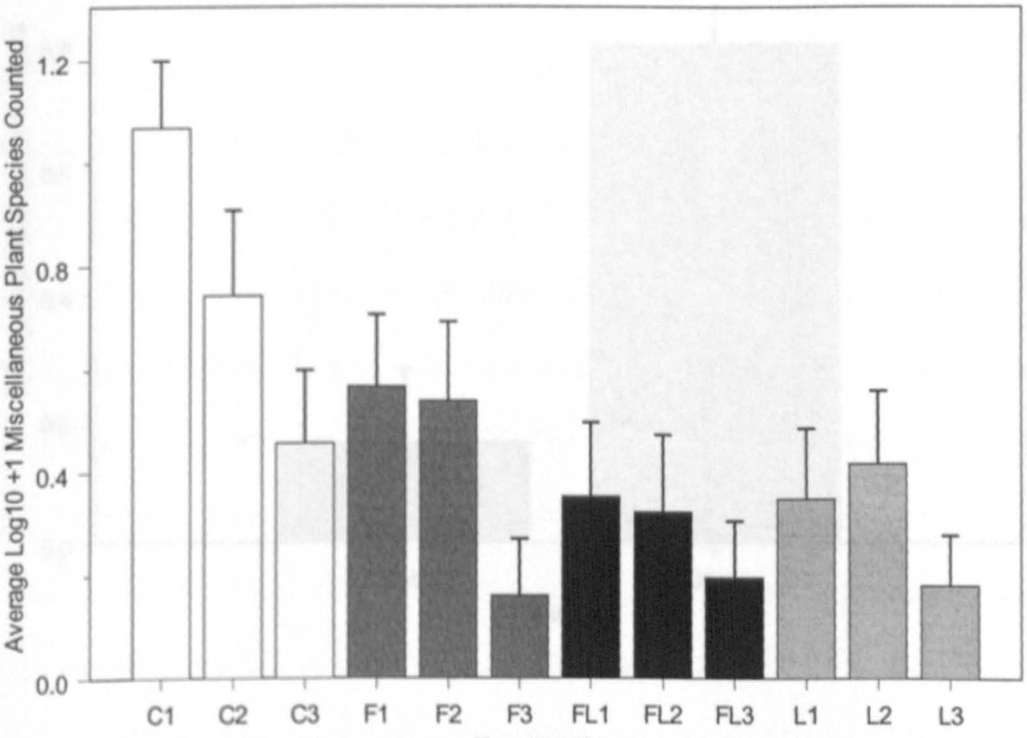
Figure 2.12. The number of heather contacts in the experimental plots over time.



2.4.9.4 Miscellaneous species

The presence of plant species that do not fall in to the dominant groups increased after the first application of lime and decreased in the third year ($F_{2,92} = 3.85$, $P = 0.026$, figure 2.13). The control and other treatment groups showed a steady decrease over time ($F_{2,92} = 15.82$, $P < 0.001$).

Figure 2.13. The number of contacts of minority species over time.

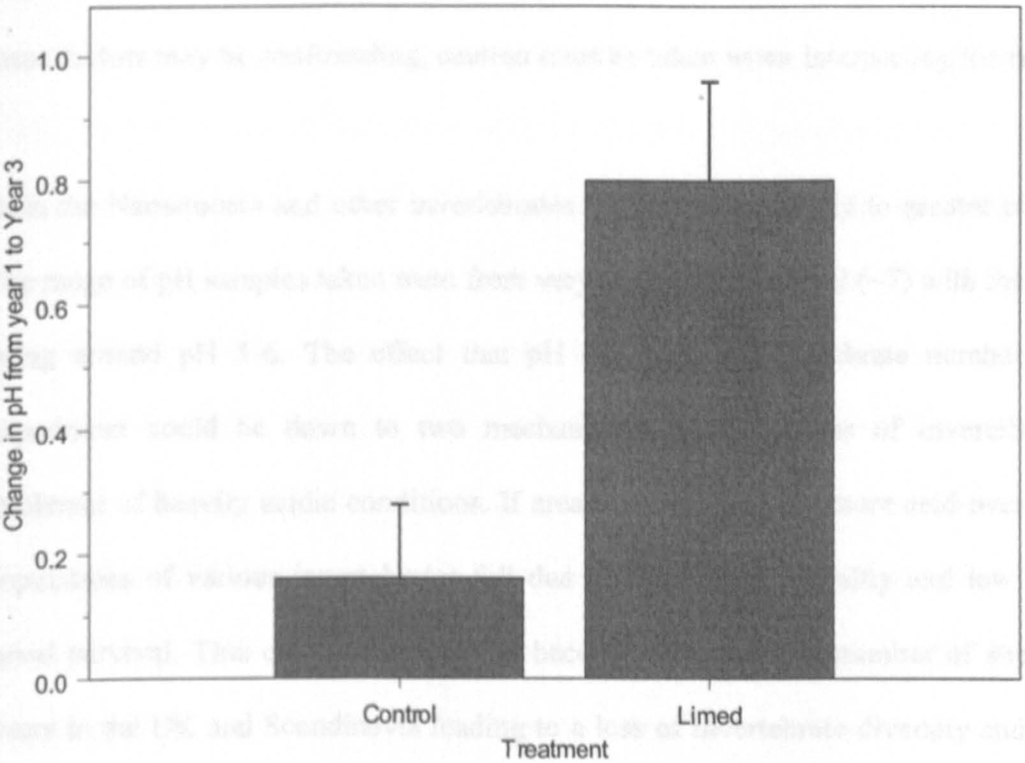


C = Control, F = Fertilised, FL = Fertilised & Limed, L = Limed, Numbers = Year of study

2.4.9.5 pH

The pH status of the experimental plots was raised by the addition of lime over time ($F_{2,92} = 4.76$, $P = 0.013$, figure 2.14) but remained unchanged by application of fertiliser ($F_{2,47} = 0.38$, $P = 0.669$).

Figure 2.14. The change in average pH from year one to year 3.



2.5 Discussion

2.5.1 The effects of physical variables on invertebrate abundance

This study suggests that a number of different factors play a role in determining the relative abundance of invertebrates on heather dominated moorland. Sanderson *et al.* (1995) demonstrated that both aspects of substrate and the plant community were responsible for the invertebrate distribution on moorland, however, they warn that, as these factors may be confounding, caution must be taken when interpreting the results.

Both the Nematocera and other invertebrates responded positively to greater pH values. The range of pH samples taken went from very acid (~4) to neutral (~7) with the majority being around pH 5-6. The effect that pH has had on invertebrate numbers in this experiment could be down to two mechanisms. Many species of invertebrates are intolerant of heavily acidic conditions. If areas become steadily more acid over time the populations of various invertebrates fall due to loss of egg viability and low levels of larval survival. This chain of events has become common in a number of streams and rivers in the UK and Scandinavia leading to a loss of invertebrate diversity and biomass and a subsequent fall in fish numbers. In a number of the affected water courses experimental applications of lime have been used to reverse the loss of invertebrate numbers and diversity (Bradley & Ormerod 2002, Fjellheim & Raddum 2001, Miskimmin *et al.* 1995, Walseng *et al.* 2001) and in one case increase the number of fish present (Walseng *et al.* 2001). The results gathered in the first year of this experiment led to the application of lime being decided upon as an experimental treatment.

Having a low pH value may also affect invertebrates by effectively restricting the amount of nutrients available to the vegetative community. Peat acts as a simple cation exchange that effectively strips the water moving through it of nutrients (Bragg 2002). This process is more severe at low pH readings resulting in nutrient poor habitats in acidic conditions. Invertebrate numbers and diversity can be affected by levels of nutrients in food plants or the structural diversity of the vegetative community (Haysom & Coulson 1998, Lawton 1983, Richardson *et al.* 2002). Both of these things are affected by nutrient availability and therefore, fertiliser application was considered a worthwhile experimental treatment.

The number of other invertebrates trapped in the first season was greater in plots that were more sheltered. The explanation for this may be subtle changes in habitat with exposure leading to more favourable micro-climatic variables in sheltered areas. However, the difference may be down to the efficiency of water traps in different air flows. Water traps work by attracting invertebrates to them (Southwood 1978). In more exposed areas various invertebrate groups may have difficulty on windy days manoeuvring to the trap thereby lowering the catch.

The number of other invertebrates trapped in the first season was also affected by the height of the canopy. The greater the height of sward the larger the number of invertebrates trapped. Lawton (1983) predicts that greater structural diversity, including plant height, could lead to greater numbers and diversity of invertebrates, furthermore Haysom & Coulson (1998) showed that the number and diversity of lepidopteron larvae living on heather plants increased with greater height.

In this study the level of the water table was correlated with the number of Nematocera trapped in year 2. However, the relationship ran in the opposite direction of the one expected, i.e. the drier the area the greater the number of nematocerans trapped. This relationship is unusual as many of the common upland dipterans have larvae that are adapted to semi-aquatic conditions (Coulson & Whittaker 1978). However, recording the water table level may not necessarily be the best measure of substrate wetness. The dominant ground cover of the study sites is made up of various mosses. These mosses, especially *Sphagnum spp.* are known for their associations with wet conditions (Phillips 1980). They are also known for their water holding abilities and can remain wet long after surrounding soil dries out, with a mat of Sphagnum plants being able to hold approximately 8 times its own weight in water. This theory is lent support by the data that shows, although not significantly, that more nematocerans are trapped in areas where the ground cover is dominated by mosses.

Over time it was seen that the amount of grasses and sedges increased in all areas and that this was associated with a decline in heather cover. Whether this was due to some environmental or climatic variables not measured is unknown. However, the possibility exists that as the plots were visited frequently and were relatively small, physical damage of the heather present could have resulted in the promotion of grass and sedge species and loss of heather cover. Despite a noticeable change in vegetation no related change in invertebrate numbers was seen.

2.5.2 The effects of experimental treatments on invertebrate numbers and habitat

The exclusion of vertebrate grazers has led to an increase in the number of invertebrates in moorland fringe habitats (Baines 1996, Baines *et al.* 1994). The mechanism by which grazer exclusion might affect the invertebrate community is by firstly preventing the loss of important food plants. For example Richardson *et al.* (2002) demonstrated that increasing the grass component of a dwarf shrub community led to a large increase in hemipterans. This relationship may be important as moorland grazers are known to, selectively browse grasses rather than heather (Alonso & Hartley 1998). Secondly the greater the structural complexity of the vegetation the greater the diversity and/or number of invertebrates present (Lawton 1983). This has been demonstrated for different height classes of heather with lepidopteran larvae (Haysom & Coulson 1998). Lastly grazers may inadvertently remove large numbers of invertebrates directly when browsing, this is most likely to have the greatest effect when egg cases are ingested. In this experiment the exclusion of grazers had no detectable effect on the invertebrate community. The amount of grasses and sedges present increased when plots were fenced and fertilised. This result was expected although a greater increase would have been predicted.

The addition of fertiliser in order to boost invertebrate production was broadly successful in both years two and three. The reason why this strategy was successful is unknown, although it may be due to a number of factors depending on which invertebrate group was being considered. Fertiliser may benefit invertebrate production in a number of ways. The main ones being the improvement of food plant quality and subsequent organic matter quality and the increased structural complexity of the habitat by an increase in growth rates and possibly composition.

These ideas have been seen to have an impact on invertebrates in dwarf shrub communities (Haysom & Coulson 1998, Power *et al.* 1998, Richardson *et al.* 2002). In this study no nutrient analysis of the plant material present was undertaken, however, in another experiment in adjacent areas the increase in N and P content of heather, when fertilised, was demonstrated (Chapter 3). Fertilisation, when in conjunction with fencing, led to an increase in the grass/sedge component of the habitat giving a similar result to other researchers (Alonso & Hartley 1998, Richardson *et al.* 2002).

Counter-intuitively fertiliser, when applied with lime, was seen to have a negative relationship on sward height over time. The most likely explanation is that the increased nutrition led to an increase in grazing pressure in the control plots and the effect of grazer exclusion was not strong enough to prevent the result in the minimal model.

The evidence suggests that the increased nutrition of the system could be responsible for the boost in the number of invertebrates trapped. This explanation is also most likely for the increase in nematocerans recorded, as the common species are bryophyte or organic matter feeders.

The change of the pH status by the addition of lime was shown to have no detectable effects on the invertebrate community. However, due to the limes effect on pH and the relationships shown between invertebrates and pH in the first year a response from the invertebrate community would be predicted over time. The lack of a detectable effect so far may be due to the coarse scale of invertebrate classification. The change in pH may have caused a loss of some acid tolerant species and caused a replacement with acid intolerant ones. This change if not noticeable in numbers would not have been seen with the identification undertaken. Liming was shown to increase the pH over time and also boost the amount of non-dominant plant species, at least in the first year. Altering the competitive abilities of some species or scorching others due to the nature of hydrated lime may have caused this. The gradual fall of miscellaneous species over time in control and other treatment plots could be due to physical damage from repeated visitation of the sites or a shift in competitive ability towards the grasses and sedges.

Two studies have shown a correlational relationship between grouse productivity and the base status of underlying rocks (Jenkins *et al.* 1967, Picozzi 1968), with the higher the base status index correlating with greater production of grouse. These researchers suggest that the mechanism behind this relationship is due to increases in the heather's plane of nutrition on areas with greater base status. This would suggest that increasing pH would act as a fertiliser and would in turn benefit the invertebrate community. It is therefore, hypothesised that liming areas could be beneficial for both the vegetative and invertebrate communities, and in turn red grouse. The reasons why changes such as these were not seen in this experiment could be due to the type of lime used (hydrated lime rather than limestone grit), the time scale of the experiment or the level of application.

2.5.3 Ramifications for the management of moorland

Moorland management has evolved in the past decade in respect to parasite control. However, the main tasks performed by grouse keepers, predator control, grazing regimes and muirburn, have remained essentially the same for many years. The level of domesticated grazing pressure on a grouse moor can be carefully controlled and guidelines to timing and number of animals per unit area is readily available (Hudson 1986). However, in the Scottish highland system the presence of large numbers of wild red and roe deer and mountain hares *Lepus timidus* makes the total grazing pressure hard to ascertain.

This study has not shown a benefit to the invertebrate community by removing grazing pressure. However, the results may be different if a longer time scale was considered or larger exclusion areas set up. If the hypothesis that reduction of grazing pressure on moorland leads to better invertebrate availability and subsequently to better grouse production, estate managers would need to make important decisions. The trade off becomes one of revenue due to the possibility of increased grouse shooting against the assured income acquired from livestock production. It is most likely that at some point grazing becomes beneficial to invertebrate and grouse production by holding moorland in a pre-climax successional stage. If the benefits of reduced grazing pressure are eventually shown to directly impact grouse production the Scottish system may be in prime position to have the best of both worlds. That is because the removal of livestock will reduce grazing pressure benefiting invertebrates and grouse, whilst the deer and hares left behind could maintain the structural integrity of the heather moorland without overgrazing.

This experiment has shown that the addition of fertiliser to moorland benefits invertebrate production, especially the Nematocera. The widespread application of fertiliser to what is wrongly thought of as a wild system (SNH 2002) may be controversial due to problems of eutrophication and plant community change. However, its ability to effect invertebrate numbers, as shown in this study and others, and grouse numbers (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984) will be of interest in an area where grouse bags have been declining steadily for a number of years (Hudson 1988). This experiment does not suggest a regime for the application of fertiliser but suggests that it could benefit grouse production if invertebrate food is in some way limiting. If done with sensitivity to the environment the consideration becomes one of cost. The cost of fertiliser and its application would have to be offset by revenue generated by increased shooting.

This experiment has shown that the invertebrate community is governed by a number of biotic and abiotic factors. It also demonstrates that some of these can be manipulated in order to increase invertebrate production.

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Chapter 3

The Effect of Fertiliser Application on Red Grouse Production, Invertebrate Abundance and the Plant Community: A Large Scale Experiment

3.1 Abstract

Fertiliser was spread in April 2002 on four ½ Km^2 plots of moorland following results gained from a small scale experiment carried out in the previous year. The effects of fertiliser on red grouse production, invertebrate abundance and plant community composition were monitored by comparison with untreated areas of moor.

The number of chicks produced per hen was significantly larger on fertilised areas than controls (2.6±0.11 to 1.5±0.1). This difference is speculated to be due to the improved nutritional status of the heather rather than maternal nutrition or invertebrate diet.

The number of invertebrates trapped was lower on treated plots than controls. This result was opposite to the findings of the small scale experiment carried out in the previous year. It is hypothesised that the result is due to differing methodologies and that the effects of the fertiliser on invertebrate numbers is most likely to be seen in 2003.

With the application of fertiliser the amount of nitrogen and phosphorous in heather shoots increased, although the level of potassium was not affected. The plant community composition and structure on fertilised and control plots was similar in all respects except for lower levels of lichens on fertilised plots. It is known that some lichen species are sensitive to nitrogen pollution and this may have caused the lower levels of lichens recorded on treated areas, however, the short time span over which the change would have had to happen for it to be due to fertiliser application is discussed.

3.2 Introduction

The Red Grouse, *Lagopus lagopus scoticus*, is a game bird of conservation and economic importance in the uplands of the United Kingdom (Hudson 1992). It is a sub-species of the widespread Willow Grouse, *Lagopus lagopus lagopus*, but is itself endemic to the uplands of Britain. It is further restricted to moorland dominated by heather *Calluna vulgaris* a scarce habitat type that is internationally recognised as requiring protection (Thompson *et al.* 1995).

3.2.1 Factors affecting the harvesting of red grouse

The harvesting of grouse as an economically viable crop relies on sustained recruitment from chicks to juvenile birds. Grouse mortality rates are highest in the first 15 days post hatch (Moss *et al.* 1981). The probability of the transition from chick to fledgling occurring is affected by a number of different factors, with their relative importance being dependent on the species in question and the local conditions. Food availability is known to be of importance to many species, e.g. great tits *Parus major* (e.g. Perrins 1991), golden plover *Pulvialis apricaria* (Pearce-Higgins & Yalden 2003) and red grouse (Erikstad & Spidso 1982), as are disease (Hudson *et al.* 1995) and predation (Redpath 1991, Redpath & Thirgood 1997). Man made factors such as pollution (Janssens *et al.* 2003) and more general influences such as weather (Erikstad & Andersen 1983) can also play a role.

The quality of females before and during egg laying can have a large influence on chick survival in many bird species due to energetic investment in egg production, for example, female quality has been shown to affect clutch sizes in the collared flycatcher *Ficedula albicollis* by up to 25% (Price 1998). Nutrient intake and heavy burdens of the caecal nematode *Trichostrongylus tenuis* can influence hen grouse quality and this may affect egg production (Delahay & Moss 1996, Hudson 1986a, Jenkins *et al.* 1965, 1967, Moss *et al.* 1981, Shaw & Moss 1990). The timing of egg laying may also cause differences in fledging success, for example the snow goose *Anser caerulescens atlanticus* has a five fold decrease in fledging success if hatched late in the season (Lepage *et al.* 2000).

3.2.2 The heather diet of red grouse and its improvement

Adult red grouse are herbivorous and feed almost entirely on heather *Calluna vulgaris* (Lovat 1911), although they are known to take small amounts of invertebrate food (Butterfield & Coulson 1975). The percentage cover of heather and the age structure of its stands is correlated with spring densities of grouse (Miller *et al.* 1966). Furthermore, territories in habitat with a large proportion of heather stands are smaller than those in areas with sparse cover, allowing a greater density of grouse per unit area (Miller & Watson 1978). Despite these observations heather biomass is not thought to be a limiting factor to grouse populations on moorland (Moss 1972).

It is the quality of the heather present that may play the major role in governing the usage patterns of moorland by grouse. Usage patterns by herbivores are often determined by the nutrient quality of the browse available, for example moose *Alces alces* respond to nitrogen levels (Ball *et al.* 2000). Adult grouse selectively graze heather shoot tips that have a higher proportion of nitrogen (N) (crude protein) and phosphorous (P) than average (Moss 1972). The N and P content of heather have been shown to be related to breeding success (Moss, Watson & Parr 1975).

With these things in mind a number of fertilisation experiments of grouse moors have been undertaken (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984). These studies focused on the effects of improved heather quality on the territory settlement rate of cocks and the breeding success of hens after they had had an extended period of feeding on nutrient enriched heather. The main assumptions made in these works were that the fertilisers' main effects were firstly to attract immigrating birds due to improved heather quality and secondly an increase in the plane of nutrition of breeding females before, during and after egg production. The effect of fertiliser application on chick survival was investigated only in terms of hen fitness. This was due mainly to the lack of control for hen fitness making any chick survival data confounded.

3.2.3 Red grouse chick survival with improved heather quality

The addition of nutrients may increase chick survival directly in a number of ways. Red grouse are nidifugous and chicks begin feeding within hours of hatching. The chicks' diet consists mainly of heather, approximately 80%, and other types of vegetation. Fertilised heather contains more crude protein (N) and P than untreated plants (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984). This increase in nutrients should benefit the chicks in terms of growth rate and, in turn, survival. Savoury (1977) showed that both adults and chicks grazed heather selectively, eating tips higher in N and P than average local levels. He also demonstrated that chicks select shoot tips higher in N and P than adult birds do, presumably due to their high growth requirements. The higher levels of nutrients in fertilised heather could aid chick development by decreasing the effort required to graze selectively and it could, if selectivity is maintained, supply more protein which is believed to be limiting (Savoury 1977, 1989).

3.2.4 Invertebrate prey in chick diets

Although their diet essentially mimics that of adults, a small proportion of the chicks' diet is made up of invertebrates. The inclusion of invertebrates in the diet lasts for about 3 or 4 weeks (Savoury 1977, 1988). Approximately 5% by dry weight of crop contents were made up of arthropods from a sample of chicks from Northeast Scotland (Savoury 1977). This invertebrate food appears to be essential to maintain the fast growth rates seen in young chicks. Park *et al.* (2001) demonstrated that when invertebrate consumption increased, chicks' growth rates increased, which in turn is correlated with better survival. Invertebrate food has a higher digestible protein content than plant material and higher concentrations of the two sulphur based amino acids, methionine and cystine, which are essential for feather synthesis (Bolton & Blair 1974, Savoury 1989). An example of the difference in nutritional content between invertebrate food and plant food is *Tipula subnidicornis*, a usual prey item, which contain nine times the nitrogen and seven times more phosphorous than heather (Butterfield & Coulson 1975).

Many bird species are known to have increased fledging success when food quantity is high, e.g. the Seyschelles magpie robin (Komdeur 1996). The mechanism by which increased food levels improve survival in most cases is unlikely to be simple avoidance of starvation, for example grey partridge *Perdix perdix* chicks resistance to chilling has been shown to improve with weight gain, and their weight is governed by the amount of protein they consume (Richards *et al.* 2002) a similar mechanism to this may occur in grouse (Savoury 1989).

Though the invertebrate food taken by red grouse chicks is varied, Diptera (true flies) make up a large percentage of the diet. Of these the Tipulidae makes up the majority of invertebrate food consumed (Grimshaw 1911, Savoury 1977, Hudson 1986a, Savoury 1989, Park *et al.* 2001). Tipulids may be preferred, as many species are relatively sedentary and conspicuous making them vulnerable to predation (Butterfield & Coulson 1975).

3.2.5 The invertebrate response to fertilisation

The small-scale fertilisation experiment carried out in the area of study (Chapter 2) demonstrated that additional nutrient input led to an increase in both the Nematocera and the combined numbers of the other invertebrate orders trapped. This increase has been mirrored in other dwarf shrub communities although Richardson *et al.* (2002) noted a decline in diversity, if not numbers, after extended periods of repeated fertilisation. There are three main ways in which invertebrate abundance might increase due to nutrient addition.

By altering the nutrient status of a substrate the competitive abilities of individual plants will change proportionately with their ability to utilise the source (Alonso & Hartley 1998). Increases in the abundance of a certain plant may lead to an increase in the invertebrates that utilise it (Lawton 1983). For example an increase in the amount of grass cover present led to a 400% increase in the gramnivorous Homoptera in a 9-year fertilisation experiment in a related dwarf shrub community (Richardson *et al.* 2002).

The nutrient status of a food plant, and not just its abundance, is likely to be important. Power *et al.* (1998) investigated the response of the heather beetle *Lochmaea suturalis* to the addition of nitrogen on lowland heath. As heather nutrient content increased larval growth rate and weight of adult beetles increased. It is proposed that these two results are an indirect measure of survival. If this relationship is repeated in other invertebrate species then the impacts could be wide-ranging for both phytophagous insects and detritovores.

The structural complexity of the environment can be important for invertebrate abundance by providing both larger surface area and greater diversity of niches to occupy (Lawton 1983). On heather moorland Haysom & Coulson (1998) showed that the abundance and diversity of lepidopteran larvae increased with greater heather height. As fertilisation of heather has been shown to increase its annual growth rate (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984) a similar increase in invertebrates may be observed.

The increase in abundance of possible prey items may benefit grouse as consumption rate is correlated with availability and indirectly survival (Park *et al.* 2001). The possible increase in size of an individual could also benefit grouse chicks by increasing intake rate and/or improve foraging efficiency. The chicks of the related Cappercallie *Tetrao urogallus* have been shown to have growth and survival rates more heavily correlated to size of prey items rather than abundance (Picozzi *et al.* 1999).

3.2.6 Other possible benefits of fertiliser for grouse chicks

Heather cover, growth rate and flowering have been shown to increase with the addition of fertiliser (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984), as have grasses commonly found on moorland (Alonso & Hartley 1998). In the absence of grazers, the addition of fertiliser has also been shown to increase the density of heather canopy (Alonso & Hartley 1998). Savoury (1978) showed that the type of heather stand used at different times of the year by grouse changed. Longer, denser heather was selected in summer and winter than in spring and autumn. This is proposed to be due to the need for extra shelter in winter and as a defence mechanism in summer when chicks are young, naïve and vulnerable. The addition of fertiliser could possibly lead to a denser heather canopy and therefore, a better refuge in which to avoid predation.

3.2.7 Aims of study

This study examines the changes caused by large-scale fertilisation of a grouse moor. A replicated experiment is used to investigate changes in habitat, grouse production and invertebrate abundance.

3.3 Materials and Methods

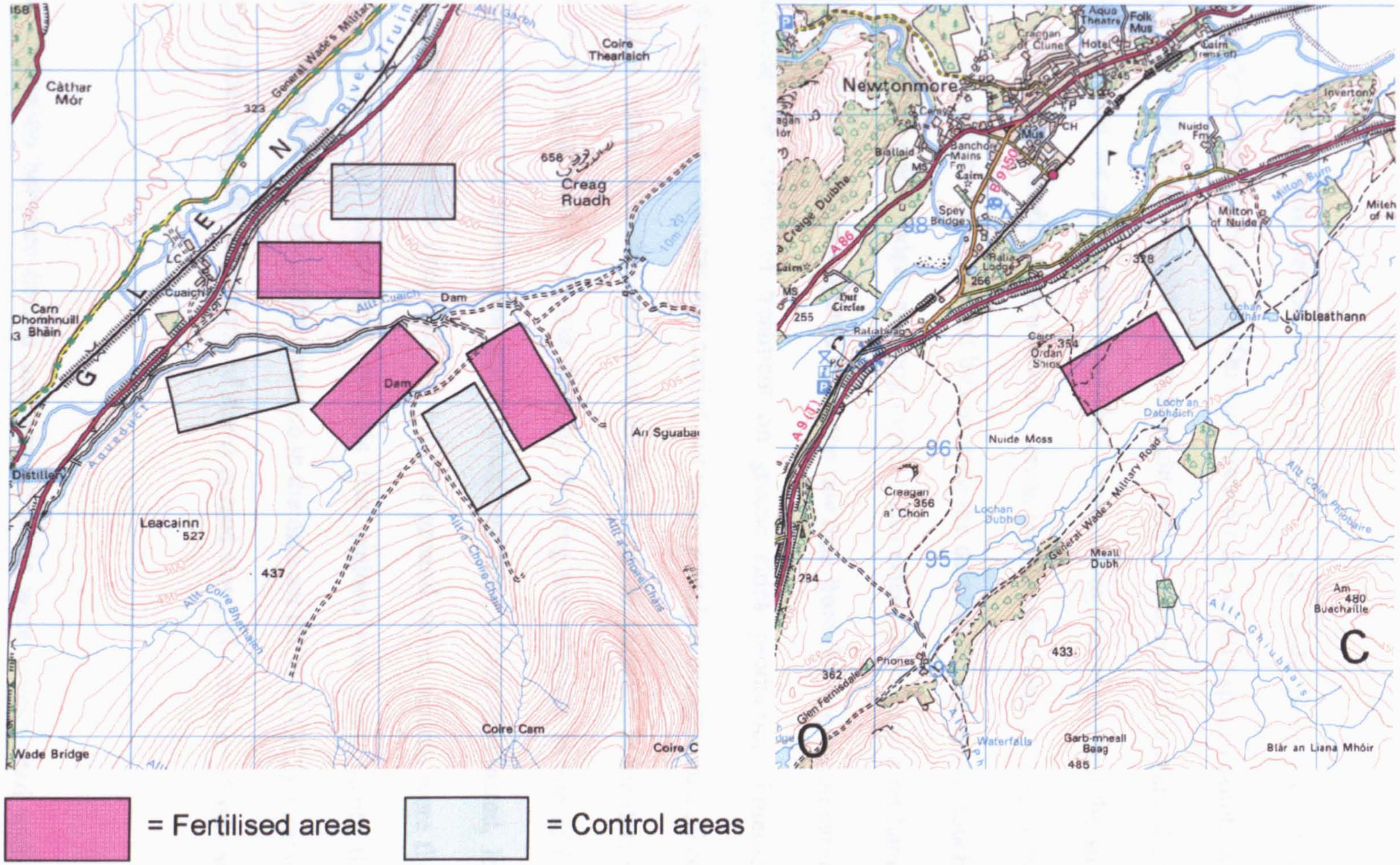
3.3.1 The Study Site

The study site is in the Spey Valley in the Scottish Central Highlands. The study used two contiguous moorland estates managed intensively for driven grouse shooting, Phones and Ralia. The areas used on the Phones estate have an altitudinal range of between 410 – 440 metres and are characterised as wet heath with patches of blanket bog. The Ralia site has a central altitude of 280 metres and is a flat mosaic of dry and wet heath.

3.3.2 The Fertiliser Application

Four ½ Km^2 blocks (500m X 1000m) were designated to receive an application of generic blended 17,17,17 N,P,K fertiliser, a standard agricultural product used on silage fields. The application rate was derived from a series of smaller experiments carried out on the same estates in the previous two years (Chapter 2). Three of these blocks were located on the Phones estate, with the remaining one on Ralia (figure 3.1). Each of these treated areas had an associated ½ Km^2 control block chosen for its closeness in distance and vegetation characteristics to itself. The fertiliser was applied in mid-April 2002 by tractor. The application process was completed on the four experimental sites in nine days before the heather growing season had begun. Maternal condition would not have been affected by the fertiliser due to the timing of application (Chapter 4).

Figure 3.1. Maps showing the position of the fertilised and control areas.



3.3.3 Vegetation Surveys and Nutrient Testing

Basic vegetation surveys were carried out in late July in all eight plots. Two 1 Km transects were walked through each plot. On each transect 25 equally spaced points were used to measure a number of variables. Sward height was measured with a marked cane with the record being at the point where the tallest piece of vegetation touched the stick. The amount of heather, including *Erica tetralix* (cross-leaf heather) and *E. cinera* (bell heather) which were sparse, was classified by counting the number of shoots that touched the cane, as were grasses and sedges and bog myrtle. The effect of treatment on habitat and invertebrate numbers was investigated using the raw data from the vegetation survey. When investigating the effects of treatment on grouse chick production dimension reduction of the vegetation measures was carried out using principal component analysis. The result was two components that accounted for 78.7% of the variance in the data set (V1 & V2). Classifying ground cover was done by allotting the substrate to one of five categories; moss (other than *Sphagnum spp.*), *Sphagnum spp.*, lichen dominated, leaf litter dominated and berry cover (*Vaccinium spp.*). The ground cover records were then condensed using a principal component analysis that yielded two components that between them accounted for 82.1% of the variance in the data set (GC1 & GC2). Grazing was measured by calculating the proportion of stems grazed along 10 1m lines (5 on each transect).

Differences in vegetation between treated and control areas were investigated with a binomial general linear mixed model (GLMM) controlling for experimental site. Analysis was carried out in GenStat 6th edition. The maximal model (Model 1), simplified in analysis by stepwise deletion of insignificant terms was:

Treatment ~ Heather*Grass/Sedge*Sward Height*GC1*GC2*Grazing

(* signifies interaction terms. All 2 way interactions were considered)

Nutrient analysis was carried out on heather collected from the eight plots in April before application of the fertiliser and again in August. Ten samples of heather were taken from each plot and then mixed, dried and milled to form a single sample. This sample was then analysed at the Scottish Agricultural College in Edinburgh. Due to the small sample size (n=8) controlling for many factors was impossible. Therefore, 1-tailed binomial exact tests were carried out looking at the effects of treatment in S- Plus 6 Professional release 1.

3.3.4 Red Grouse Production Counts

Red grouse were counted in late July on the treated and control plots to determine breeding success (Jenkins *et al.* 1963). The effect of treatment, vegetation characteristics and invertebrate food abundance on red grouse production was investigated with a quasi-likelihood general linear model (GLM) with a log link and variance function mu^2 in S-Plus 6 Professional release 1. The maximal model was (Model 2):

Brood size (of each hen seen) ~ Treatment*V1*V2*Nematocera

(* signifies interaction terms. All 2 way interactions were considered)

3.3.5 Invertebrate Monitoring

Invertebrates were trapped for a 50-day period from the 3rd May 2002. They were trapped in bright yellow water traps (Chapter 2) that were collected every 10 days. Each ½ Km^2 block had a transect of five evenly spaced water traps running along the centre line of the plot. The first trap on the transect was 100m from the edge of the experimental plot, with each further trap being 200m from the last.

The samples were sorted into orders or sub-orders in the laboratory. The Nematocera were differentiated from the other dipterans due to their importance as chick food insects. The main nematocerans trapped on the study areas were Tipulidae (crane flies) and Chironomidae (non-biting midges), the two major groups identified in faecal samples of chicks in the area by Park *et al.* (2001).

The invertebrate counts were transformed to achieve normality and homoscedasity using natural log transformations. The abundance of nematocera and of total non-Nematocera abundance and the factors affecting them were investigated using restricted maximum likelihood models (ReML) in GenStat 6th Edition. The effect of site and $time^2$ (as the relationship between invertebrate abundance and time is not linear) were controlled for as random terms in the model. The maximal model was (Model 3):

Ln Invertebrate measure ~ Treatment*Heather*Grass/Sedge*Bog Myrtle*Sward Height*
GC1*GC2*Grazing

(* signifies interaction terms. All 2 way interactions were considered)

3.4 Results

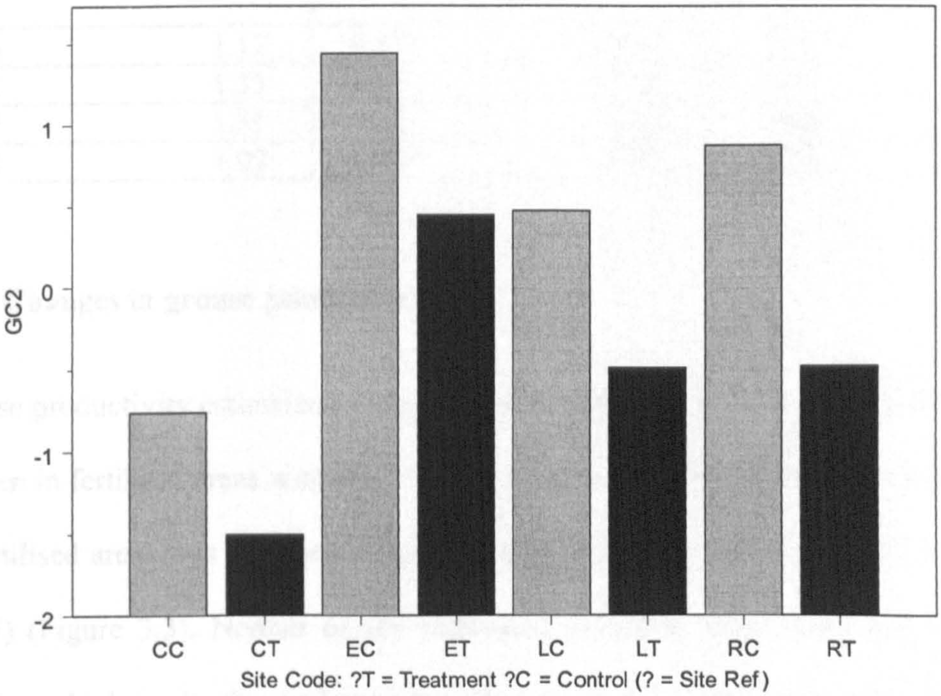
3.4.1 Changes in vegetation

The vegetation characteristics, determined by survey, were compared between the treatments whilst controlling for site (see Table 3.1). A principle component of ground cover was the only significant term in the model (Binomial GLMM, Wald Statistic = 13.45, P <0.001) (Figure 3.2). The significant component described 18.8% of the variance in the ground cover data set and was characterised by a negative correlation with lichen abundance ($r = -0.930$, $F_{1,6} = 38.4$, $P < 0.001$). The analysis showed that the application of fertiliser lowers the recorded abundance of lichen species.

Table 3.1. Wald statistics and probability values of vegetation characteristics in response to treatment.

Vegetation Variable	Wald Statistic	P - Value
Heather	0.00	0.951
Grasses/Sedges	0.00	0.954
Sward Height	0.00	0.989
GC1	0.39	0.531
GC2	13.45	<0.001**
n = 400		

Figure 3.2. Second principle component of ground cover recorded in the treated and control plots in July. The dark bars are plots that have been treated with fertiliser, the lighter bars are the corresponding control plots.



3.4.2 Nutrient analysis results

Nitrogen and phosphorous levels were consistently higher in all treated plots compared to their control, however, due to the small sample size the 5% level of significance was not reached (Binomial exact test, P=0.0625, trials = 4). There was no difference in the potassium levels between the treated and control plots (Binomial exact test, P=1, trials = 4) (see Table 3.2).

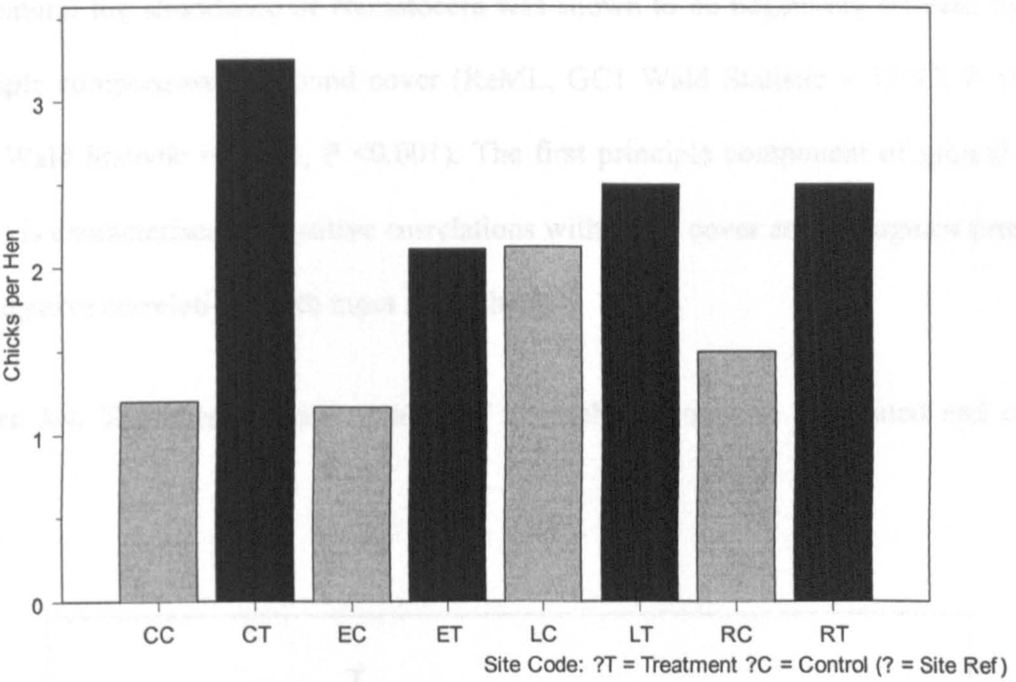
Table 3.2. Percentage dry matter of N, P and K in heather samples collected in August from the experimental plots.

Nitrogen % dry matter		Phosphorous % dry matter		Potassium % dry matter	
Treated	**Control**	**Treated**	**Control**	**Treated**	**Control**
1.46	1.17	0.17	0.08	0.70	0.52
1.32	1.31	0.11	0.08	0.61	0.41
1.37	1.31	0.12	0.07	0.48	0.51
1.08	1.07	0.09	0.08	0.40	0.54

3.4.3 Changes in grouse productivity

Grouse productivity estimated by dog counts in July gave an average of 2.6±0.11 chicks per hen in fertilised areas with only 1.5±0.1 in control plots. The increase in productivity in fertilised areas was significantly greater than in control plots (GLM, $F_{1,58} = 4.13$, $P = 0.047$) (Figure 3.3). Neither of the vegetation principle components had a significant effect on chick production and were therefore, deleted from the model (GLM, V1, $F_{1,57} = 0.367$, $P = 0.547$, V2, $F_{1,55} = 0.02$, $P = 0.884$). The number of Nematocera trapped was used as a measure of chick food insect availability. This measure was used due to their importance in chick diet (Park *et al.* 2001) and because of the strong correlation between them and other invertebrate groups sampled ($r = 0.842$, $F_{1,187} = 455.33$, $P <0.001$). The average number of Nematocera was not related to the grouse counts in model 2 (GLM, $F_{1,56} = 0.009$, $P = 0.924$).

Figure 3.3. Grouse productivity estimated from July counts for the four sites. The dark bars are plots that have been treated with fertiliser, the lighter bars are the corresponding control plots.



3.4.4 Changes in invertebrate production

The treatment had a significant effect on both the total number of invertebrates sampled (ReML, Wald Statistic = 6.78, P = 0.009) (Figure 3.4) and the number of Nematocera sampled in a season (ReML, Wald Statistic = 10.16, P = 0.001) (Figure 3.5). Both measures of invertebrate food availability were shown to be higher in the control plots. Invertebrate abundance was also shown to be negatively related to the amount of grass present (ReML, Wald Statistic = 6.94, P = 0.008) and a principle component of ground cover (GC2) (ReML, Wald Statistic = 11.92, P <0.001) when controlling for time of invertebrate collection, as a quadratic function and experimental site. The significant principle component of ground cover is strongly associated with the absence of lichens and this relationship is most likely seen due to an effect of treatment (see 2.3.1).

The natural log abundance of Nematocera was shown to be negatively affected by both principle components of ground cover (ReML, GC1 Wald Statistic = 12.97, P <0.001, GC2 Wald Statistic = 21.53, P <0.001). The first principle component of ground cover (GC1) is characterised by positive correlations with berry cover and *Sphagnum* presence, and negative correlations with moss and lichens.

Figure 3.4. The average total number of invertebrates trapped on treated and control plots.

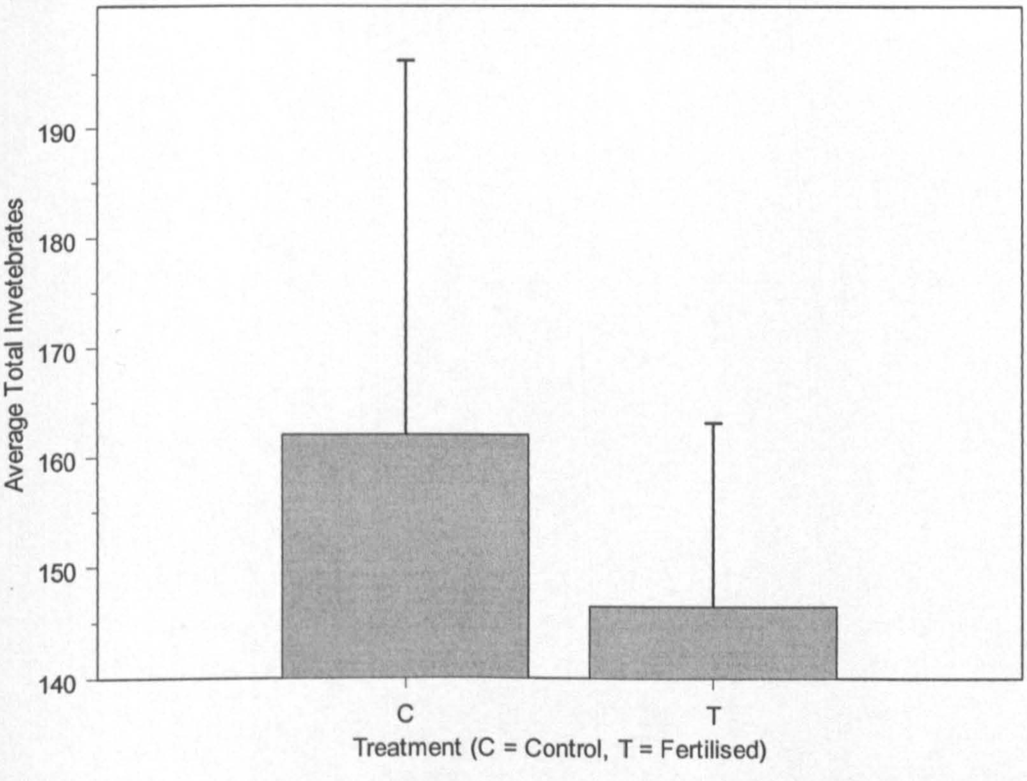
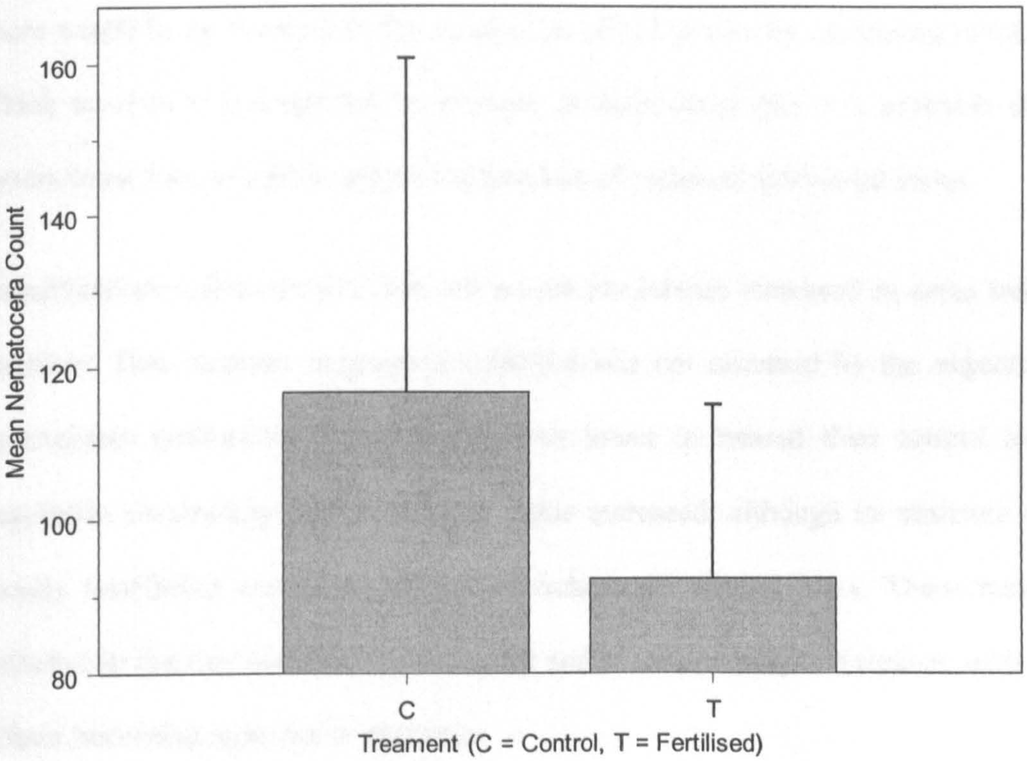


Figure 3.5. The average number of Nematocera trapped on treated and control plots.



3.5 Discussion

This study investigated the possibility that by increasing the nutrient status of moorland, there would be an increase in the production of red grouse by increasing chick survival. Chick survival was suspected to increase in these areas due to a probable rise in the invertebrate food available and be independent of maternal nutritional status.

Experimental studies showed that red grouse production increased in areas treated with fertiliser. This increase in grouse production was not mirrored by the expected rise in invertebrate production, which in fact was lower in treated than control areas. The vegetation community had its nutrient status increased, although its structure remained mostly unaffected except for a loss of lichens on treated plots. These results were gathered in the first season after treatment and therefore, maybe transient, with different effects becoming apparent in the future.

3.5.1 Changes in vegetation

The application of fertiliser to a related dwarf shrub ecosystem has been shown to increase the amount of litter deposition and grass cover (Power *et al.* 1998, Richardson *et al.* 2002), although this invasion depends on the state of the heather canopy on grouse moors (Alonso & Hartley 1998). In this study the vegetation surveys did not show any increase in the abundance of grasses or sedges in fertilised plots. The lack of change is most likely due to this study using only one application of fertiliser and being monitored for just one season. Other works investigating the impact of fertiliser on the vegetation community have had repeated nutrient inputs and have been monitored over a number of years.

The only change that was detected by vegetation survey in the make-up of the plant community was a loss of lichens in fertilised areas. Some lichen species are sensitive to high levels of nitrogen and have been used in the past as a tool for mapping ammonia pollution (Benfield 1993, Van Herk 1998). The large loss in the lichen community is a major obstacle to using large-scale fertiliser application as a management technique. Furthermore, in long term studies of nutrient application to dwarf shrub communities the abundance and production of bryophytes initially increased but then fell dramatically as they became shaded out (Chapin *et al.* 1995, Richardson *et al.* 2002). As well as being of conservation concern, loss of bryophytes might make the technique counter-productive over time as many larval stages of chick food insects feed on them. Further work in to the mechanisms of the fertilisers effect on moorland and chick survival and its role in improving maternal nutrition should be pursued in order to be able to deliver a more focused management tool.

Nutrient analyses of heather samples taken from the treated and control plots showed differences in the nutrient status of the grouse's main food plant, although due to the low number of samples tested the power of the analysis was low. However, in terms of nitrogen accumulation heather in the treated plots was consistently greater. This greater accumulation was mirrored in the percentage dry matter of nitrogen in the treated plots in August. This pattern was also seen in the phosphorous levels. Despite a high level of potassium in the fertiliser there appeared to be no effect on the concentration of this element in heather. The reason for the apparent lack of uptake is unclear. However, Moss

(1972) demonstrated that nitrogen and phosphorous were the limiting elements in the vegetative diet of red grouse.

The change in nutrient status of the heather would have occurred to late too benefit breeding females before or during egg laying and therefore, it is assumed that benefits to chick survival are independent of maternal nutritive status.

3.5.2 Changes in grouse productivity

Grouse productivity was higher in all fertilised plots when compared to their controls, this result was mirrored in an intensive study of radio tagged broods in the same areas (Chapter 4). On average the control plots produced only 59% of the chicks per hen as the treated plots, with a range of 37% to 85%. A change in productivity in the first season after treatment, when application occurred in late spring, did not show an effect on breeding production in work carried out by Watson *et al.* (1984), the reasons why the two studies differ so markedly is unknown. The difference may grow in 2003 as the effects of maternal nutrition also begin to play an increased role in chick production. As invertebrate production was lower in fertilised plots it is assumed that the role of dietary invertebrates was not a factor in the shown increased survival probability. This would suggest that the effect was caused by either an increase in diet quality and therefore, body condition derived from the intake of nutrient enriched vegetation matter or a decrease in predation pressure by a more complex vegetation structure. Although vegetation density was not measured directly, the number of heather shoots at a given point was. This is an indirect measurement of density and as such there was no difference between treatments.

In bird surveys carried out on the plots in June no aerial predators of grouse were seen. Ground predators were also assumed to be at low levels as only one nest was predated and this was not complete (n=32). The data therefore, suggest that the nutritive vegetation quality is the factor influencing chick survival in this experiment.

Grouse chicks selectively graze heather tips for those higher in N and P than average (Savoury 1977). By increasing the N and P levels by fertilisation, selectivity may decrease and therefore, the energetic costs of feeding. Selectivity may also be maintained leading to a greater intake of these two elements leading to faster developmental times and a supposed consequence of greater survival rates.

3.5.3 Changes in invertebrate productivity

Invertebrate abundance has been shown in previous studies to increase with the addition of nitrogen to the system (Chapter 2, Hartley *et al,* 2003, Richardson *et al.* 2002). The prediction that this relationship would occur in this experiment was unfulfilled. An explanation for this may lie in the timing of the application of the fertiliser.

Chick faecal analysis from the same areas (Park *et al.* 2001) shows that the majority of chick food invertebrates are taken in their adult stages. The chances of this being mainly due to digestibility differences are small due to crop content sampling in other areas showing similar results (Grimshaw 1911, Savoury 1977). The majority of chick food insects feed mainly in the larval stages that live in the substrate. Therefore, any benefit of nutrient addition via diet would need to occur when the larval stages were feeding. The fertiliser was applied in mid-April when the final instar larvae would be close to pupation for metamorphosis and finally adult emergence in May. The result seen in the small-scale experiment carried out in the same area (Chapter 2) is most likely due to the application of fertiliser being given in two stages, i.e. in late August and again in April.

Power *et al.* (1998) showed that heather beetle larvae increased in growth rate with nutrient addition, leading to bigger adults. They allude to the fact that this would increase survival between life stages and therefore, increase the population. If the same relationship occurs in other invertebrate groups feeding on plant material then the effect of improved diet should be seen in 2003.

However, on average the control plots had a greater number of invertebrates than the treated areas. The reasons why this may have occurred are unclear and maybe due to a number of factors. The simple mechanical damage of the application of fertiliser may have had an effect. Unfortunately, due to cost, the tractors could not be driven over the control plots or an inert pelleted formula spread. The amount of damage created by the tractors appeared to be minimal and the type of fertiliser used is not known to have an insecticidal effect. The placement of the traps may also have played a role as the distribution of invertebrates in the environment is patchy (Erikstad 1985, Hudson 1986). Only two of the four control plots showed higher levels of invertebrates than their corresponding treatment area. The strength of these differences, and the lack of difference in the other plots, was enough to give a significant relationship. Of greatest importance may simply be a lack of baseline data making it is impossible to say whether or not the treatment and control plots have always shown the difference observed in this experiment. It therefore remains unclear what effect, if any the application of fertiliser had on the invertebrate community.

The distribution of invertebrates was also related to some measures derived from the vegetation surveys. When looking at the total abundance of invertebrates, the amount of grass present was shown to have a negative effect. This relationship runs contrary to what would have been expected from other studies in dwarf shrub communities (Hartley *et al.* 2003, Richardson *et al.* 2002) where greater levels of grass boosted invertebrate abundance. The reason for the relationship observed in this relationship is unknown. The loss of lichens was also shown to be related to lower trap catches of invertebrates. As some lichens are known to be sensitive to nitrogen application (Benfield 1993, Van Herk 1998) the result may be confounded with that of treatment. The abundance of Nematocera was also shown to be related to the presence of lichens. The nematoceran distribution was also related to the first principal component of ground cover. Unfortunately this component is characterised by four relatively strong correlations making interpretation difficult. The positive correlations are with the presence of *Sphagnum spp.* and berry shrubs (*Vaccinium spp.*). Many tipulids are thought to feed on *Sphagnum* in their larval stages and although no relationship between berry cover and chick food invertebrates is seen another experiment in the same area has shown a similar relationship (Chapter 5). The negative correlations in the PCA component are with moss (other than *Sphagnum*) and lichens. As above the lichen component is likely to be confounded. The negative relationship with moss is difficult to explain but could be due to the semi-aquatic larval stages of many of the nematocerans. *Sphagnum spp.* grow in very wet areas, whereas many of the other moss species are found in drier areas.

3.5.4 Summary and Conclusions

The addition of fertiliser has been shown to have a significant effect on the survival chances of red grouse chicks, although this experiment has not investigated the causal mechanism. Unlike previous work the addition of fertiliser did not have a positive detectable effect on invertebrate abundance, in fact any effect caused ay have been negative. It is hypothesised that an increase of invertebrates will be seen in the season following application, 2003, due to the benefits higher nutrient levels may have on larvae feeding in the substrate and litter layers.

Additional work is required if this technique is to be developed in to a management tool for poorly producing grouse moors. Information required includes long-term impacts of nutrient addition on the vegetation community and the mechanisms that are working to improve grouse chick survival.

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Chapter 4

The Mechanistic Effects of Fertiliser on Grouse Chick Survival

4.1 Abstract

The addition of fertiliser to moorland intensively managed for red grouse has been shown to increase productivity; this has been mainly attributed to maternal nutrition and increases in settlement rates of dispersing birds. In 2002 on four ½ Km^2 plots of moorland fertiliser was spread in order to monitor its effects on grouse chick survival.

Survival of radio-tagged broods was greater in areas where fertiliser had been applied. Chick weight at day 5 was shown to be of importance, with larger chicks having a better chance of survival. An unexpected result was seen when it was observed that the level of invertebrate fragments in the faeces was negatively related to survival. The number of sheep tick larvae parasitising grouse chicks lowers the survival probability of broods. This reduction of survival chances is most likely due to the mechanical effects of parasitism as louping ill was not detected. The effect of a given tick burden on survival of grouse chicks was lower for broods in treated areas than those on control plots. This suggests that access to a better diet enables chicks to resist parasitism more effectively.

The implications of fertilisation as a widespread management tool are discussed.

4.2 Introduction

The red grouse *Lagopus lagopus scoticus* is a gallinaceous gamebird essential in terms of the economics and conservation of large areas of upland Great Britain (Hudson 1992, Thompson *et al.* 1995). Grouse are restricted to habitats dominated by their major food plant, heather *Calluna vulgaris.*

4.2.1 Factors influencing red grouse production

Maintaining a harvestable surplus of red grouse is dependent on maximising survival chances of both adult grouse and chicks. Predator control, muirburn and control of the parasitic nematode *Trichostrongylus tenuis* are standard practice to maintain a large population. The greatest level of mortality occurs whilst the grouse are chicks, with the majority of deaths being recorded in the first 15 days post hatch (Moss *et al.* 1981). Factors that can affect a chick's survival probability are numerous; the tick-bourne virus louping ill can cause losses of up to 80% in infected populations (Hudson *et al.* 1997), and locally, predation by predators such as the hen harrier *Circus cyanus* can be important (Redpath 1991, Redpath & Thirgood 1997). Insect food availability, which can be affected by the weather, can govern the rate of growth and in turn survival of grouse chicks (Erikstad & Spidso 1982, Park *et al.* 2001), as can the fitness of the hen before and during egg laying (Delahay & Moss 1996, Hudson 1986, Jenkins *et al.* 1963, Moss *et al.* 1981, Shaw & Moss 1990).

4.2.2 Red grouse breeding biology

Breeding females usually begin laying eggs in late April or early May. Hens tend to lay an egg on most days until the clutch is complete. Once complete, incubation begins and lasts for approximately 22 days. Chicks are moved from the nest soon after hatching and from then on only rely on the hen for brooding due to their inability to thermoregulate (Erikstad and Spidso 1982).

There is some debate in the literature to whether or not the red grouse is a capital or income breeder, as defined by Drent and Dann (1980). Thomas (1982) showed that willow grouse, of which red grouse is a sub-species, were dependent on food supplies during egg laying and were therefore, income breeders. However, Savoury (1975) showed that the clutch mass produced by captive red grouse hens was directly related to the intake of food in the five weeks before egg laying commenced, suggesting that they were relying on reserves in the egg production phase and are therefore, capital breeders. Savoury's work is supported by work on experimental infections of *T. tenuis* by Shaw & Moss (1990), which showed that an infection 5 weeks before egg laying had more of an effect on egg production than an infection during egg laying. However, Delahay & Moss (1996) showed that food intake during laying was important, although hen body weight prior to laying was also significant.

4.2.3 The importance of maternal effects

Whether grouse are capital or income breeders, it is likely that maternal effects play an important role in governing chick survival. Maternal effects have been shown to be important in man species, e.g. Atlantic salmon (Einum 2003), common lizard (Uller & Olsen 2003) and the common frog (Pakkasmaa *et al.* 2003). In birds maternal effects can influence the number of eggs produced, the immunocompetence of offspring and their body mass (Price 1998). For example, female quality has been shown to affect clutch sizes in the collared flycatcher *Ficedula albicollis* by up to 25% (Price 1998). In grouse and ptarmigan *Lagopus mutus* weight of eggs has been shown to affect chick survival and this implies that the feeding condition of the mother may be important (Moss *et al.* 1981, Moss & Watson 1984). Furthermore in a cross-fostering experiment Smith (in prep.) demonstrated that hen quality had a large direct effect on chick survival regardless of post hatch conditions. These findings are at odds with those of Delahay & Moss (1996) whose results showed that hen body condition suffered greatly due to parasitic infection but egg production was maintained. They do however, suggest that this may be due to the plentiful and easily digestible food source the captive birds had access to and that conditions in the wild may prevent this trade-off.

4.2.4 Food intake in red grouse

An important factor in determining the quality of females is the quality of food intake. Red grouse eat a diet almost entirely made up of heather (Leslie 1911). The abundance of heather has been used to explain the between moor variation in spring grouse densities (Miller *et al.* 1966). The size of territories is also dependent on heather cover with smaller territories being taken in areas with dense heather cover (Miller & Watson 1978). This suggests that food resources are a limiting factor, however, Moss (1972) showed that heather biomass is not a limiting factor to red grouse in the uplands of Scotland. Grouse are selective grazers of heather, focusing on shoot tips with higher than average crude protein (N) and phosphorous levels (P) (Moss 1972). Furthermore levels of N and P have been related to breeding success (Moss, Watson & Parr 1975). It is therefore, suggested that it is quality rather than quantity that is the important factor in grouse diet.

4.2.5 Fertilisation experiments on grouse moors

Due to the observed relationships between grouse biology and N and P levels, fertilisation of moorland was carried out in a series of experiments in the late 1960's and early 1970's (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984). These experiments used the territory settlement rate of cocks and the improved breeding status of the hen to explain the improved breeding success that was observed in areas applied with fertiliser. Due to the nature of the experimental designs and the lack of an effect in the first season of application, factors affecting hen quality and those working on chick survival post hatch could not be measured independently.

4.2.6 Fertilisation and the vegetative food of grouse chicks

The experiment described in this paper was designed to look at the effects of fertilisation on chick survival independently of maternal effects. Nutrient input may influence chick survival in a number of ways. The increase in nutrients should benefit the chicks in terms of growth rate and in turn survival. Savoury (1977) showed that both adults and chicks grazed heather selectively eating tips higher in N and P than average local levels. He also demonstrated that chicks select shoot tips higher in N and P than adult birds do, presumably due to their high growth requirements. The higher levels of nutrients in fertilised heather could aid chicks by decreasing the effort required to graze selectively and it could, if selectivity is maintained, supply more protein which is believed to be limiting (Savoury 1977, 1989).

4.2.7 Fertilisation and the invertebrate food of grouse chicks

Red grouse chicks begin to feed themselves soon after hatching. Although their diet essentially mimics that of adults, a small proportion of the chicks' diet is made up of invertebrates, approximately 5% by dry weight. This intake rate is maintained in the first 3 to 4 weeks post hatch (Savoury 1977, 1989). It is believed that this easily digestible and rich source of protein is necessary to enable fast growth rates (Savoury 1989). Park *et al.* (2001) demonstrated that when invertebrate consumption of a chick increased the growth rate increased, faster growth rates were correlated with a better survival probability.

In an experiment carried out in the area of study in the previous two years the abundance of invertebrates after fertilisation had been shown to increase (Chapter 2). However, in a related dwarf shrub community Richardson *et al.* (2002) showed that after periods of repeated fertilisation diversity, but not abundance, can fall. The survival rates of heather beetle *Lochmaea suturalis* have been indirectly shown to benefit by addition of nitrogen by increasing the larval growth rate and increasing the average weight of an adult (Power *et al.* 1998). The increase in abundance of possible prey items and a possible increase in the size and therefore, nutrient content of an individual could be beneficial by increasing foraging efficiency. If invertebrate food is a limiting factor on chick growth rates, and in turn survival (Park *et al.* 2001), then an increase in invertebrate abundance could increase production.

4.2.8 Fertilisation and predation risk

The increase in heather cover, growth rate and flowering has been shown to increase with the addition of fertiliser (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984), as have grasses commonly found on moorland (Alonso & Hartley 1998). In the absence of grazers the addition of fertiliser has also been shown to increase the density of heather canopy (Alonso & Hartley 1998). Savoury (1978) showed that the type of heather stand used at different times of the year by grouse broods changed. Longer, denser heather was selected in summer and winter than in spring and autumn. This is proposed to be due to the need for extra shelter in the winter and as a defence mechanism in summer when chicks are young and naive. If fertiliser increased heather density then a benefit in terms of a reduction in predation risk might be observed.

4.2.9 Aims of study

This study focuses on the mechanisms that may play a role in chick survival after fertilisation. Effects of maternal nutritive status, invertebrate diet, ecto-parasite burden and weight are investigated with respect to treatment.

4.3 Materials and Methods

4.3.1 The Study Site

The study site is in the Spey Valley in the Scottish Central Highlands. The study used two contiguous moorland estates managed intensively for driven grouse shooting, Phones and Ralia. The areas used on the Phones estate have an altitudinal range of between 410 – 440 metres and are characterised as wet heath with patches of blanket bog. The Ralia site has a central altitude of 280 metres and is a flat mosaic of dry and wet heath.

4.3.2 The Fertiliser Application

Four ½ Km^2 blocks (500m X 1000m) were designated to receive an application of blended 17,17,17 N,P,K fertiliser, a standard agricultural product used on silage fields. The application rate was derived from a series of experiments carried out on the same estates in the previous two years (Chapter 2). Three of these blocks were located on the Phones estate, with the remaining one on Ralia (Chapter 3, figure 3.1). Each of these treated areas had an associated ½ Km^2 control block chosen for its closeness in distance and vegetation characteristics to itself. The fertiliser was applied in mid-April 2002 by tractor. The application process was completed on the four experimental sites in nine days before the heather growing season had begun.

4.3.3 The Radio-tagging of Red Grouse Hens

Red grouse hens were captured by lamp light in late March and early April within the treated and control plots (Hudson & Newborn 1995). These females were fitted with radio-transmitters suspended on a necklace. These radio tags were of the same type used by Thirgood *et al.* (1995) who showed that they had no effect on survival or breeding success. At capture the hens were given an oral dose of the drug Levicide. The application of Levicide (active ingredient Levamisole Hydrochloride at 7.5%) was given in order to remove the parasitic gut nematode *Trichostrongylus tenuis*, which is known to have an effect on body condition and reproductive effort (Delahay & Moss 1996, Hudson 1986, Shaw & Moss 1990).

4.3.4 Nest Monitoring

The radio-tagged females were monitored in late April in order to test the collars and to monitor the survival rates of study birds. Each individual was flushed only once in this period in order to minimise disturbance prior to nesting. After the first week of May the study animals were monitored closely in order to locate their nests. Birds that were heard to be moving from the transmitters pulse rate were not flushed. Those that did not move when approached were possibly incubating eggs. These hens were flushed, and if a nest was found it was marked. A bamboo cane ten metres north of the nest was used as a marker in order to prevent the attention of nest predators such as carrion crows *Corvus corone*. The nest had the number of eggs laid recorded and weights, lengths and breadths of five randomly drawn eggs measured.

From these measurements of egg size a predicted hatch date and lay weight could be derived from an equation by Furness & Furness (1981) and calibrated by Smith (in prep) on moors in the immediate vicinity of the study area. The predicted hatch weights were used as a guide on which to base a nest-monitoring programme. The nest marker was visited every other day, starting 8 days before the predicted hatch date. Radio telemetry equipment was used to ascertain whether the hen was still sitting on the nest. If the female was judged to be away from the nest, the eggs were located and checked to see whether they had hatched, the nest had been abandoned or the female was away feeding. If the nest had hatched the number of successfully hatched eggs was recorded. Hatch date was determined as the day the nest was visited if the eggshells were still wet and the hens droppings' fresh and the previous day if the eggs and faeces had dried. Nest success was classified as the number of chicks that had left the nest, therefore, not only unhatched eggs were considered but also dead chicks in and about the nest. The effect of treatment on clutch size and measures of egg size were analysed using generalised linear models (GLM), clutches that had no successful hatches were excluded, as was one nest part predated. The effect of treatment on hatching success was analysed with a logistic regression. These analyses were performed in S-Plus 6 Professional release 1.

4.3.5 Chick Capture, Measurements and Survival

The chicks produced by the radio-tagged females were captured on days 5, 10 and 15 after their assumed hatch date. The chicks were located by using the radio telemetry equipment to find the hen and then trained pointing dogs to locate the chicks. Chicks were not disturbed if the weather was poor, i.e. raining or excessively windy.

The chicks were placed in cotton bags from which faecal samples were collected. Each chick was weighed, had wing length measured and the number of sheep ticks *Ixodes ricinus* counted.

The number of chicks located with a dog was not a good measure of survival as the number of chicks located on day 5 was on a number of occasions smaller than that on day 10. This was most likely to do with the conditions and level of scent the dogs were working with. To get a more robust measure of survival the broods were flushed on day 50. The survival estimate is more robust at this age as the brood flies from the encounter and can be easily counted.

Broods were designated to treatment or control groups if the hen nested in either area and on two of the three occasions of capture they were in one or other of the experimental sites.

The effects on brood survival were investigated using generalised linear mixed models (GLMM) with binomial errors for data from each of the three age groups. The analysis was carried out in this way as the relatively small data set did not allow the model to be either stepwise deleted or built in to a definitive minimal model. The random terms in the model were the average predicted lay weight for each brood), weight of faeces (to control for sample amount and as a proxy measure of the number of chicks caught) and the experimental site they were in. The maximal model was (an example for chicks at day 5):

Chick Survival ~ Treatment * Weight at day 5 * Mean no. of tick larvae at day 5 * Invertebrate parts in faeces at day 5

* all 2 way interactions considered

Factors influencing weight of chicks were investigated with restricted maximum likelihood models (ReML). Both analyses were carried out in GenStat 6th Edition. The random terms in the model were the average predicted lay weight for each brood, the weight of faeces collected and the experimental site they were in. The maximal model was (an example for chicks at day 5):

Weight at day 5 ~ Treatment * Mean no. of tick larvae at day 5 * Invertebrate parts in faeces at day 5

Table 4.1 is a key for model terms and their abbreviations for use in the results section.

Table 4.1. Model key

Model Term	Abbreviation
Survival (chicks at day 50/Chicks off nest)	S
Weight at days 5, 10, 15	W5, W10, W15
Weight differences between catches	WD5-10, WD5-15, WD10-15
Mean number of tick larvae parasitising a chick in a given brood at days 5, 10,15	L5, L10, L15
Number of invertebrate parts in faeces at days 5, 10, 15	I5, I10, I15
Weight of plant material in faeces at days 5,10, 15	P5, P10, P15
Treatment	F

4.3.6 Blood Sampling and Louping Ill Tests

73 red grouse shot in August 2002 on the Phones study area had blood taken for louping ill tests. Five birds sampled in 2000 and 3 mountain hares *Lepus timidus* shot in 1999 from Ralia were also tested. All samples were analysed at the Moredun Institute.

4.3.7 Invertebrate Monitoring

Invertebrates were trapped for a 50-day period from the 3rd May 2002. They were trapped in bright yellow water traps (Chapter 2) that were collected every 10 days. Each ½ Km^2 block had a transect of five evenly spaced water traps running along the centre line of the plot. The first trap on the transect was 100m from the edge of the experimental plot, with each further trap being 200m from the last.

The samples were sorted into orders or sub-orders in the laboratory. The Nematocera were differentiated from the other dipterans due to their importance as chick food insects. The main nematocerans trapped on the study areas were Tipulidae (crane flies) and Chironomidae (non-biting midges), the two major groups identified in faecal samples of chicks in the area by Park *et al.* (2001).

The data was truncated into the time period when the chicks had hatched and used in a quasi-likelihood GLM to investigate the relationship between amount of invertebrates caught and the amount of invertebrate material recovered from the faeces. Analysis was done in S-Plus 6 Professional release 1.

4.3.8 Faecal Analysis

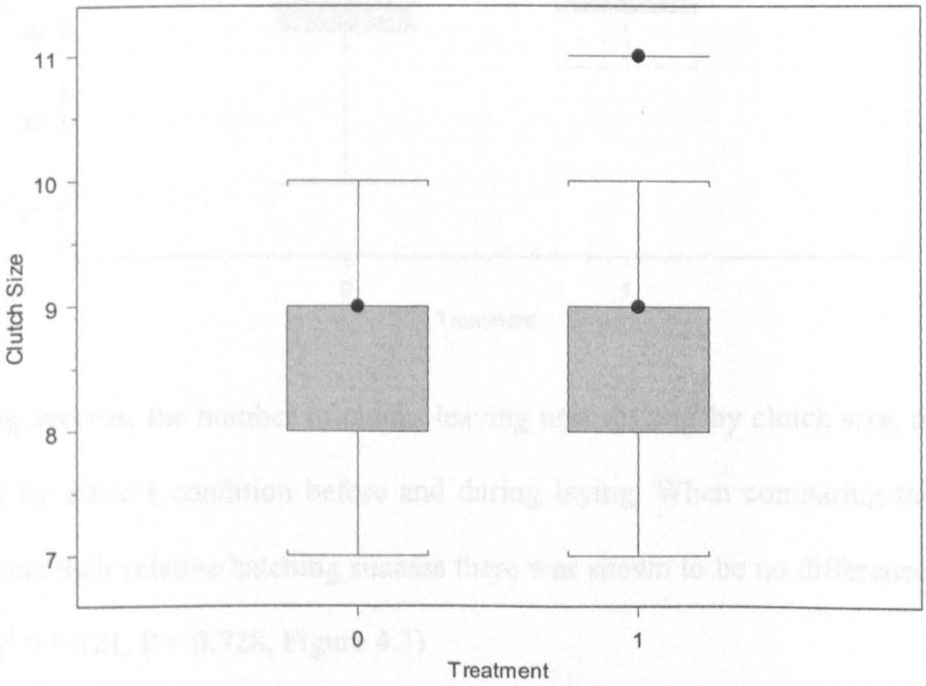
The faeces collected from the chicks was soaked in water for three days and then separated in to its plant and animal components under a microscope. The plant portion was dried and weighed. The amount of invertebrate fragments in 0.1 grams of faeces was counted as the samples were too small to register an accurate mass. The weight of the plant faecal matter acted as a proxy control for the number of chicks caught.

4.4 Results

4.4.1 Looking for the effects of maternal nutrition

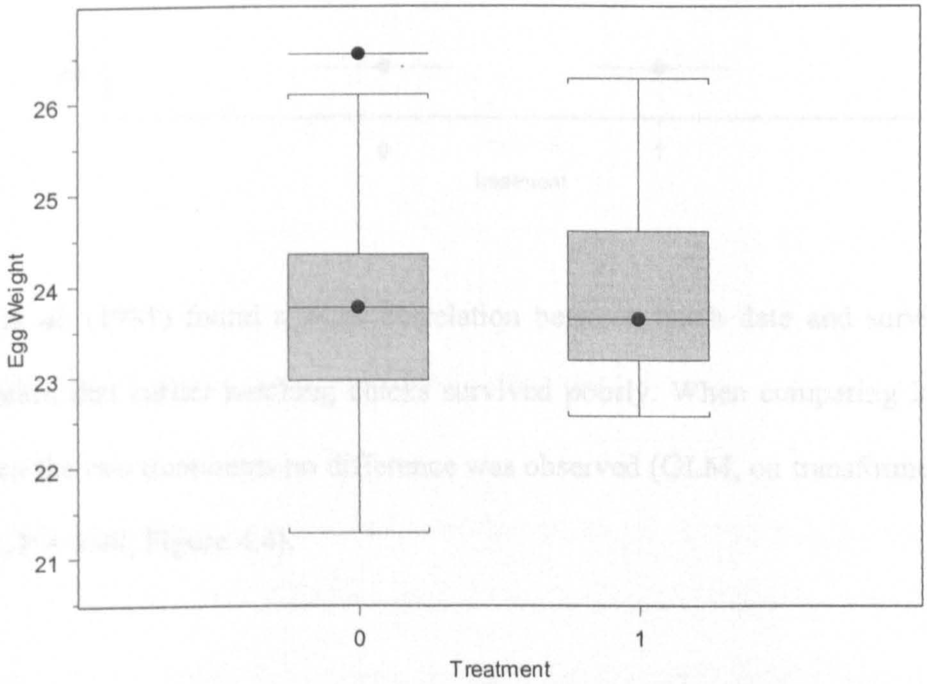
The effect of fertilisation on the quality of red grouse hens was investigated by comparing clutches laid in treated and control areas. Delahay and Moss (1996) showed that hen's weight and food intake was significantly related to the number and weight of eggs produced. When clutch size of hens with nests in treated and control areas were compared there was no difference in clutch size (GLM, $F_{1,27} = 0.280$, $P = 0.601$, Figure 4.1).

Figure 4.1. Clutch sizes from 28 hens in the two treatment groups. Treatment 0 is the control and 1 is the fertilised area. (—•— = outliers)



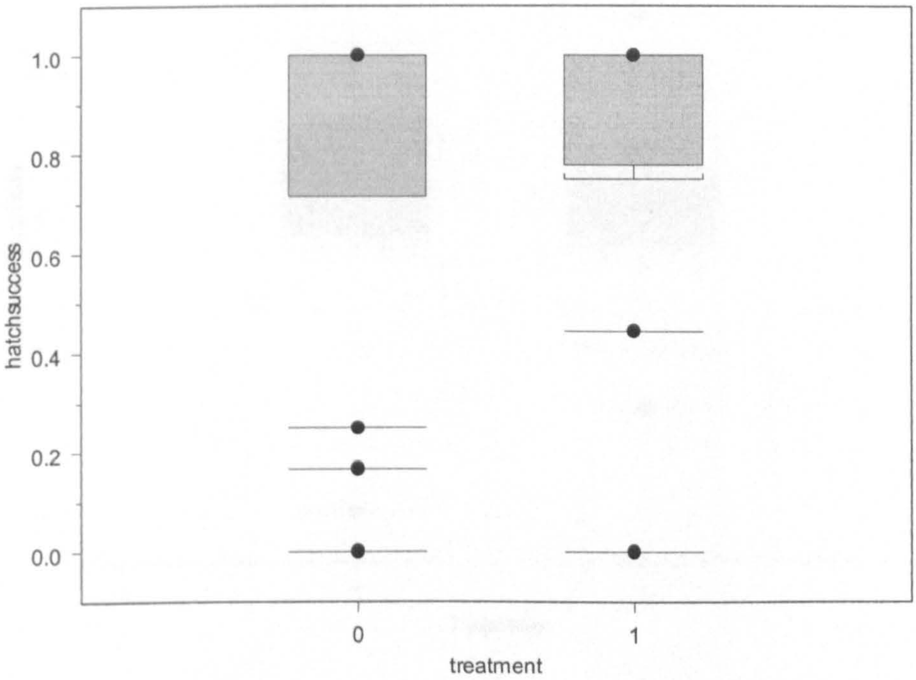
There was no difference in the predicted average lay weight of an egg from the 28 clutches measured (GLM $F_{1,28} = 0.11$, $P = 0.74$) (Figure 4.2). Two other measures of egg size were also considered, neither average egg length (Wilcoxon rank-sum test, $Z = 0.31$, $P = 0.76$) nor breadth (Wilcoxon rank-sum test, $Z = 0.12$, $P = 0.91$) were significantly different.

Figure 4.2. Average predicted lay weight of an individual egg from each of the 28 clutches measured. (—•— = outliers)



Hatching success, the number of chicks leaving nest divided by clutch size, may also be affected by a hen's condition before and during laying. When comparing the treatment groups and their relative hatching success there was shown to be no difference (Binomial GLM, $\chi^2 = 0.121$, $P = 0.728$, Figure 4.3)

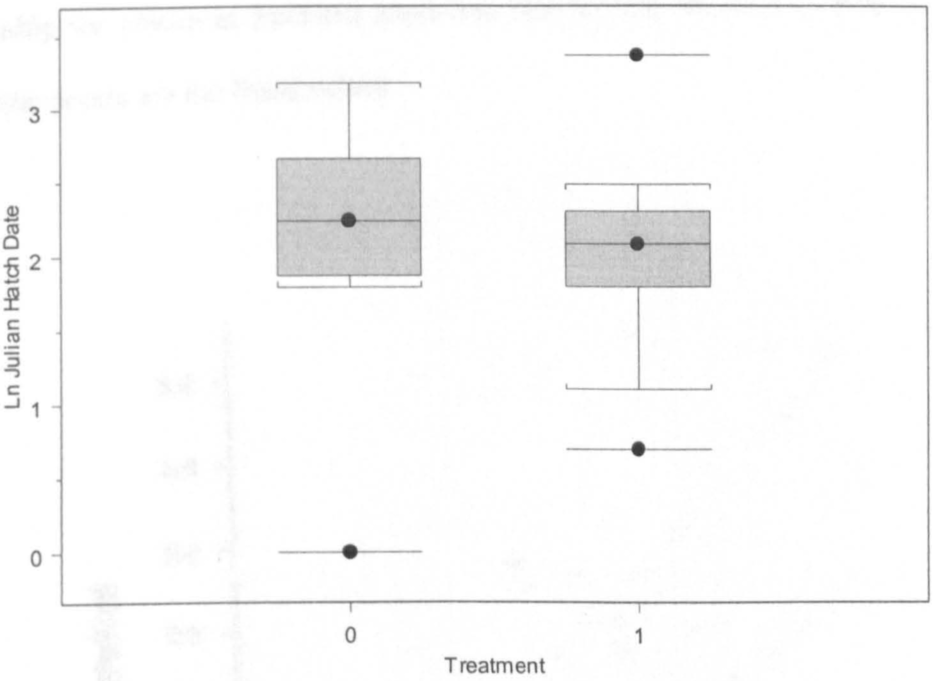
Figure 4.3. The proportion of chicks leaving the nest / number of eggs laid in 32 nests on the treated and control plots. (—•— = outliers)



Moss *et al.* (1981) found a weak correlation between hatch date and survival. With a suggestion that earlier hatching chicks survived poorly. When comparing ln hatch date between the two treatments no difference was observed (GLM, on transformed data, $F_{1,31} = 0.72$, $P = 0.40$, Figure 4.4).

Figure 4.4. Hatch date (Julian days from May 21st ln transformed) in the two treatments.

(—•— = outliers)



4.4.2 Factors affecting grouse chick survival at day 5

Chick survival at day five is positively effected by treatment with fertiliser (Binomial GLMM, Wald Statistic = 5.74, P = 0.017), and average chick weight (Binomial GLMM, Wald Statistic = 8.32, P = 0.004, figure 4.5). The average number of tick larvae parasitising a chick is negatively related to survival (Binomial GLMM, Wald Statistic = 8.42, P = 0.004, figure 4.6) as is the amount of invertebrate fragments in the faecal material (Binomial GLMM, Wald Statistic = 7.16, P = 0.007, figure 4.7).

Figure 4.5. The fits for the proportion of chicks surviving at day 5 with respect to weight at day 5 in, grams, for the minimal model; S ~ F+W5+I5+L5. (For more information on model term abbreviations see table 1). The green line is the estimated relationship for chicks in fertilised areas and the red line represents those in control areas. The points are the fitted values.

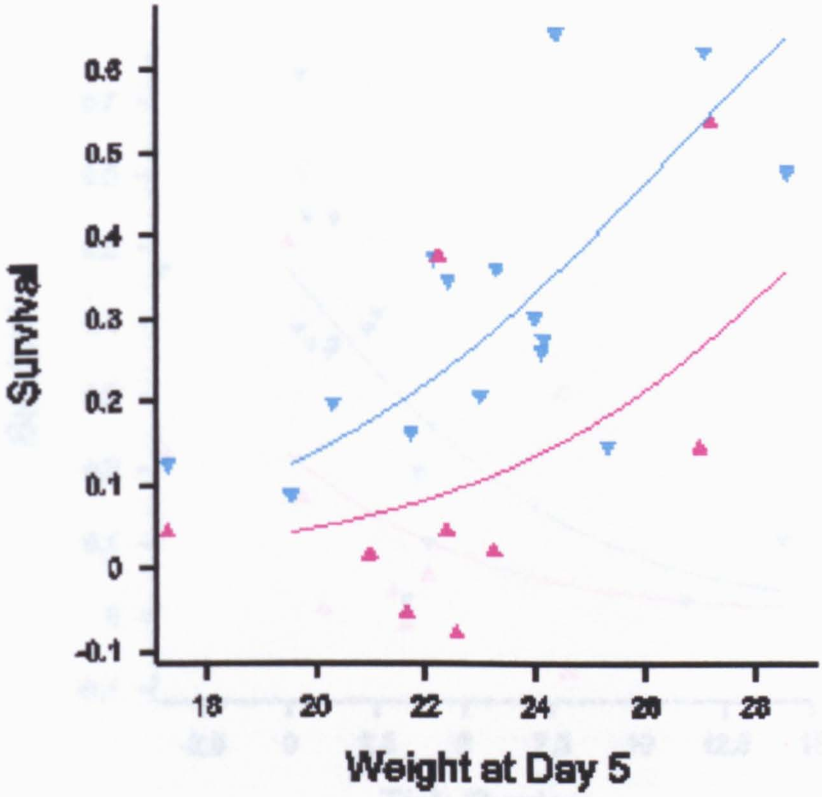


Figure 4.6. The model fit for the proportion of chicks surviving at day 5 with respect to the number of tick larvae parasitising at day 5 for the minimal model; S ~ F+W5+I5+L5. (For more information on model term abbreviations see table 1). The green line is for chicks in fertilised areas and the red line represents those in control areas. The points are the fitted values.

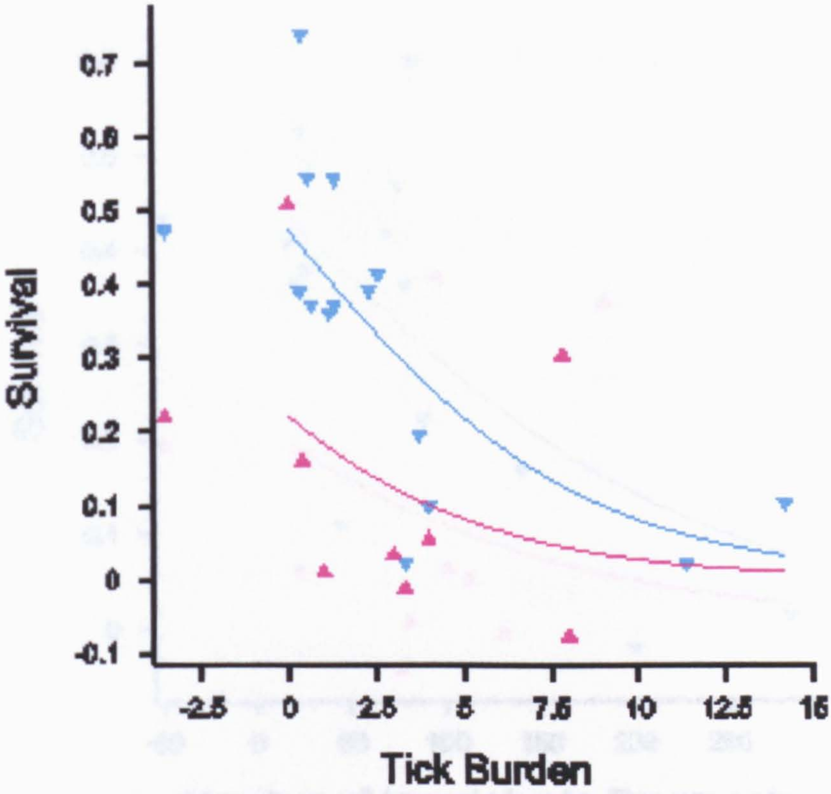
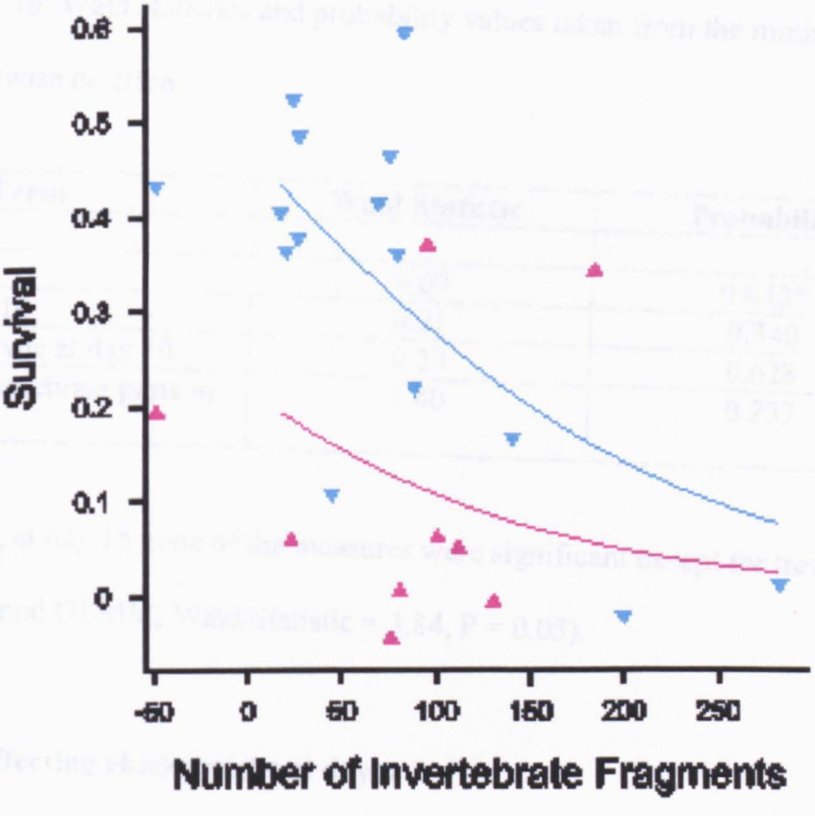


Figure 4.7. The model fits for the proportion of chicks surviving at day 5 with respect to weight at the amount of invertebrates in the faeces at day 5 for the minimal model; S ~ F+W5+I5+L5. (For more information on model term abbreviations see table 1). The green line is for chicks in fertilised areas and the red line represents those in control areas. The points are the fitted values.



4.4.3 Factors affecting grouse chick survival at day 10 and 15

Survival at day 10 is positively affected by the application of fertiliser (Binomial GLMM, Wald Statistic = 4.09, P = 0.043). No other terms in the maximal model were significant (Table 4.1) when lay weight and experimental site were controlled for.

Table 4.1. Wald statistics and probability values for terms in the model encompassing data from day 10. Wald statistics and probability values taken from the minimal model or at time of stepwise deletion.

Term	Wald Statistic	Probability
Treatment	4.09	0.043*
Weight at day 10	0.91	0.340
Number of Larvae at day 10	0.23	0.628
Number of invertebrate parts in faeces	1.40	0.237

As with day 10, at day 15 none of the measures were significant except for treatment fertiliser (Binomial GLMM, Wald Statistic = 3.84, P = 0.05).

4.4.4 Factors affecting chick weight at day 5

Weight at day 5 is not affected by the application of fertiliser (ReML, Wald Statistic = 0.99, P = 0.321). The number of invertebrate parts in the faeces interacts significantly with the number of tick larvae (ReML, Wald Statistic = 6.23, P = 0.013, figures 4.10 &

4.11). Both of these factors have a positive relationship with chick weight when predicted lay weight, weight of faeces and site are controlled for.

Figure 4.10. The number of invertebrate parts in the faecal samples with chick weight at day 5, in grams, for the minimal adequate model; W5 ~ I5+L5+I5.L5. (For more information on model term abbreviations see table 1).

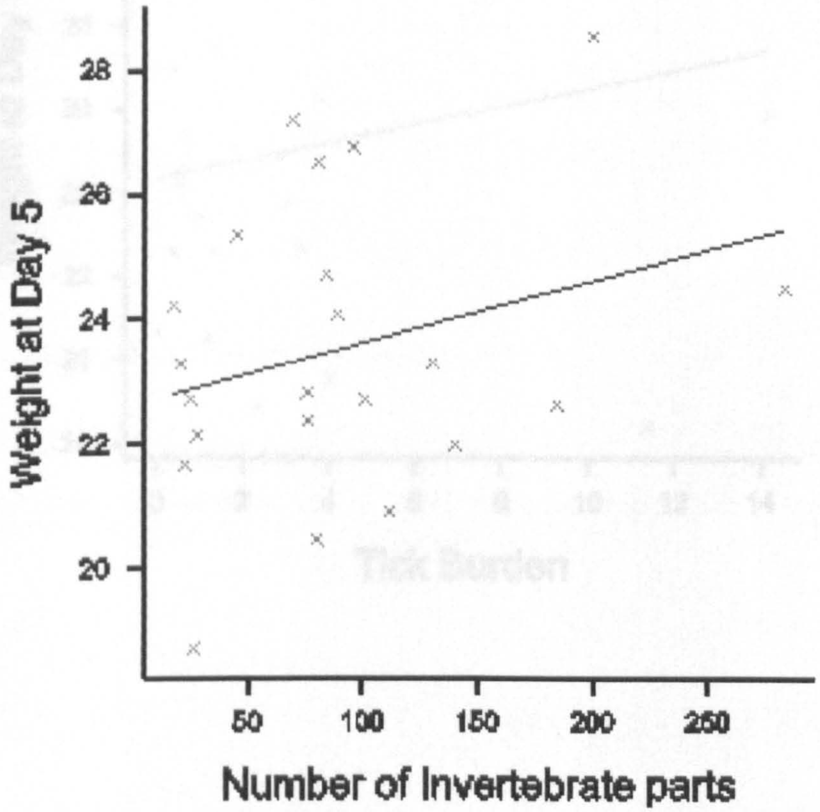
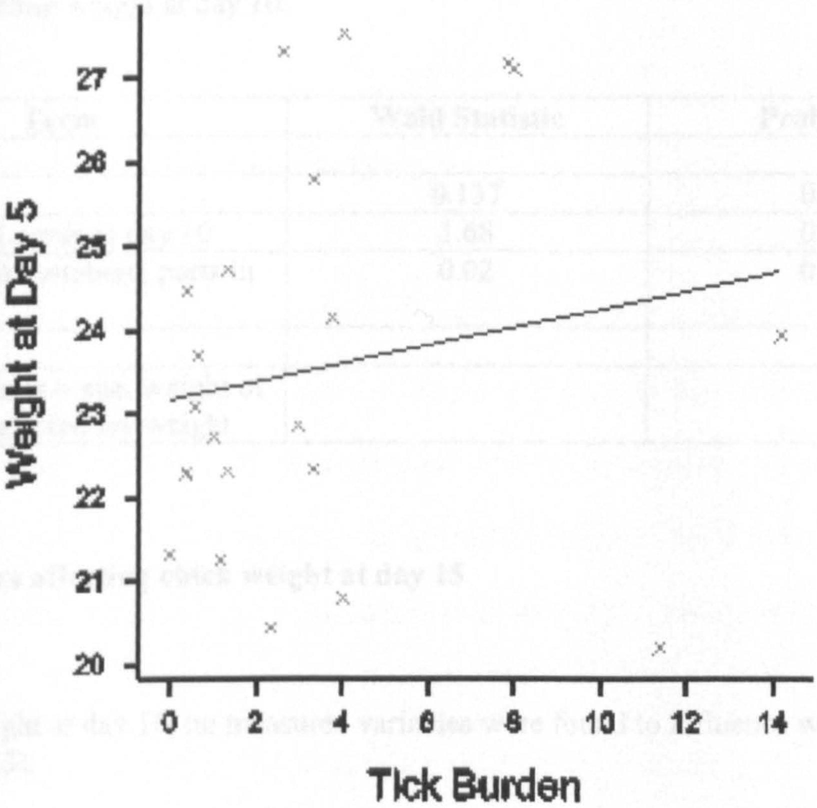


Figure 4.11. The number of tick larvae parasitising chicks against weight at day 5 for the minimal adequate model; W5 ~ I5+L5+I5.L5. (For more information on model term abbreviations see table 1).



4.4.5 Factors affecting chick weight at day 10

No measured variables were seen to affect the average weight of a chick at day 10 (table 4.2).

Table 4.2. Wald statistics and probability values from the ReML analysis investigating factors effecting weight at day 10.

Term	**Wald Statistic**	**Probability**
Treatment	0.137	0.390
Number of Larvae at day 10	1.68	0.195
Number of invertebrate parts in faeces	0.02	0.878
Random Terms = site, weight of faeces & predicted lay weight		

4.4.6 Factors affecting chick weight at day 15

As with weight at day 10, no measured variables were found to influence weight at day 15 (Table 4.3).

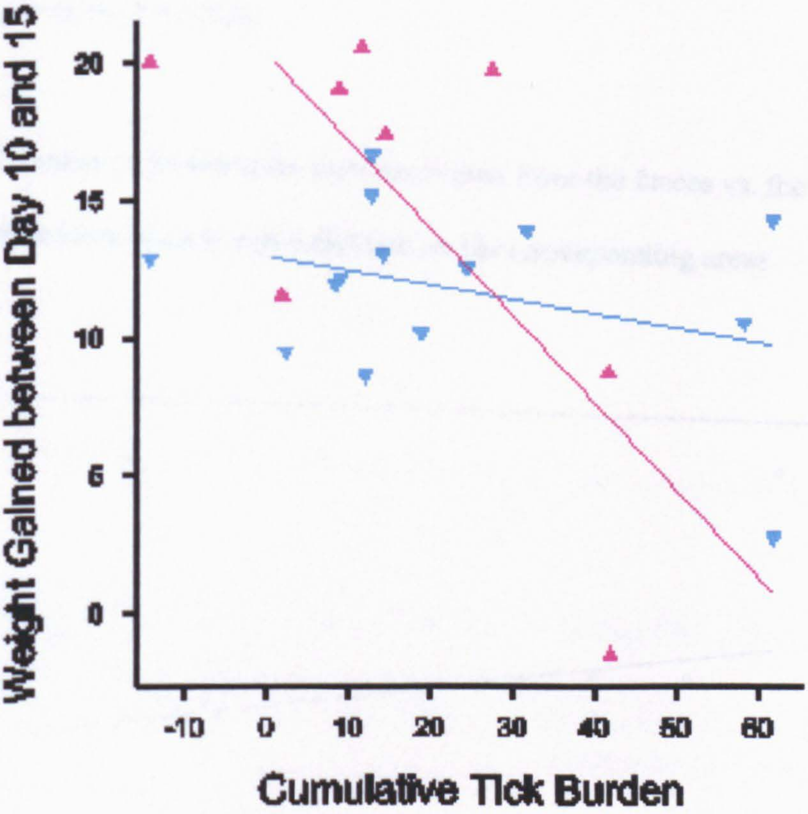
Table 4.3. Wald statistics and probability values from the ReML analysis investigating factors effecting weight at day 15.

Term	Wald Statistic	Probability
Treatment	0.20	0.653
Number of Larvae at day 10	0.05	0.831
Number of invertebrate parts in faeces	0.17	0.678
Random Terms = site, weight of faeces & predicted lay weight		

4.4.7 Factors affecting chick weight gain

No variables measured related significantly to differences in the average weight gain of a chick in a brood between day 5 and 10 and day 5 and 15. The difference between day 10 and 15 was characterised by a significant interaction between treatment and the difference in larval numbers between day 10 and 15 (ReML, Wald Statistic = 3.82, P = 0.051) when lay weight and site were used as random terms in the model (figure 4.14).

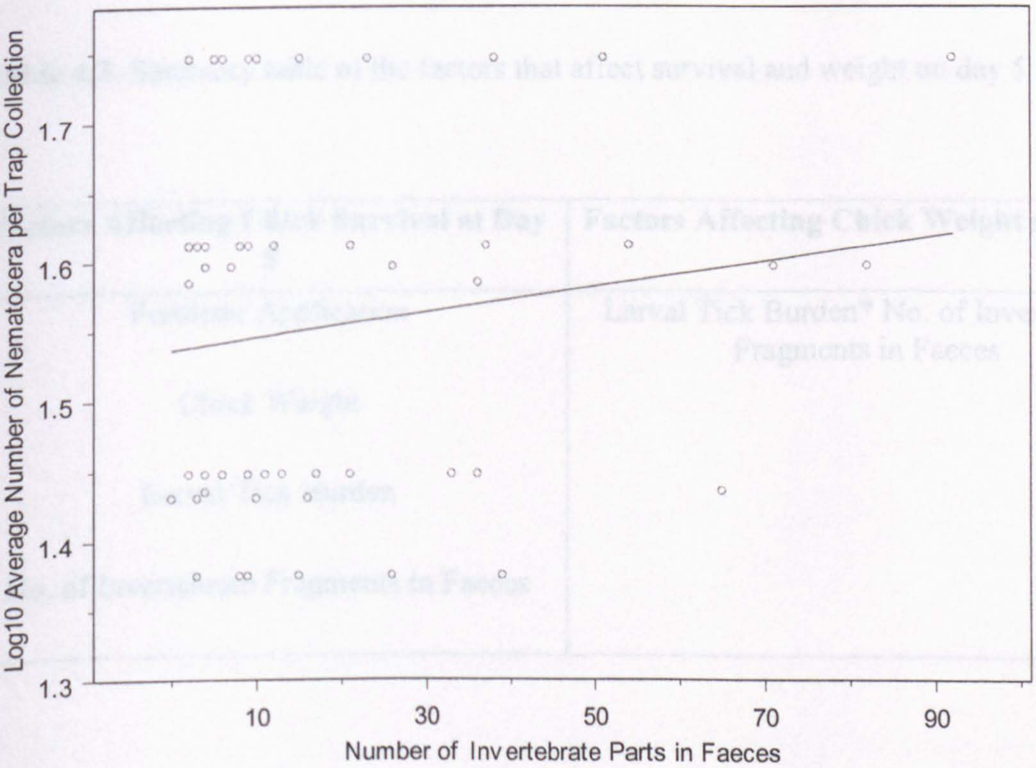
Figure 4.14. The relationship between the difference in tick larval parasitism from day 10 to 15 against chick weight gain between day 10 and day 15 for the minimal model; WD10-15 ~ F+L10-15+F.L10-15. (For more information on model term abbreviations see table 1). The green line represents chicks from fertilised plots and the red line are those from the control. Points are fitted values.



4.4.8 Invertebrate make-up of faecal samples and invertebrates trapped

The number of invertebrate fragments in the faeces is positively related to the amount of Nematocera trapped on the corresponding site (Quasi-likelihood GLM, link = log var = mu^2, $F_{1,20}$= 5.81, P = 0.026, figure 4.15). The amount of plant material in the sample is not related to the levels of invertebrate parts recovered (Quasi-likelihood GLM, link = log var = mu^2, $F_{1,20}$= 0.26, P = 0.62).

Figure 4.15. Number of invertebrate parts recovered from the faeces vs. the average number of Nematocera in each trap collection on the corresponding areas.



4.4.9 Louping ill tests

All 73 red grouse shot and tested on the Phones estate, including the study areas, tested negative for Louping ill. On the study area on Ralia, no birds were shot or tested in 2002. However, in 2000 the 5 birds tested were negative and in 1999 the 3 mountain hares shot were also negative.

4.4.10 Summary tables

Tables 4.3, 4.4 and 4.5 are summary tables of the analyses investigating factors affecting chick survival and weight at days 5, 10 and 15.

Table 4.3. Summary table of the factors that affect survival and weight on day 5

Factors Affecting Chick Survival at Day 5	**Factors Affecting Chick Weight at Day 5**
Fertiliser Application Chick Weight Larval Tick Burden No. of Invertebrate Fragments in Faeces	Larval Tick Burden* No. of Invertebrate Fragments in Faeces

Table 4.4. Summary table of the factors that affect survival and weight on day 10

Factors Affecting Chick Survival at Day 10	Factors Affecting Chick Weight at Day 10
Fertiliser Application	No Significant Terms

Table 4.5. Summary table of the factors that affect survival and weight on day 15

Factors Affecting Chick Survival at Day 15	Factors Affecting Chick Weight at Day 15
Fertiliser Application	No Significant Terms

4.5 Discussion

This study investigated the effects of fertilisation on chick survival in red grouse and the mechanisms that might be influencing this relationship. Unlike past fertilisation experiments (Miller *et al.* 1970, Watson & O'Hare 1979, Watson *et al.* 1984) an effect on grouse production was seen in the first season after application. This was despite the fact that the predicted increase in the amount of invertebrate food produced due to fertilisation was not detected and in fact appeared to be reversed (Chapter 3).

4.5.1 The effects of maternal nutrition

In past work the effect of fertilisation has been attributed mainly to the improved nutritional status of the hen grouses food in the run up to, and during laying. The effects of improved food intake on females, in the absence of the gut parasite *T .tenuis*, has been shown to increase the number, lay rate and weight of eggs produced (Delahay & Moss 1996) and these aspects have been shown to be related to chick survival (Moss *et al.* 1981).

However, the fertiliser application in this experiment began in mid-April and was probably too late to improve the condition of breeding females in 2002. Indirect measures of hens' breeding fitness, biometric measures of eggs, were compared between the treated and control plots. There was seen to be no difference in the eggs' physical size between the treated and control areas, measured by predicted lay weight, length and breadth.

Clutch size, hatch success and hatch dates were also shown to have no significant differences between the control and fertilised areas. These measures were used in order to ascertain any relations between this experiment and previous work on the relationships between nutrient status and egg quality. As no differences were observed it is assumed that the fertiliser application was too late to benefit this seasons breeding females. These results allow a clearer investigation of the factors that are influencing chick survival post hatch.

4.5.2 Fertiliser, chick survival and weight

The data from the radio-tracked grouse broods gives an insight in to the ways in which fertilisation may be affecting chick survival. Moss *et al.* (1981) showed that mortality was at its highest in the first 5 days of life, with considerable mortality occurring till day 15. A chick's chance of survival, in this experiment, was influenced by a number of factors. The addition of fertiliser had a large positive effect on chick survival when other factors at days 5, 10 and 15 were taken in to account and the lay weight, weight of faeces and experimental area controlled for. Fertilisation may affect chick survival in number of ways.

4.5.2.1 The effect of improved nutrient status of heather

As the majority of grouse chick diet is made up of heather (Savoury 1977) the improved plane of nutrition could influence chick survival. The assumed increase in N and P levels in the dietary intake of grouse chicks in treated areas, should have been seen as an increase in chick weight. Chick weight was not shown to be directly related to treatment, although it was shown to be linked with survival. As predicted when the lay weight of eggs was used as a control in the model, as an approximation of hatch weight, the significance of chick weight post hatch to survival probability suggests that a dietary mechanism is in effect. The lack of direct evidence between treatment and weight may be due to the loss of individual detail as data was collected at the brood level.

4.5.2.2 Fertilisation and invertebrate diet

Invertebrate intake was shown to increase in areas where more insects were available. This suggests that a grouse chick's intake rate is governed by what is in the environment and, therefore, many chicks are likely to be eating less invertebrates than is optimal. It follows that an increase in the amount of invertebrates in the environment may be of benefit to chicks and could possibly increase their weight and in turn survival chances.

There was no recorded increase in invertebrates in the fertilised plots so it is assumed that improvements in survival rates were not due to the abundance of invertebrate prey (Chapter 3). However, no chemical analysis of invertebrates was undertaken to see whether the nutritional value of prey items had increased with the addition of fertiliser, although this is perhaps unlikely as invertebrate quality is likely to be largely defined by juvenile conditions prior to fertilisation.

Weight was shown to be an important factor in chick survival at day 5. At this stage of life weight positively related to the amount of invertebrate remains in the faecal material. This result suggests that the role of invertebrates in weight gain, and in turn survival, is significant. However, the probability of survival decreased with increased intake of invertebrate food. This unexpected relationship is likely to be due to the inaccurate estimate of invertebrate food that faecal analysis will provide. These contradictory results are difficult to interpret, however, evidence from other researchers has pointed to the link between invertebrate intake, chick weight and survival (Park *et al.* 2001).

4.5.2.3 Fertilisation and predation risk

The effect of treatment on habitat structure in decreasing predation risk was not measured in this experiment. However, derived results (Chapter 3) show that this is unlikely to have caused the increase in survival probabilities, as there was very little difference in the vegetation structure.

4.5.3 The effect of tick parasitism on grouse chicks

As tick burden increases, survival of chicks at day 5 decreases. This lowering in survival probability is the first time that grouse chicks have been shown to be effected by ticks in the absence of louping ill. Reduction in survival probability by non-viraemic tick biting could be due to mechanical or physiological reasons. Ticks mainly parasitise chicks around the eyes and beak (Hudson 1986). Bites can frequently cause swelling that can lead to eyes becoming closed; it is possible that this may cause problems with feeding or hen location. Alternatively the stress of tick biting on the immune system may leave the chick weakened and therefore, less likely to survive. Whatever the mechanism of reduced survival probability due to tick biting, the effect is shown prior to chick loss as a reduction in weight gain. The reduction in weight with increasing tick burden could be consistent with either a mechanical or physiological explanation of loss of survival chances.

The weight gain between days 10 and 15 is characterised by an interaction between tick burden and treatment. As tick burden rises the level of weight gain falls. This result is not in itself surprising. However, the application of fertiliser seems to buffer the effect of parasitism. It may follow that a more nutritious diet enables chicks to resist the negative effects of higher tick burdens. This result is consistent with the theory that excessive tick biting weakens the chick through challenges to the immune system and/or loss of blood leading to a reduction in survival.

Tick burden has been shown at various chick ages to be related to invertebrate intake. The positive relationship between invertebrate food and tick burden suggests that greater foraging levels increase the chance of parasitism. Ticks require areas that have high humidity levels, over 85%, in order to avoid desiccation (Sonnenshine 1991), this need overlaps with the boggy environments where most moorland tipulids are present (Coulson & Whittaker 1978).

4.5.4 Fertilisation and habitat change

Repeated application of fertiliser, as a management tool would most likely impact heavily on the vegetative community, mainly by favouring grasses at the detriment of shrubs and bryophytes (Richardson *et al.* 2002, Chapin *et al.* 1995, Alonso & Hartley 1998). Changes in the vegetation community brought about by nutrient addition may lower red grouse production by leading to a loss of heather and therefore, the main source of food and cover. The reduction in bryophyte abundance may also be detrimental as many larval stages of invertebrate food are thought to be associated with them (Coulson & Whittaker 1979). If nutrient input was to become a widely practised management tool then it would have to be spatially and temporally focused to avoid ecosystem damage.

4.5.5 Summary and Conclusions

The addition of fertiliser has been shown to have a significant effect on the survival of red grouse chicks. The causal mechanism of this relationship remains unclear, although diet is the most likely cause. The amount of invertebrates in the faeces was highest in areas where more invertebrates were available. This result coupled with that from chapter 3 that showed that invertebrate abundance was greater in control areas raises an interesting question about the benefits given by consuming invertebrates.

In addition to diet, chick survival was related negatively to non-viraemic tick biting. However, its effects can be reduced by fertilisation, as better nutrition appears to buffer the effect of parasitism. The benefits to chick survival from fertilisation could lead to it being developed as a management tool. Before a management prescription can be formulated further work is needed to determine which aspects controlling chick survival are most important and easily manipulated. This would allow a more tailored approach to fertiliser application to be employed, reducing costs to land managers and the environment.

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Chapter 5

The Spatial and Temporal Relationships between Red Grouse Chicks and Their Invertebrate Food

5.1 Abstract

The spatial and temporal relationships between red grouse production and the invertebrate food supply utilised by chicks was investigated with a natural experiment using altitude to vary invertebrate timing.

The numbers, biomass and weight of individual nematoceran prey items were related to altitude with sites classified as being of medium height (approximately 500-600m) producing the largest amounts. This pattern was largely repeated for grouse production counts both on the experimental sites and from counts gathered from 22 moorland estates.

The factors affecting the spatial patterns of grouse production were mainly comprised of altitude and vegetation variables. When invertebrate data was added to the model after it had been subsetted to sample the times when grouse chicks had been utilising it, a weak relationship was shown between numbers trapped, biomass and the number of chicks produced by each grouse hen.

When investigating the temporal relationships it was seen that a strong correlation exists between the degree of difference between chick hatch and the availability of large prey items, with the greater the degree of synchrony leading to greater grouse production figures.

The consequences of climate change to red grouse are discussed in light of the findings.

5.2 Introduction

Red grouse *Lagopus lagopus scoticus* and the associated moorland management are of both economic and conservation importance in the Scottish uplands (Hudson 1992). Despite this, numbers of grouse in the Spey valley in the central Scottish highlands have been declining since the mid 1970's (Hudson 1988). The subsequent loss of sporting interest has been associated with loss of heather moorland as levels of game management fall (Robertson, Park & Barton 2001). The change in abundance of red grouse is not evenly distributed over their range in Scotland. Anecdotal reports from game managers suggest grouse densities have been maintained on moors with higher altitudes (Smith pers. comm).

5.2.1 Questions of climate change

Over the past ten years both rainfall and temperature have increased in Scotland, with temperatures rising over half a degree centigrade when compared to the 1961 to 1990 average and a precipitation increase of almost nine percent (Scottish Executive National Statistics 2001). The effects of these changes are likely to be most obvious in upland areas where temperature lapse rates are greatest (Manly 1970). Changes in climate can affect habitat and micro-climate and these factors are known to effect invertebrates (Coulson 1988). This study investigated the hypothesis that grouse abundance increases with altitude and investigated whether grouse production was associated with differential invertebrate availability, both spatially and temporally, over a range of altitudes.

5.2.2 The invertebrate diet of red grouse chicks

Red grouse rely on invertebrate food in the first few weeks after hatching. A grouse chicks diet consists of approximately 5%, by dry weight, of invertebrate food. However, this food appears essential to maintain fast growth rates (Savoury 1977). Park *et al.* (2001) demonstrated that when invertebrate consumption increased chick growth rates increase, which in turn was correlated with better survival. Invertebrate food has a higher digestible protein content than plant material and higher concentrations of the two sulphur-based amino acids, methionine and cystine, which are essential for feather synthesis (Bolton & Blair 1974, Savoury 1989). The adult stage of *Tipula subnidicornis*, a usual prey item, contains nine times the nitrogen and seven times more phosphorous than heather *Calluna vulgaris*, which is the main food source of both adults and chicks (Leslie 1911, Butterfield & Coulson 1975, Savoury 1977).

Though the invertebrate food taken by red grouse chicks is varied, Diptera make up a large percentage of the diet. Of these the Tipulidae make up the majority of invertebrate food consumed (Grimshaw 1911, Hudson 1986, Savoury 1977, 1989, Park *et al.* 2001). Tipulids may be preferred, as many species are relatively sedentary making them vulnerable to predation (Butterfield & Coulson 1975).

5.2.3 The spatial distribution of invertebrates on moorland

The intake of invertebrates by grouse chicks can be influenced by the prey's availability both spatially and temporally. The abundance of invertebrates spatially is governed by habitat, with factors such as substrate type and vegetation characteristics playing the major roles (Coulson & Whittaker 1978, Sanderson *et al.* 1995). Hudson (1986) recorded the greatest abundance's of chick food insects in bog flushes on moors in the North York Moors. Changes in temperature may alter the spatial distribution of invertebrates by changing the vegetation characteristics and/or the substrate. Michelsen *et al.* (1996) showed that plant growth increased when temperatures were raised. The direct effect of temperature on growth rates may well have been reinforced by the increase in nutrient availability caused by increased organic matter decomposition and nutrient cycling in warmer weather (Rustad *et al.* 2001). Both these effects may cause changes in vegetation structure by altering the relative competitive abilities of the species present (Richardson *et al.* 2002). These changes are likely to alter the pattern of distribution and community structure of moorland invertebrates.

5.2.4 The temporal distribution of moorland invertebrates

Red grouse chicks predominantly target invertebrates in their adult stage. Adult invertebrates are present in the environment for relatively short periods. For example *T. subnodicornis* emerges over a period of about 3 weeks (Coulson 1962), with *Molophilus ater* emerging over approximately 11 days (Hadley 1969), both these species have been identified as important prey items of grouse (Coulson & Whitaker 1979, Grimshaw 1911). Furthermore, these two species along with an annelid worm, *Cognettia sphagnetorum*, form 75% of the invertebrate biomass on areas of blanket bog on a moorland reserve in the north of England (Coulson & Whittaker 1979). Over 80% of the invertebrate biomass is gained and lost in the 6 weeks from mid May until the end of June. The main source of chick food insects is therefore, transient and so it is assumed that chick hatch is timed to correspond with the emergence of the invertebrate food. There is some evidence that the date of chick hatch is earlier in years when April temperature is high (Moss *et al.* 1981) the same cue that causes earlier invertebrate pupation and therefore, emergence in these invertebrates (Coulson & Whittaker 1979). However, in the great/blue tit system the same temperature cues are used but do not guarantee synchronisation between peak invertebrate biomass and the chick's window of major reliance on their caterpillar food. This is because the caterpillars hatch and development is much more flexible than that of the birds (Van Noordwijk *et al.* 1995). This inflexibility causes the tits to hatch to late in years where it is warmer than average (Van Balen 1973). A time lag of 2-3 days can have a marked effect on great tit fledging success (Van Noordwijk *et al.* 1995). The larger the time lag the lower the nestling weight and fledging success (Dias & Blondel 1996). Perrins (1991) showed that the temporal relationship between the tits and the caterpillars was more important to fledging success than the sheer abundance of food.

In the grouse/crane fly system the emergence times fluctuate between years, habitats and altitude. Hadley (1969) showed that *M. ater* emergence fluctuated between the years of study by up to 8 days and this was correlated with temperature. Temperature also caused different emergence times at different altitudes with each graduation of 300 ft (approximately 100m) leading to differences in emergence of between 7 and 9 days. The type of substrate the larval stages inhabit can also affect the emergence by up to a week (Hadley 1969).

5.2.5 The abundance and size of prey

Red grouse chicks eat more invertebrates when more are available (Chapter 4, Park *et al.* 2001). However, the size of an average prey item may also play an important role in the red grouse/invertebrate prey system. Picozzi *et al.* (1999) correlated capercaillie, *Tetrao urogallus*, chick survival to the size rather than abundance of invertebrate prey in mid-June. The size of prey items and not just the number have also been shown to be important in nestling weight and fledging success of Great tits *Parus major* and blue tits *Parus caeruleus* (Naef-Daenzer & Keller 1999). Larger prey items may increase overall intake of invertebrate food or lead to greater foraging efficiency allowing chicks to minimise energy expenditure due to feeding.

5.2.6 Study aims

This study examines the spatial and temporal relationships between invertebrate food availability and red grouse production. The relative importance of the abundance and biomass of invertebrate prey to red grouse production is investigated. The importance of synchrony between grouse hatch and invertebrate emergence is also examined. Altitude is used as a tool to observe the relationship at different temperatures and times.

5.3 Materials and Methods

5.3.1 The study site

The study site is in the Spey Valley in the Scottish Central Highlands. The study used two contiguous grouse moors managed intensively for driven grouse shooting, Cuaich and South Drumochter. Both moors are characterised as wet heath with patches of blanket bog.

On each of the moors two transects were assigned on neighbouring corries, Corrie Chais, Corrie Caim on Cuaich and Corrie Illieum and Corrie Bhutre on South Drumochter. Each transect consisted of three ½ Km^2 plots (500m X 1000m) categorised as being at low, medium and high altitudes. The mid-point of plots classified as low was between 400-440m, medium plots between 520-560m and high plots between 660-700m. The range of altitudes chosen run from the lowest points on each moor to the upper limit of grouse nesting distribution.

5.3.2 Vegetation surveys

Basic vegetation surveys were carried out in late July in all twelve plots. Two 1 Km transects were walked through each plot. On each transect 25 equally spaced points were used to measure a number of variables. Sward height was measured with a marked cane with the record being at the point where the tallest piece of vegetation touched the stick. The amount of heather, including cross-leaf heather *Erica tetralix* and bell heather *Erica* *cinera* which were sparse, was classified by counting the number of shoots that touched the cane, as were grasses and sedges. Grazing was estimated by looking at the ratio of grazed to ungrazed shoots along a 25cm line at each of the 50 points. Classifying ground cover was done by allotting the substrate to one of five categories; moss (other than *Sphagnum spp.*), *Sphagnum spp.*, lichen dominated, leaf litter dominated and berry cover (*Vaccinium spp.*). For the models investigating the factors effecting grouse production principle component analysis (PCA) was used in order to condense the vegetation variables. Ground cover was split from the other vegetation variables and had a separate PCA carried out. All PCA was carried out in S-Plus 6 Professional release 1. The effect of altitude on the vegetation community was investigated with a generalised linear model (GLM) in S-Plus 6 Professional release 1.

5.3.3 Invertebrate monitoring

Invertebrates were trapped from May 1st to June 24th 2002. They were trapped in bright yellow water traps (Chapter 2) that were collected every 3 days. Each trap was placed as close to the mid-point of the plot as possible. All the traps were placed in areas that were dominated by heather with a canopy of 20-30cm in height. The ground cover was moss dominated.

The samples were sorted into orders or sub-orders in the laboratory. The Nematocera were differentiated from the other dipterans due to their importance as chick food insects. The main nematocerans trapped on the study areas were Tipulidae (crane flies) and

Chironomidae (non-biting midges), the two major groups identified in faecal samples of chicks in the area by Park *et al.* (2001). The nematocerans were counted and their mass taken.

The factors affecting the abundance of Nematocera were investigated using Reidual Maximum Likelihood models (ReML) in GenStat 6th Edition. This was done so that site and collection time could be added in to the model as random factors. Collection time was added as a quadratic term as a better approximation of the relationship than using it as a linear term.

5.3.4 Grouse hatch date

The hatch date of red grouse in the study area was determined by locating nests with a trained pointing dog in May. Five eggs in each nest were weighed and had length and breadth measured. These morphometrics were used in an equation to estimate hatch date formulated by Furness & Furness (1981), the equation has been tested and confirmed as accurate for red grouse in the area of this study (Smith in prep.). The equation works out the volume of the egg and from this predicts the weight when it would have been laid. As eggs lose moisture and become lighter as incubation progresses the percentage weight loss from the predicted initial weight, along with the average incubation period for grouse, can be used to predict time of hatch. The effect of altitude on estimates of hatch date was investigated with a GLM in S-Plus 6 Professional release 1.

5.3.5 Grouse production

Extensive data on grouse productivity were collected on 22 moorland sites (14 estates) where there was management for red grouse (predator control and heather burning). The distribution of these sites was determined by the availability of grouse abundance data for Scottish central highland moors with five-years of continuous data. These count areas are distributed throughout the Scottish central highlands. Red grouse production was carried out in the same fashion as above (Jenkins *et al.* 1963). The count sites were classified into areas of low, medium, and high altitude sites as in the intensive study. The data were analysed using ReML as the data are mixed and unbalanced, year was added as a random term. Analysis was carried out in GenStat 6th Edition.

Red grouse were counted in late July on the twelve plots to determine breeding success (Jenkins *et al.* 1963). The counts of grouse were converted to the ratio of chicks per hens. This was done as a measure of production that is independent of the density of grouse in the study areas. The effect of altitude, vegetation characteristics and invertebrate food abundance on red grouse production was investigated with a quasi-likelihood GLM in S-Plus 6 Professional release 1. The invertebrate data used was from the sub-order Nematocera as they have been shown to be the most important chick food insects in the study area (Park *et al.* 2001). Two sets of analyses were carried out, one using the data for the whole season and again when the nematoceran data had been subsetted to reflect the time when grouse chicks were utilising invertebrate food.

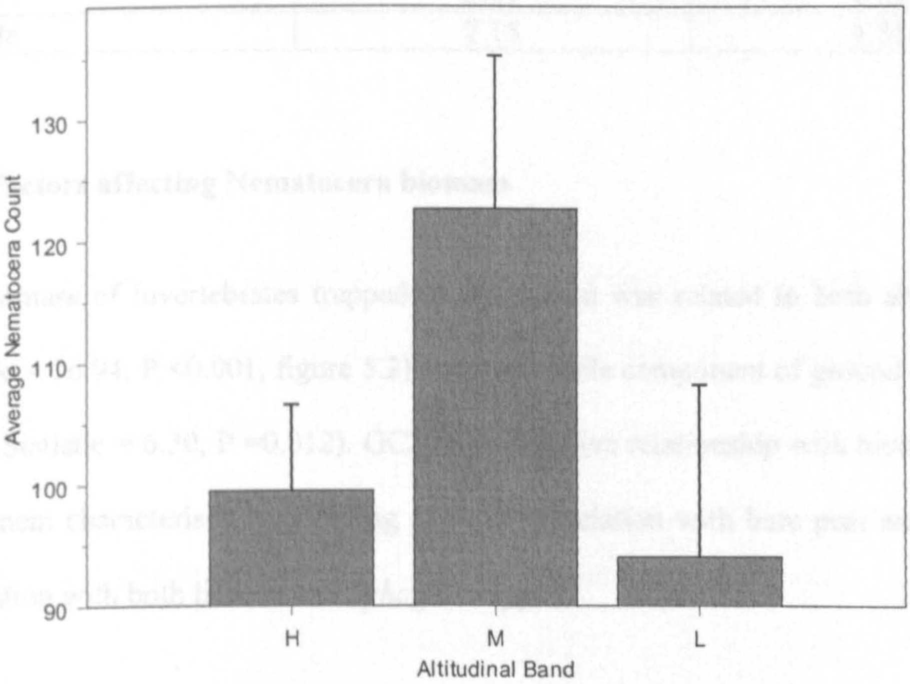
For use in the investigation of temporal relationships between grouse and invertebrates the peak level of a number of measures of invertebrate production were ascertained by creating general additive models (GAM). The splines that were fitted to the data had 6 degrees of freedom (n/3) to reflect the fluctuations in the time series. These values were used in GLMs with various error structures to look at the affect of altitude on timing in availability of Nematocera and whether the degree of difference between peak invertebrate food availability affected the number of chicks produced per grouse hen. These analyses were carried out in S-Plus 6 Professional release 1.

5.4 Results

5.4.1 Factors affecting Nematocera abundance

The number of invertebrates captured in the period of trapping is significantly affected by altitude (Wald Statistic = 6.04, P = 0.049, figure 5.1) when plot number and collection day^2 are controlled for as random factors. None of the variables explaining the vegetation or ground cover make-up had a significant affect in the model.

Figure 5.1. The average count of Nematocera at High (H), Medium (M) and Low (L) altitudes.



When the data was subsetted to consider the invertebrates trapped in the period from the time of peak grouse hatch until their demand for invertebrate food diminishes, there were no significant terms in the model (table 5.1), although altitude came the closest to being significant.

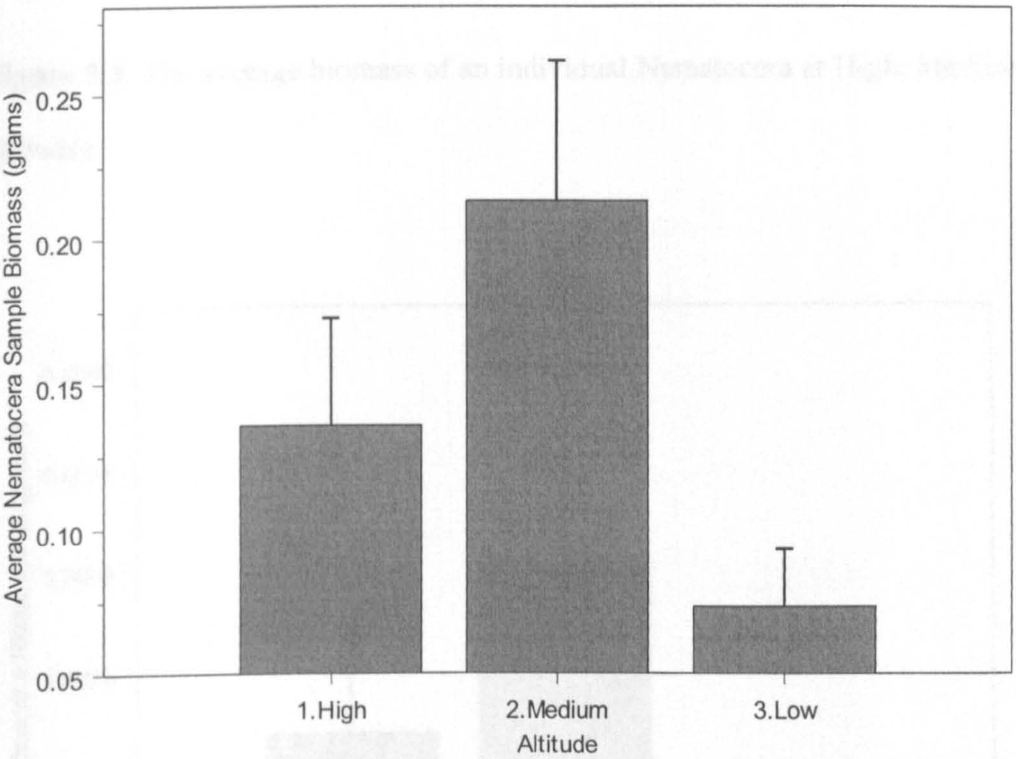
Table 5.1. The Wald statistics and probability values for the truncated nematoceran counts after stepwise deletion.

Model Term	Wald Statistic	Probability Value
Vaccinium spp. presence	0	0.999
Grass/Sedge presence	0	0.999
Grazing	0	0.963
Heather presence	0.12	0.731
Ericoid presence	0	0.999
Miscellaneous	0.2	0.656
Average sward height	1.64	0.201
GC1	0.84	0.361
GC2	0.73	0.392
GC3	1.49	0.223
Altitude	2.15	0.116

5.4.2 Factors affecting Nematocera biomass

The biomass of invertebrates trapped in the season was related to both altitude (Wald Statistic = 16.94, P <0.001, figure 5.2) and a principle component of ground cover (GC2) (Wald Statistic = 6.30, P =0.012). GC2 has a negative relationship with biomass and is a component characterised by a strong positive correlation with bare peat and a negative association with both lichens and *Sphagnum spp.*

Figure 5.2. The average biomass of Nematocera at High, Medium and Low altitudes.

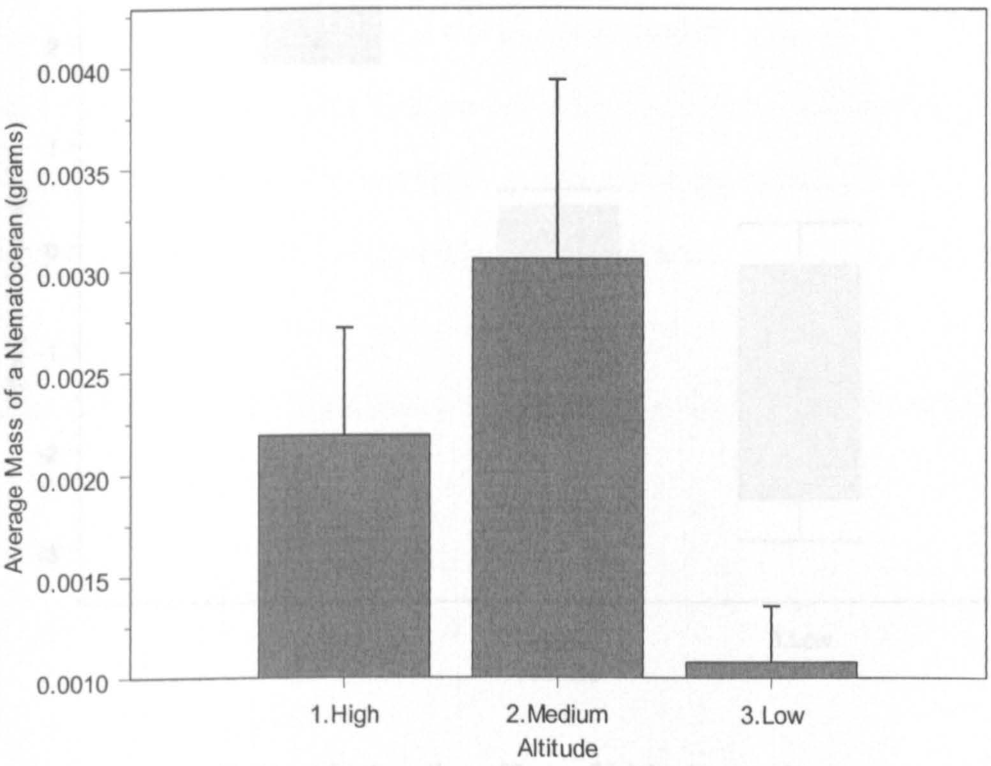


When the data was subsetted the same pattern of relationships was observed with altitude (Wald Statistic = 8.22, P = 0.016) and GC2 (Wald Statistic = 5.67, P = 0.017) being significant.

5.4.3 Factors affecting the average individual weight of a prey item

The same relationships present for factors affecting total biomass of Nematocera are repeated for the average weight of a nematoceran prey item. Altitude (Wald Statistic = 9.29, P = 0.01, figure 5.3) and GC2 (Wald Statistic = 5.10, P = 0.024) show a significant relationship when the data set is whole and when the response was subsetted (Altitude: Wald Statistic = 8.97, P = 0.011, GC2: Wald Statistic = 5.46, P = 0.019).

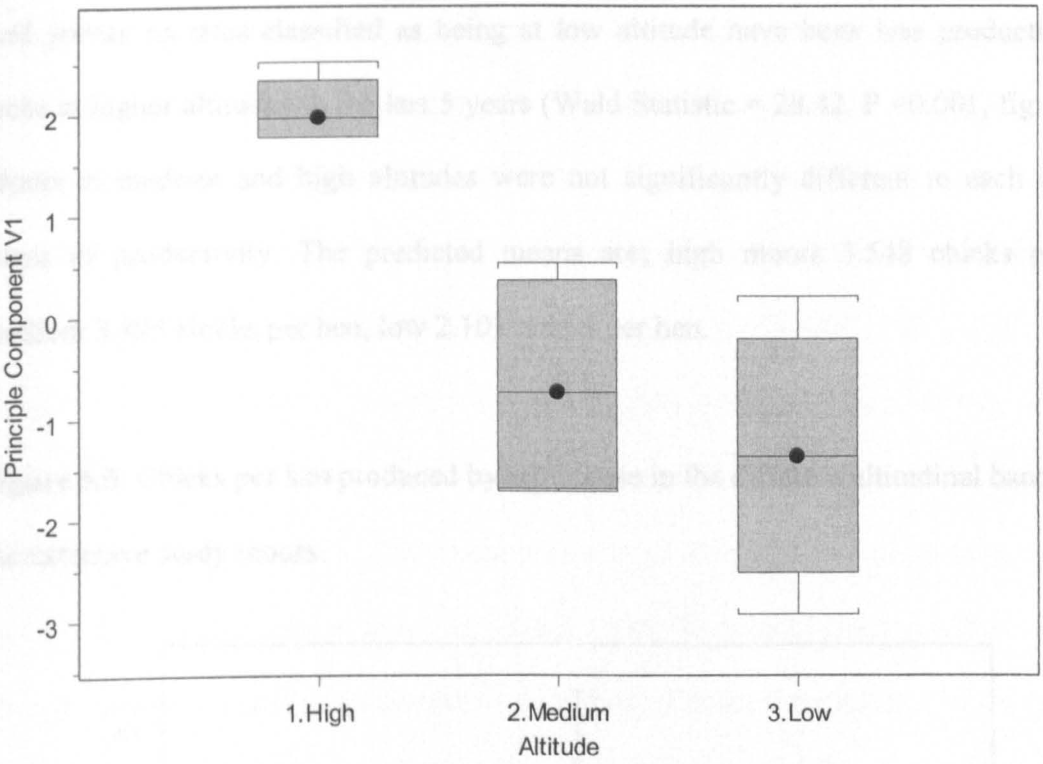
Figure 5.3. The average biomass of an individual Nematocera at High, Medium and Low altitudes.



5.4.4 Differences in vegetation with altitude

The vegetation characteristics that were included in the survey were condensed with a principle component analysis in to three variables (V1, V2, and V3). Altitude only had an affect on V1 ($F_{2,9} = 11.042$, P = 0.0038). In this analyses high and medium sites differed significantly ($t_9 = 3.54$, $P < 0.05$), as did high and low sites ($t_9 = 3.42$, $P < 0.05$). Medium and low sites did not differ significantly ($t_9 = 0.7$, $P > 0.05$, figure 5.4).

Figure 5.4. The principle component scores of V1 at different altitudes.



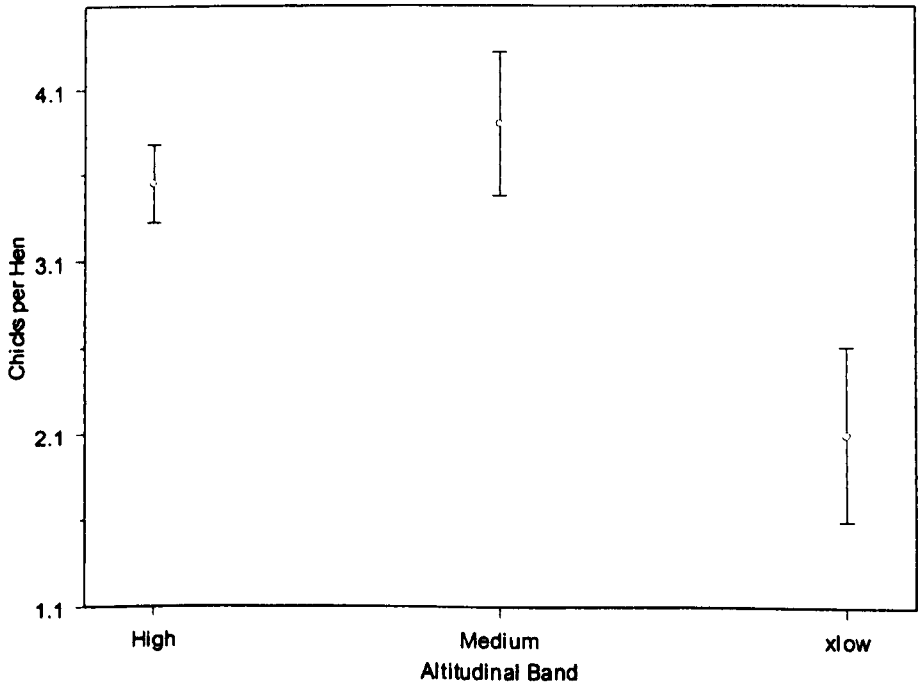
In order to investigate whether the effect of altitude on the nematoceran count and biomass data was masking an effect of vegetation, the important variables in V1 were compared with altitude. Patterns present in the data were compared with those of the Nematocera; e.g. medium height areas were much greater in abundance and biomass. Although there were significant differences in some of the vegetation characteristics between altitudinal bands none of the patterns reflected those in the invertebrate data.

GC2's relationship with altitude was also investigated, as it was a significant term in some of the models. GC2 does not differ significantly with altitude ($F_{2,9} = 0.168$, $P = 0.848$).

5.4.5 Extensive grouse production counts

Red grouse on sites classified as being at low altitude have been less productive than those at higher altitudes in the last 5 years (Wald Statistic = 28.42, $P < 0.001$, figure 5.5). Moors at medium and high altitudes were not significantly different to each other in terms of productivity. The predicted means are; high moors 3.548 chicks per hen, medium 3.895 chicks per hen, low 2.101 chicks per hen.

Figure 5.5. Chicks per hen produced by red grouse in the different altitudinal bands of the extensive study moors

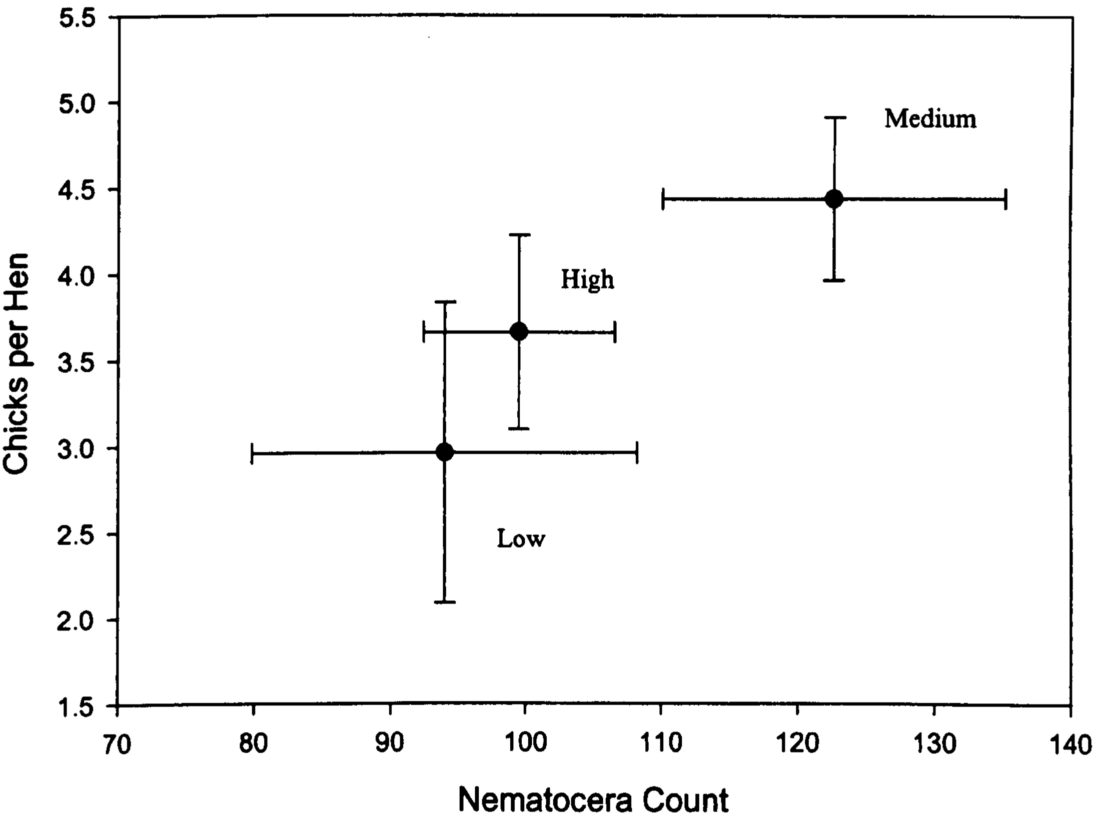


5.4.6 Factors affecting red grouse production

The major factors influencing red grouse production on the study sites were altitude ($F_{1,11}$ = 15.89, P = 0.004), two principle components of vegetation (V1: $F_{1,11}$ = 2.57, P = 0.01, V3: $F_{1,11}$ = 7.33, P = 0.035), and the principle component of ground cover GC2 ($F_{1,11}$ = 7.35, P = 0.035). Any measure of invertebrate availability drops out of the model as insignificant. This indicates that although there is correlation between grouse production and invertebrate availability it is unlikely to be causal but jointly influenced by altitude and its effects on microclimate and vegetation. Grouse production has a negative relationship with V1 which is a principle component of vegetation characterised by negative correlations with sward height, the amount of grasses and sedges and the presence of miscellaneous sparsely represented plant species. V1 is positively related to the amount of *Vaccinium spp.* present. V3 is positively related to grouse production and is characterised by a positive correlation with ericoid shrubs (i.e. *Calluna vulgaris, Erica tetralix, Erica cinera*) and negative correlations with the level of grazing and the presence of miscellaneous sparsely represented plant species. Unlike the measures of nematoceran biomass, grouse production is positively associated with GC2.

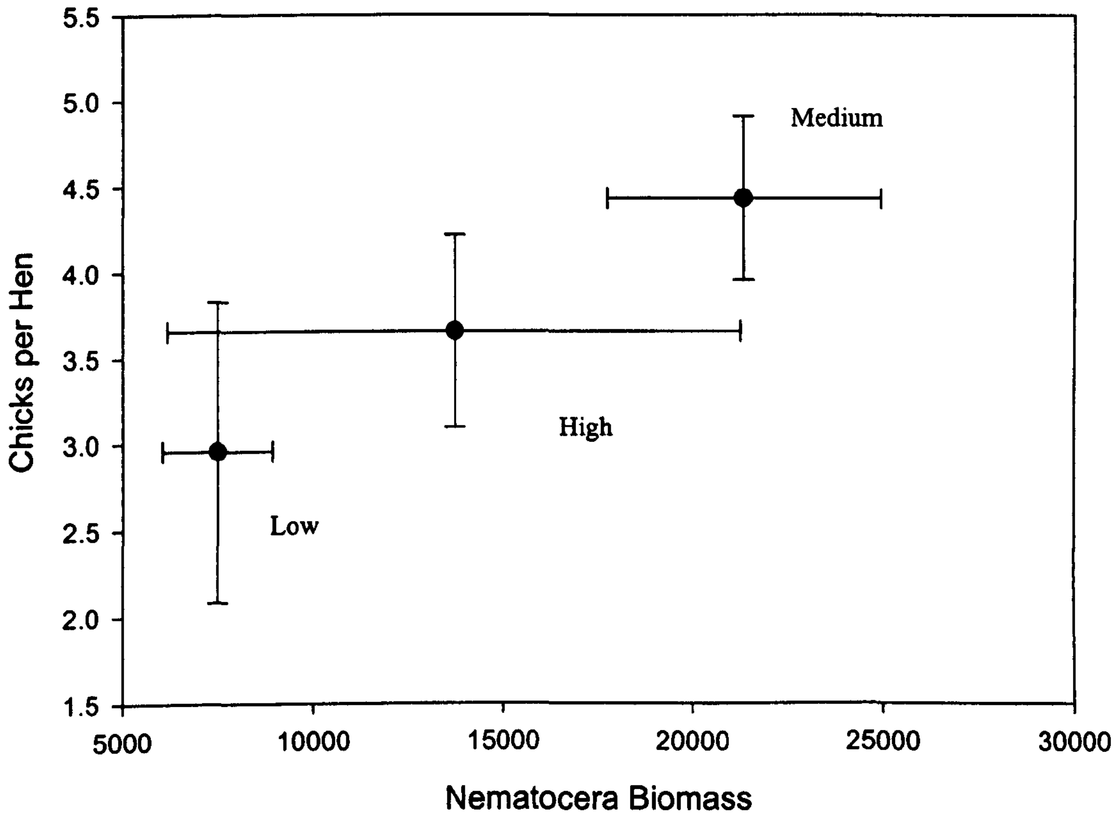
When using the subset of invertebrate data from the time in which red grouse chicks will be utilising the nematocerans as food, the minimal models change. When the model contains the subsetted Nematocera counts the significant terms in the model are; altitude ($F_{1,11}$ = 19.95 , P = 0.004), two principle components of vegetation, v1 ($F_{5,11}$ = 8.12 , P = 0.035) and V3 ($F_{1,11}$ = 10.52 , P = 0.023) and GC2 ($F_{1,11}$ = 13.84, P = 0.014). The last term to drop out of the model is the Nematocera count, however, it is significant at the 10% level ($F_{1,11}$ = 13.84, P = 0.01, figure 5.6).

Figure 5.6. The number of chicks per hen in the three altitudinal bands in relation to the counts of Nematocera.



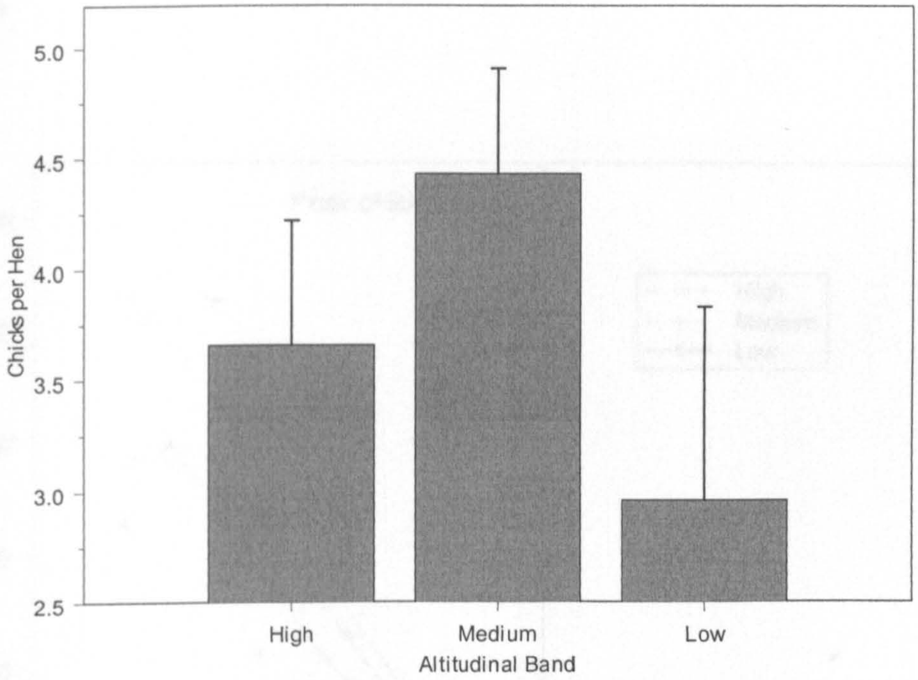
When replacing the nematoceran count with the biomass of the sample, altitude ($F_{1,11}$ = 9.44, P = 0.014), V1 ($F_{1,11}$ = 0.018, P =0.018) and V3 ($F_{1,11}$ = 7.33, P = 0.035) are still significant terms in the model. The last term to be deleted is the nematoceran biomass itself. At this point it is significant at the 10% level ($F_{1,11}$ = 3.79, P = 0.099, figure 5.7).

Figure 5.7. The number of chicks per hen in the three altitudinal bands in relation to the biomass of Nematocera.



When replacing the biomass with the average weight of an individual nematoceran the minimal model achieved does not contain a measure of invertebrate availability. The two significant terms in the model are altitude ($F_{1,11} = 5.13$, $P = 0.037$) and V1 ($F_{1,11} = 7.79$, $P = 0.024$, figure 5.8).

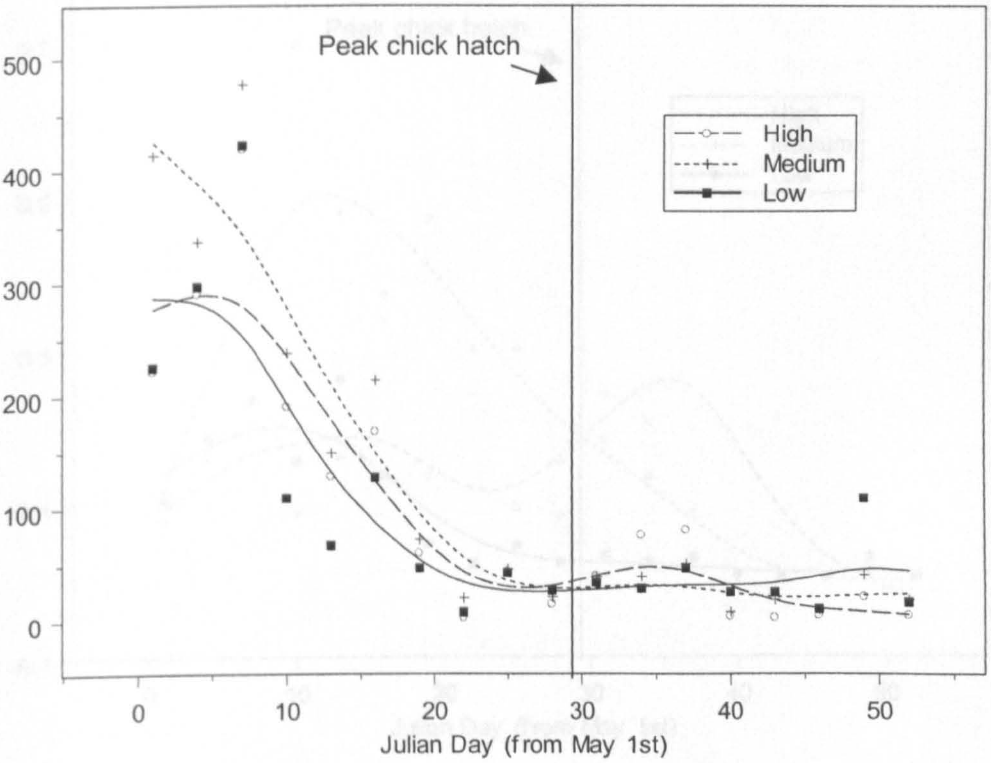
Figure 5.8. The number of chicks per hen at High, Medium and Low altitudes in the intensive study areas.



5.4.7 Temporal relationships between Nematocera abundance and altitude

The time at which Nematocera reach their peak numbers appears to occur before the trapping of invertebrates began at low and medium altitudes. It appears that at higher altitudes the peak comes later. However, without a data set with a greater range it is impossible to say whether the peak seen at high altitudes is the maximum or a fluctuation (figure 5.9).

Figure 5.9. The mean Nematocera count in each altitudinal band throughout the trapping season.



The timing of the peak biomass of Nematocera is related to altitude (Negative binomial GLM; $\chi^2_{2,9} = 6.25$, $P = 0.044$, figure 5.10), as is the peak weight of an individual nematoceran (Poisson GLM; $F_{2,9} = 9.21$, $P = 0.007$, figure 5.11). The pattern of both measures of invertebrate abundance is to reach its peak first on low sites and latest at the highest altitudes, the medium sites peak in between the high and low ones.

Figure 5.10. The mean Nematocera sample biomass (grams) in each altitudinal band throughout the trapping season.

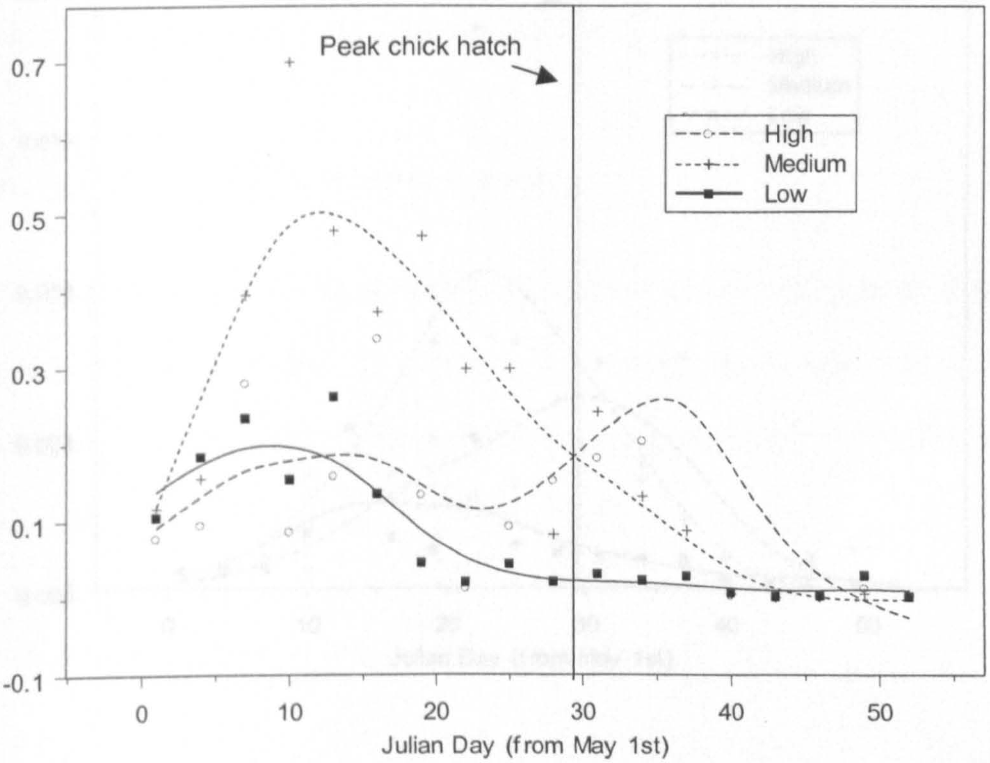
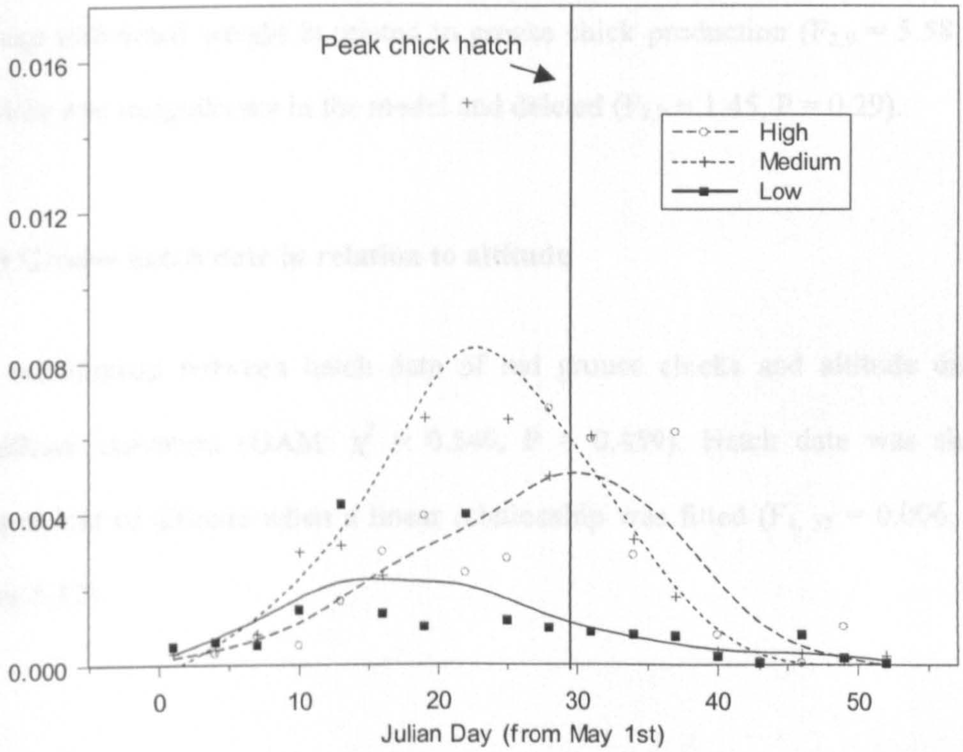


Figure 5.11. The mean individual nematoceran biomass (grams) in each altitudinal band throughout the trapping season.



The number of Nematocera trapped peaks significantly earlier than either total biomass ($t_{33} = 3.96$, $P < 0.05$) or average weight of an individual ($t_{33} = 2.41$, $P < 0.05$). The total biomass and average weight of an individual do not differ ($t_{33} = 1.55$, $P > 0.05$).

5.4.8 Temporal relationships between grouse hatch and invertebrate emergence

The degree of difference between chick hatch and nematoceran peaks in numbers and biomass is not related to chick production (counts: $F_{2,9} = 0.337$, $P = 0.574$, biomass $F_{2,9} =$

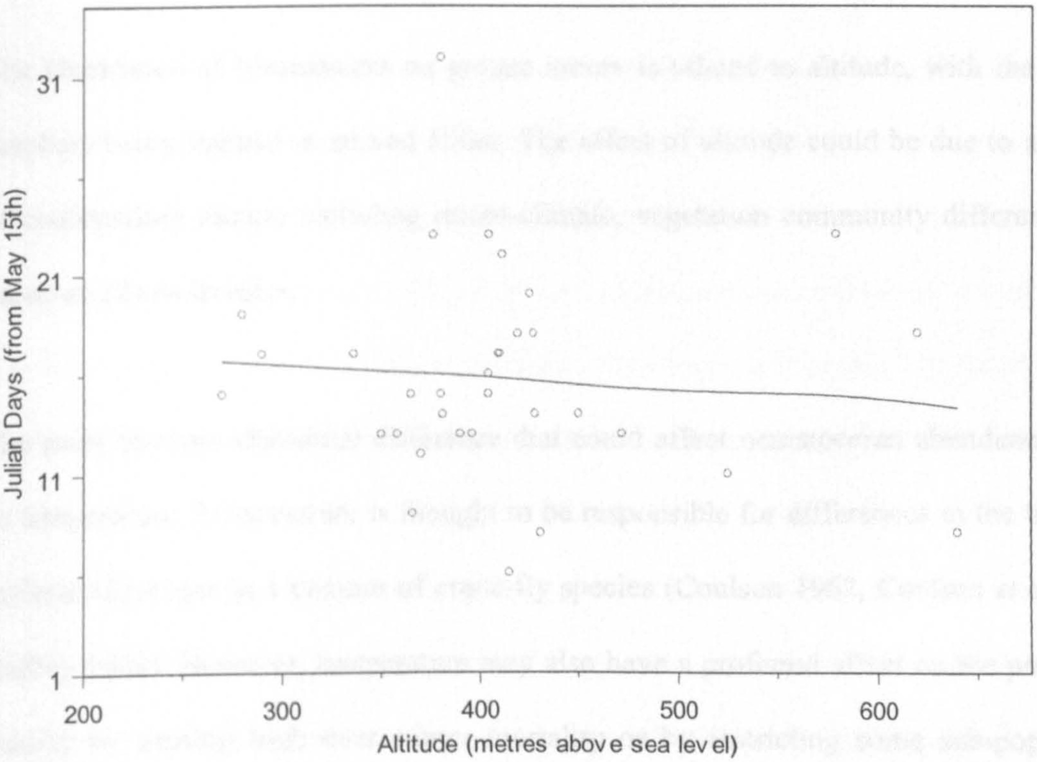
0.348, P = 0.571) or altitude (counts: $F_{2,9}$ = 1.29, P = 0.326, biomass $F_{2,9}$ = 1.251, P = 0.332).

The difference between chick hatch and the point at which nematocerans reach their peak average individual weight is related to grouse chick production ($F_{2,9}$ = 5.58, P = 0.04). Altitude was insignificant in the model and deleted ($F_{2,9}$ = 1.45, P = 0.29).

5.4.9 Grouse hatch date in relation to altitude

The relationship between hatch date of red grouse chicks and altitude did not have significant curvature (GAM: χ^2 = 0.549, P = 0.459). Hatch date was shown to be independent of altitude when a linear relationship was fitted ($F_{1,35}$ = 0.006, P = 0.937, figure 5.12).

Figure 5.12. The Julian day on which individual broods hatched in relation to the altitude of the nest. The line is the model fit of a GAM with 3 degrees of freedom.



5.5 Discussion

5.5.1 Factors affecting Nematocera abundance and biomass

The abundance of Nematocera on grouse moors is related to altitude, with the greatest numbers being trapped at around 500m. The affect of altitude could be due to a number of confounding factors including micro-climate, vegetation community differences and substrate characteristics.

The most obvious altitudinal difference that could affect nematoceran abundance would be temperature. Temperature is thought to be responsible for differences in the timing of various life stages in a number of crane-fly species (Coulson 1962, Coulson *et al.* 1976, Hadley 1969). However, temperature may also have a profound affect on the population density by causing high over-winter mortality or by restricting some sub-populations completing regular life cycles (Coulson *et al.* 1976).

The vegetative community may be affected by altitude due to temperature changes, water table and substrate differences. Callaghan & Jonasson (1995) showed that temperature could limit vegetation growth in arctic terrestrial ecosystems. Differential changes in biomass of the vegetation community could lead to differences in competitive ability and lead to species exclusion (Alonso & Hartley 1998). Any differences in the vegetative community can lead to differences in the invertebrate community in dwarf shrub communities (Richardson *et al.* 2002). Possibly of greatest importance to the Nematocera are the species making up the ground cover. *Tipula subnodicornis* larvae are known to feed on various liverworts (Coulson 1962), and these may be susceptible to changes in the canopy above (Chapin *et al.* 1995, Richardson *et al.* 2002).

The only principle component of vegetation that was significantly related to altitude was V1. Due to this the important terms that made up the component were individually compared to altitude. Despite a number of differences between altitudinal bands being present, none of these mirrored the pattern in the Nematocera counts and were therefore, discounted as being of importance. However, the broad-scale vegetation survey carried out does not necessarily reflect the constraints on the invertebrate community.

Substrate changes can occur with differing temperatures. Rustad *et al.* (2001) used a meta-analysis to show that temperature rise not only directly increases the growth and development of organisms but also soil nutrient mineralisation. The impact of increased nutrients on invertebrate communities in dwarf shrub communities can be marked leading to greater production and/or diversity (Chapter 2, Power *et al.*1998, Richardson *et al.* 2002). However, the increased nutrient addition could also negatively affect some prey species as their larval stages feed on lichens, some of which can be sensitive to nitrogen levels (Benfield 1994, Van Herk 1999).

Unlike the nematoceran counts the biomass of the sample was related to the type of ground cover present as well as altitude. This was true when the season was considered as a whole and for when a subset of the data representing the times in which they would be possible prey for red grouse chicks were used. The significant ground cover component was not itself related to altitude and so it can be assumed that the link between it and biomass are independent.

The relationship between ground cover and biomass is interesting as it associates greater biomass with increased levels of *Sphagnum spp.* and lichens. *Sphagnum spp.* are associated with areas that are utilised by grouse chicks for invertebrate feeding (Hudson 1986) and bryophytes are present in the diet of *Tipula subnodicornis* larvae (Coulson 1962). The negative association between biomass and bare peat may suggest those areas without a vegetative covering may not be able to provide any food for the developing larvae of the species present.

The factors affecting nematoceran biomass were also important in the model using the average weight of an individual Nematocera.

In general altitude could be both a proximate and ultimate cause of invertebrate prey distribution. However, in this study the extremes of altitude are neither as high nor low as used by Coulson *et al.* (1976) who managed to collect both the major crane-fly species at all their sites. More fine scale work is needed to determine how the distribution of invertebrate food species is governed.

5.5.2 Spatial factors affecting red grouse production

Using grouse count data from the past five years from estates throughout the Spey valley it was shown that moors at medium and higher altitudes had a greater grouse production than low lying moors. Medium altitudinal areas were the most productive but were not significantly different to high sites. This pattern mirrors the anecdotal reports received from game managers in the Spey valley (Smith pers. com). The pattern of grouse production with altitude on the extensive sites was mirrored in the experimental areas. At these sites it was also noted that the measures of invertebrate availability follow the same pattern as grouse production i.e. medium and high sites produce more invertebrates than low lying areas.

The factors affecting grouse production were many. When looking at factors affecting grouse production, including the entire invertebrate data set, altitude and a number of vegetation variables were shown to have a significant effect, with measures of nematoceran abundance being deleted from the minimal model. Altitude is likely to be having an indirect affect on another factor such as a change in vegetation, substrate richness or invertebrate availability. The vegetation variables significant in the models do not appear to be classically related to grouse production. The most important vegetation variable to red grouse production has always been shown to be type and abundance of heather (Miller *et al.* 1966, Moss 1972, Savoury 1978) and this variable did not have an effect in the models. The type of survey carried out may be masking any relationship present.

When the invertebrate data is subsetted to represent the period when grouse chicks are utilising the food source the models change. Both the Nematocera count and the biomass weakly related to the number of chicks per hen (at the 10% level) in their respective models. The positive correlation between these measures and nematoceran availability do not necessarily suggest a causal relationship, although taken in context with other researchers results (Hudson 1986, Park *et al.* 2001) provide a good hypothesis. The hypothesis is; grouse production is greatest in areas that produce more invertebrate food.

5.5.3 Temporal relationships between nematoceran prey and red grouse production

The hypothesis suggested above is likely to be an oversimplification of the system if it proves to be correct. The amount of invertebrate food available is strongly affected by a number of other variables; the greatest of these is time.

The estimated average hatch date of red grouse was not discernibly affected by altitude, despite the assumed change in average temperature. Watson & O'Hare (1979) found a correlation between April temperature and hatch date for red grouse in Ireland with warmer weather causing eggs to hatch earlier. The maximum difference of mean April temperatures was just 0.8°C in the four years of the study and the associated change in hatch date with the greatest difference was 13.4 days. The lack of difference in hatch date in this study is puzzling if the 1°C change for every 207m of altitude at the Moorhouse National Nature Reserve in May is roughly similar to the Scottish Highlands. The reasons why no differences were detected are unknown; however the data suggest a greater level of plasticity in grouse egg production in relation to climatic variables in the population studied in this investigation. Alternatively the number of nests found was not great enough to show a pattern amongst the large amount of natural variation that is most likely in the population. Although no change was seen between altitudes the population is known to hatch at different times in different years depending on April temperatures (Kirby *et al.* in prep).

In the great tit system, higher than average temperatures causes earlier hatch of both bird and lepidopteran eggs. However, the hatch of the caterpillars has fewer constraints allowing for the hatch date to be earlier than the great tits. The subsequent development of caterpillars also increases with temperature, halving the time between hatch and pupation and therefore, halving their availability to the tits (Naef-Daenzer & Keller 1999, Van Noordwijk *et al.* 1995). The degree of synchrony between the chicks' peak demand for invertebrate food and caterpillar peak availability is related to the number of successful fledglings. An asynchrony of just 2 or 3 days is enough to show a marked effect on nestling weight in some years (Van Noordwijk *et al.* 1995).

If red grouse chicks were under similar constraints, as the data suggests, then fluctuations from average temperatures may be a problem. When looking for relationships between grouse production and the level of synchrony with peak nematoceran abundance no relationship appears to exist. The fact that the peak emergence time is a number of weeks before the peak grouse hatch also suggests that despite climate there was never any synchrony between these measures. This is because the level of plasticity in the development of nematoceran larvae would have to be inordinately large to achieve such discrepancy. When looking at between year differences of *M. ater* and *T. subnodicornis* emergence dates in the field Coulson *et al.* (1976) recorded maximum differences of 14 and 12 days respectively. These are too short to account for the greater than 3-week discrepancy in the emergence of Nematocera to the grouse peak hatch date.

The peak biomass of Nematocera trapped on the study areas peaked later than the peak in numbers. However, there was no relationship between the degree of difference in hatch times and emergence to grouse production. The data shows that the low and medium sites peak before average grouse hatch occurs and that high sites have a more constant level of biomass throughout the season.

The average size of a prey item peaks closest to when peak grouse hatch occurs. The degree of difference observed correlates with the number of chicks produced per hen, with the greater the degree of synchronisation the greater the number of chicks surviving to the juvenile stage. This relationship is interesting as it suggests that savings to chicks are made through foraging efficiency, rather than abundance of food. As chicks are mainly consuming heather it is assumed that most of the time spent feeding is required to take in the bulk of heather necessary. If the invertebrate food required could be taken in quickly with little effort then the time left to feed on vegetation is maximised. This may be of particular importance to grouse chicks, as the environment in which they live is incredibly variable. As the chicks cannot thermoregulate they require frequent brooding by the hen and this need increases if the weather is relatively cold and/or wet (Erikstad &

Spidso 1982). It is therefore, proposed that this may explain the apparent synchronisation of grouse hatch to the peak biomass of individual prey items as it would be the best trade off between brooding time and energy/protein intake.

This relationship has been shown in another tetrionid, the capercaillie *Tetrao urogallus* whose chick survival is related to the size, rather than abundance of their caterpillar prey (Picozzi *et al.* 1999). Both size and abundance are seen to be important in the great tit system as well, with synchronisation being of greatest importance (Dias & Blondel 1996, Naef-Daenzer & Keller 1999, Perrins 1991, Van Noordwijk *et al.* 1995).

The data suggest that there is some evidence for the hypothesis that altitude affects grouse production by causing differences in the availability of invertebrate food when demand by chicks is at its peak. This could lead to poor chick growth and in turn chick survival (Chapter 4, Park *et al.* 2001). This hypothesis needs further investigation due to its importance to grouse ecology.

5.5.4 Possible consequences of climate change

The possible consequences of climate change to red grouse could be marked if the correlational relationships shown prove to hold true. Climate change is likely to be most marked in upland areas (SNH Hills & Moors Report 2002) and is likely to be characterised by increased temperature, and in the area of the study increased rainfall (Scottish Executive Statistics online 2002). The increase in temperature could make the degree of asynchrony greater leading to poor grouse production. If this occurs then the outcome would be a continual range contraction to higher altitudes. The eventual result would be a loss of shooting interest and associated loss of moorland management, which would impact on many species. Increasing rainfall could further compound the problems by causing the chicks to require more brooding and therefore, reduce foraging time.

5.5.5 Conclusions

Grouse production appears to be spatially and temporally correlated with some measures of invertebrate food availability. Although the measures differ in importance when considering them either spatially or temporally there are weak patterns, despite no direct evidence of causality. The factors governing the spatial and temporal distribution of prey species is in most cases poorly understood so further work is needed if management plans to maximise grouse production via invertebrate diet are to be introduced.

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Chapter 6

General Discussion

6.1 The importance of invertebrate prey to breeding birds

Many birds rely on a source of invertebrate food to provide chicks with a high protein diet sufficient to maintain fast growth rates (Savoury 1989). Wilson *et al.* (1999) showed that the "granivorous" farmland birds in decline were also the species that relied most on an abundant supply of invertebrates on which to feed their chicks. The correlational relationship shown in farmland passerines has been shown experimentally for the gamebird the grey partridge *Perdix perdix*, where invertebrate food availability has been liked with chick survival (Potts 1986, Richards *et al.* 2002, Southwood & Cross 1969). Benton *et al.* (2002) showed that fluctuations in insect numbers over three decades are associated with changes in census data of birds in the same area. In addition small changes in invertebrate food supply, either temporally or spatially, have been shown to have a large effect on the fledging success of great tit *Parus major* broods (Dias & Blondel 1996, Naef-Daenzer & Keller 1999, Perrins 1991, Van Noordwijk et al. 1995). These researchers have provided some evidence of a generalised link between the life history and population size of a range of birds and the invertebrate food available.

Like many species of farmland birds the numbers of red grouse *Lagopus lagopus scoticus* in the Spey valley have been falling since the 1970's (Hudson 1988), this study was initiated in order to investigate whether the decline in grouse numbers could, to some extent, be attributable to invertebrate prey availability and whether this relationship was able to be manipulated.

6.2 Does invertebrate diet affect grouse production?

The data presented in these studies provides some correlational evidence that invertebrate availability may be influencing the number of chicks produced by each hen. Due to the indirect methods of the assessment of invertebrate availability, i.e. trapping, and chick dietary assessment, i.e. faecal examinations, a causal relationship is impossible to determine. However, the evidence presented here, allied with the work of others (e.g. Park *et al.* 2001) gives a sound basis on which to establish future research.

6.3 Manipulating moorland to produce invertebrates: summary of treatment results

As with previous studies a number of substrate and vegetation variables were shown to be factors in determining invertebrate abundance (Chapter 2, Coulson & Whittaker 1978, Richardson *et al.* 2002, Sanderson *et al.* 1995). Due to the nature of these variables the distribution of invertebrates in the environment is patchy, leading to small productive areas that are actively sort out by grouse broods (Hudson 1986, Savoury 1977). If manipulation of moorland to improve invertebrate availability to chicks is carried out, then the patchy distribution already seen, allows less broad-scale measures, as those carried out in this investigation (Chapter 3), to be undertaken. It follows that those things known to affect invertebrate abundance should be targeted for manipulation, however, it is only possible to affect changes easily in some of these.

6.3.1 Fertilisation experiments

The addition of fertiliser led to an increase in the amount of invertebrates trapped, including the important Nematocera. This finding is supported by similar results due to fertilisation in other dwarf shrub communities (Richardson *et al.* 2002, Power *et al.* 1998). The mechanisms responsible for the rise seen in this experiment are unknown but could be due to a number of complementary factors.

The majority of invertebrates that grouse chicks prey upon are either phytophagous or detritovores. Many invertebrates are tied to a single or small range of host plants (Lawton 1983). Altering the nutrient status alters the biomass and, therefore, the competitive abilities of certain plants, which, in turn may lead to greater abundance of them. The greater the abundance of the food plant, the larger the population of those invertebrates that utilise it can become. Richardson *et al.* (2002) documented this type of relationship, in various invertebrate groups, in response to increased grass production in a fertilised dwarf shrub community.

The addition of fertiliser in the short term is likely to have most effect on the nutrient status of the vegetative community rather than its structure. The higher the plane of nutrition in the food plant, the greater the growth and survival rates, especially in the larval stages, of the invertebrates feeding upon them. The heather beetle has been shown to respond in this way to nutrient addition (Power *et al.* 1998).

On grouse moors, in the short term, the indirect evidence gained from the comparison of the small plot trial (Chapter 2) with the large-scale fertilisation experiment (Chapter 3) suggests that, in the short term, at least, nutrient enrichment leads to greater abundance of herbivores due to better food quality, rather than fertilisation leading to greater plant biomass and therefore more habitat for specialised insects. In the small plot experiment fertiliser was added in August and then again in April with the invertebrates being monitored thereafter. A strong positive relationship between fertilisation and invertebrate numbers was seen in both years of study. No rise was seen in adult invertebrate numbers on treated areas in the large-scale experiment. This is hypothesised to be due to the fertiliser being added in April and therefore, too late to affect the over-winter survival of larvae due to emerge that season.

Despite failing to produce an increase in invertebrate abundance the production of grouse chicks rose dramatically in the large areas that had been treated with fertiliser. The reason for this is most likely to do with better heather quality resulting in a greater protein intake from vegetative sources. We hypothesise that the presence of high quality heather following fertilisation reduced the need for invertebrate food – hence the observed negative relationship between survival and invertebrate intake. However, if insect quality/quantity respond to fertilisation in the following years the intake of invertebrate food may become relatively more profitable again. This may lead to a greater difference in the productivity of grouse on treated and control areas.

Surprisingly fertiliser application did not lead to an increase in vegetation complexity as measured by sward height but did increase the amount of grass present. An increase in the grass component of the system is shown to increase the amount of invertebrates trapped. This result is mirrored by increases in invertebrates due to greater grass production in a 9-year experiment by Richardson *et al.* (2002).

6.3.2 The addition of lime

This investigation demonstrates that invertebrate production is greater in areas with higher pH levels. However, the addition of lime to experimental plots did not increase the number of invertebrates trapped despite increasing the alkalinity of the substrate. The result may be due to the coarse scale of invertebrate classification. The change in pH may have caused a loss of some acid loving species and caused a replacement with acid intolerant ones. This change if not noticeable in numbers would not have been seen with the identification undertaken. The benefits of liming may be seen in subsequent seasons as the greater base status may give a fertilisation effect by releasing nutrients locked up in the acid substrate (Bragg 2002), some invertebrates may also "choose" to lay eggs in these areas as the higher pH levels may provide more suitable hatching conditions (Coulson & Whittaker 1978).

6.3.3 Grazer exclusion

Grazers may affect invertebrate communities directly by competing for the same food plants, by reducing habitat complexity or from loss of individuals or eggs due to unintentional removal by vertebrate herbivores (Baines *et al.* 1994). In this experiment grazer exclusion led to a change in habitat with more grass being present, probably due to many herbivores selecting grasses in preference to woody shrubs (Alonso & Hartley 1998). Despite a change in habitat structure the hypothesised change in the number of invertebrates trapped was not seen. This may have been due to the sampling methods employed or time scale of the experiment.

6.4 Experimental treatments to management – real world applications

6.4.1 Fertiliser application as a management tool?

Changing the management routine of grouse moors requires a level of certainty in the new techniques being employed. It is apparent that fertilisation increases both the number of invertebrates trapped and, most importantly, the production of red grouse. The mechanisms remain unclear however, as both results did not coincide in the same experiment. Further investigation is necessary in order to understand the interactions and foresee any deleterious effects wide-scale use of fertiliser as a management tool may have. Apart from these two areas of focus, grouse and invertebrates, fertiliser application could have major implications for habitat and pollution.

In these experiments fertiliser was shown to have a positive effect on the amount of grass present. This result mirrors those of other groups researching dwarf shrub communities (Alonso & Hartley 1998, Richardson *et al.* 2002). The long-term consequences of repeated fertilisation could be a large reduction in heather cover. This change may have a negative effect on grouse populations as their density and abundance has been related positively to heather cover (Miller & Watson 1978, Moss 1967 from Savoury 1978). However, grass invasion due to fertilisation is largely governed by heather canopy integrity (Alonso & Hartley 1998) and therefore, targeted application could prevent this problem.

After large-scale fertilisation the amount of lichens present was reduced greatly. This reduction is most likely due to many lichen species being sensitive to increases in nitrogen (Benfield 1994, Van Herk 1999). Depending upon the species lost after nutrient addition the technique may prove unappealing to conservation bodies, therefore, further work is necessary in this area.

The widespread use of fertiliser on moorland may also create a nitrate problem for surrounding areas, especially watercourses. However, peat is known for its ability to remove large amounts of nutrients from water and lock them in the substrate by means of its acidity. This action also leads to water moving through peat becoming stripped of its nutrients. The effect can be strong enough to effectively clean up run-off from fertilised upland pastures before it enters local watercourses (Lundin 1998 from Bragg 2002). If fertilisation became a management technique, careful monitoring of ground water would be necessary to reduce the chances of pollution incidences.

The change from an experimental to a managerial role for fertiliser application may become reality in the future. However, a greater understanding of the mechanisms and the consequences of its use need to be gained first. Understanding the most important aspects of its benefits should lead to a more targeted, less environmentally sensitive and more cost effective application regime. Vegetative chick diet, invertebrate chick diet or maternal condition could all theoretically be the most important focus of fertiliser application, each leading to a different management solution. Despite its obvious effect on grouse production caution should be taken before further results are obtained.

6.4.2 Does base status change have a role in grouse moor management?

The addition of lime to freshwater systems has increased the presence of acid-intolerant invertebrates (Bradley & Ormerod 2002, Buckton & Ormerod 1997, Fjellheim & Raddum 2001, Miskimmin *et al.* 1995, Walseng *et al.* 2001) and fish (Walseng *et al.* 2001). However, the addition of lime in this experiment did not bring about any measured changes. This may be due to application rate, methodology or the unsuitability of the treatment itself. Red grouse are known to be more productive on areas overlying base rich rocks (Jenkins *et al.* 1967, Picozzi 1968). The erosion of underlying rock is likely to lead to a slow release of compounds keeping the substrate at an even pH state, tending to neutral, and in turn benefit the nutrient cycling ability of the habitat and nutrient accessibility to the plants present. As acid deposition is likely to have had a large affect on the already acid system of the uplands (SNH 2002), a more enlightened approach might be to change the pH state at a much slower rate in order to prevent dramatic shifts in conditions whilst increasing buffering capacity. Use of pH manipulation as a management tool is unlikely to occur in the short term, as a slow release experiment is likely to take a number of years to show results.

6.4.3 Managing grazing regimes for the benefit of chick diet

Grouse moors have long been managed with the aid of grazing. Selective browsing by deer, cattle and sheep, along with muirburn, prevent the successional community of heather moorland becoming scrub. Grazing of livestock and holding of large densities of wild deer for stalking also provide important streams of revenue. Due to this, removal of grazers in order to increase invertebrate availability and in turn grouse production would have to reap substantial benefits for it to become a major management tool. Grouse moors are sensitive to overgrazing (Hudson 1986) and so a sensitive management plan might allow benefits in both areas to be achieved. Rotation of livestock into different areas allowing various sites to recover from overgrazing and increase invertebrate populations might prove beneficial for grouse production. The major problem with a routine such as this is due to the openness of the system. Large-scale exclusion of grazers, even for a short period, would require large investments in fencing. There is also the secondary problem of increased tick parasitism in areas where the major hosts have been excluded. Perkins (2003) showed that the exclusion of deer from areas with a healthy tick population led to increased parasitism on small mammals. If this increased parasitism was seen on grouse chicks the consequences could be drastic falls in survival rates. Focused use of acaricidally-treated sheep flocks in a long-term plan could remedy such problems.

It is unlikely that grazer exclusion is an achievable goal on most grouse moors. However, if invertebrate numbers increase in a negative relationship with grazer density, as in the black grouse system (Baines 1994, Baines *et al.* 1996), then increased effort in the culling of deer and more stringent regulation of livestock numbers may give tangible benefits.

6.5 Climate change and the temporal relationship between grouse chicks and their invertebrate prey

Climate change is likely to increase both temperature and rainfall in the study area (Scottish Executive statistics online 2002). The increase in rainfall is unlikely to cause great changes in the short term as it is predicted to fall over winter and not whilst grouse chicks may be sensitive to weather (Erikstad & Andersen 1983, Erikstad & Spidso 1982). Most of the common invertebrates consumed by grouse chicks have larval stages that are adapted to damp conditions so further water logging of the substrate is unlikely to cause a problem (Coulson & Whittaker 1978).

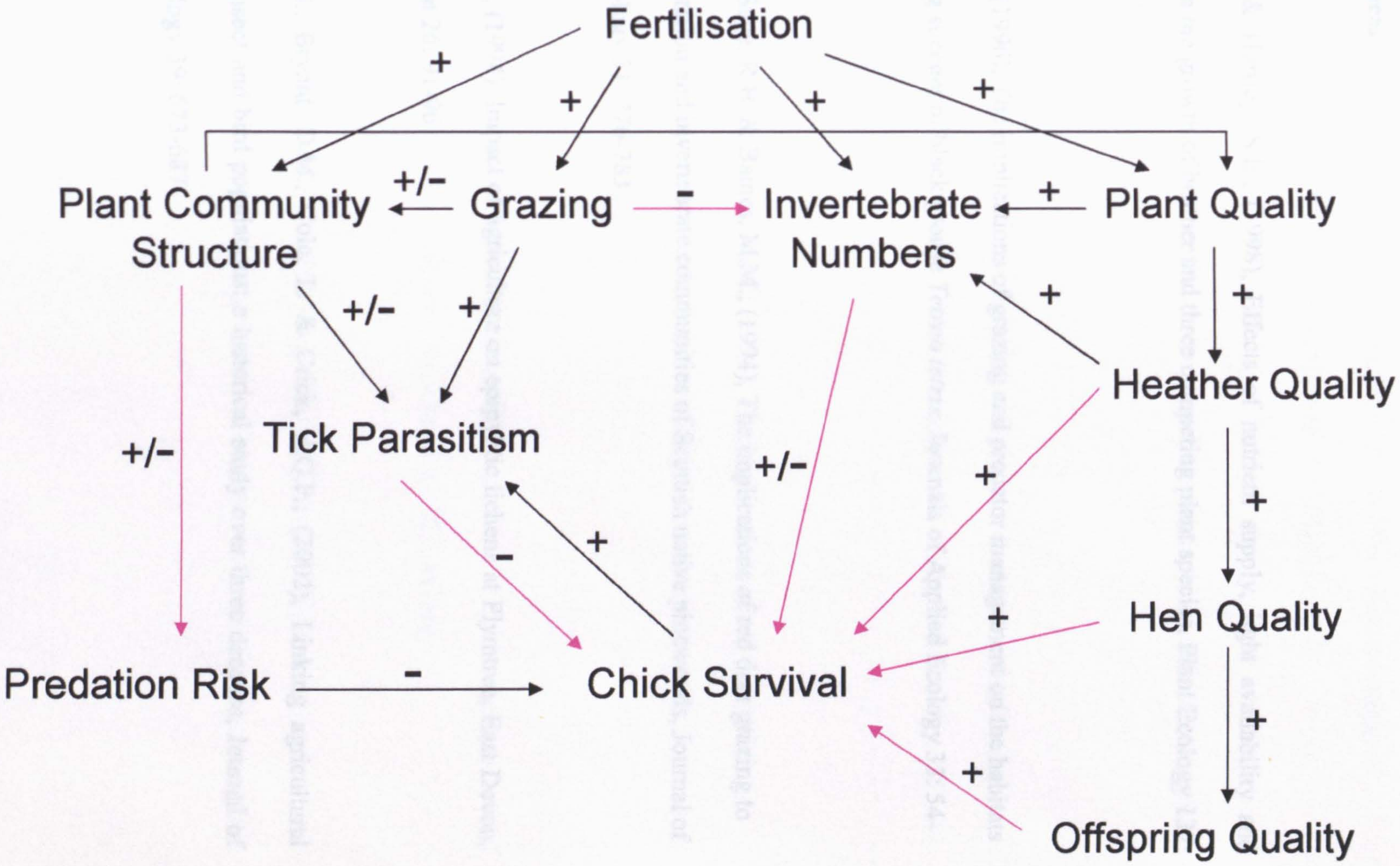
Size and timing of availability of invertebrate prey has been shown to be important in the closely related capercaillie (Moss *et al.* 2001, Picozzi *et al.* 1998) as well as the great/blue tit system (Dias & Blondel 1996, Naef-Daenzer & Keller 1999, Perrins 1991, Van Noordwijk et al. 1995). This study has shown a correlational relationship between chick production and the degree of synchronisation between chick hatch and the peak in prey item size. The change in temperature could have a major affect on the red grouse/invertebrate prey system, as it is likely to lead to greater discrepancies between peak chick hatch and invertebrate availability.

With increasing temperatures the degree of asynchrony will increase as the more flexible invertebrates respond more quickly to changes in the environment than red grouse. This may have dire consequences for grouse management. The result of climate change could be dramatic range contraction with the edge of range moving to higher altitudes and greater latitudes. The conservation status of the red grouse is unlikely to become critical in the short term, unless the degree and rate of change are greater than those predicted. However, the consequences for shooting interests and the associated conservation of large areas of low-lying Scottish moorland may become marked if grouse production falls. As fertilisation was shown to change the level of invertebrates taken, with the fewer being consumed on fertilised plots correlated with better survival, nutrient addition in order to counteract the negative effects of climate change might be a possibility.

6.6 Summary

The distribution of invertebrate abundance on heather moorland is governed by a number of biotic and abiotic factors. Some of these factors can be manipulated in order to produce greater numbers of invertebrates. In general the more invertebrates consumed by a grouse chick the greater its rate of weight gain and, in turn its survival. Chicks respond well to experimental applications of fertiliser, irrespective of the effect on invertebrate numbers and independently of maternal effects. This response is shown in greater growth rates, survival probabilities and their ability to resist ecto-parasites. Further investigation is necessary in order to ascertain the exact mechanisms behind the positive relationship between treatment with fertiliser and chick survival in order to create an effective and responsible management strategy (figure 6.1). However, if the link between grouse production and invertebrates proves to have a large effect on production then the predicted climate change could make intensive grouse management obsolete.

Figure 6.1. A flow chart of the shown/predicted relationships in the grouse/fertiliser/invertebrate system. The arrows in shown in red are the relationships that are most in need of further investigation.



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