# The interaction between demography and harvesting in red grouse

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# Abstract

Many animal populations are threatened by human activity, including habitat loss and harvesting but recent advances in population ecology show that the age- and sex-structure are important when aiming to understand population dynamics. However, research on population dynamics often focuses on species that experience relatively little human disturbance and human caused mortality is often assumed not to affect population dynamics. An increasing number of studies shows short-term and long-term evolutionary and ecological consequences of harvesting. This has not only implications for the understanding of population dynamics but also for the management and conservation of species in human-dominated landscapes.

This thesis aims to investigate the interaction between the demographic structure and harvesting in a fluctuating species, the red grouse (*Lagopus lagopus scoticus*) using a combination of empirical and theoretical approaches. The relative roles of age-related parasite burden, fecundity and shooting in driving population dynamics are assessed, and empirical data are used to parameterise a model examining the effect of harvesting on the population dynamics.

The empirical part of the thesis starts with the investigation of the intensity and distribution of the parasitic nematode *Trichostrongylus tenuis* for three age-classes of red grouse before the breeding season. The intensity of the parasite increased with host age. Parasites in two-year-old grouse were more aggregated than in one-year-old and 3+-year-old grouse. This has implications for population dynamics because the aggregation of parasites within the host influences mortality rates. Females of the oldest age class (3+-years-old) were less fecund than younger grouse and interactions with nesting habitat and year were found to affect female fecundity. The age- and sex-structure of shot birds was compared with the age- and sex-structure of the population before shooting. More old birds were shot at small bag sizes but this bias decreased as more birds were shot. Old males were highly susceptible to shooting at the beginning of the season but susceptibility decreased with number of

shooting events. A relationship between bag numbers and population density was found.

An age- and sex-structured population model was used to examine the effect of harvesting on red grouse population dynamics. Selective harvest for or against a certain age class led to a skew in the sex ratio of the population and to a decrease in fecundity and therefore to a drop in population size and harvest yield. Parasites and the exclusion of young birds through aggressiveness affected the population dynamics and led to a skew in the harvest rate at which the maximum sustainable yield was attained. Shooting early in the season resulted in a higher yield because individuals were removed from the population before they contributed to the availability of free ranging stages of the parasite. The population model demonstrated that parasites, aggressiveness and harvesting interact and that harvesting is a significant factor in population dynamics. Overall, the current practice of shooting rarely more than 50% of the population seems to be a good precautionary principle. Uncertainty in the harvesting rate increased the probability of local extirpation of the population. Therefore, reliable estimates of the population, including the age and sex structure, are invaluable parts of red grouse management. This study showed that harvesting and the age and sex structure of the population are important drivers of red grouse population dynamics and an understanding of their interactions is important for sustainable management of red grouse.

# Acknowledgements

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# Chapter 1

# General Introduction

## 1.1 Population dynamics and harvesting

Understanding the changes in abundance of populations is one of the main challenges in ecology. Population fluctuations of animals have been shown to be due to temporal variation in survival and fecundity. Density dependent and independent mechanisms influence the extent of the variation and can work at the same time in the same population (Leirs *et al.* 1997, Coulson *et al.* 2001).

Insights into population fluctuations are often derived from populations that face relatively little human disturbance (e.g. Soay sheep, Clutton-Brock and Pemberton 2004; voles, Lambin *et al.* 2006). However, many animal populations are under anthropogenic threat; human harvest has led to range contraction and extinction of many species (IUCN Red List 2007). In addition to these dramatic impacts, harvesting has been shown to affect populations in ways that are more difficult to detect; for example short-term changes in behaviour (Jedrzejewski *et al.* 2006) population growth rates (Milner *et al.* 2007) and long-term evolutionary consequences (Coltman *et al.* 2003, Proaktor *et al.* 2007). Thus anthropogenic harvesting is a major biological force in population dynamics and further research is needed to understand how it influences population dynamics.

In many cases animals are hunted for a specific phenotypic trait to maximise benefits for the hunter, e.g. trophy hunting for horns or selection for large body size. The effects of selective harvesting of a certain age or sex class on the demographic structure of the population and consequently on population dynamics have been demonstrated (Ginsberg & Milner-Gulland 1994, Kokko *et al.* 2001, Festa-Bianchet 2003). For example, selective harvesting might lead to sex ratio bias and reduction of mean age and thereby depress recruitment (Milner *et al.* 2007). Hunting systems

such as the ones above purposely target a specific age or sex class, but this is not always the case in hunting or shooting. Physiological or behavioural differences between age and sex classes of the same species may result in non-obvious selection. Therefore, selective harvesting of a specific trait or demographic group is important to understand when studying population dynamics. For example many grouse species are monomorphic and studies conflicting results. Some studies have found age-selective harvesting (Hörnell-Willebrand *et al.* 2006) whereas others found no difference between the age structure of the population before harvesting and in the shot birds (DeStefano & Rusch 1986). Susceptibility to human harvest could also depend on the fitness of the individual bird. Holmstad *et al.* (2006) found that highly parasitized grouse were less likely to show a flee response to human disturbance (e.g. hunter) and might therefore be more likely to be harvested when detected.

Harvesting theory and understanding the sustainable exploitation of fluctuating populations has a long history in applied ecology. Three classical harvesting strategies have been developed; constant harvest, proportional harvest and threshold harvest. The constant harvest strategy removes a constant number of individuals from the population, without knowing the population size. The advantage is that as long as the quota is kept small, no population estimate is needed. However, low growth rates and large stochastic fluctuations may increase the chance of overharvesting. Proportional harvesting removes a constant fraction of the population, either by knowing the population size or by using constant harvesting effort from an unknown population size. Finally, threshold harvesting exploits the population at the highest possible rate when the population size is above a certain threshold and does not harvest when the population is below this threshold. This strategy is suitable for situations in which the population size and carrying capacity are known. Mixed harvesting strategies are generally employed. Lande *et al.* (1997) show that proportional threshold harvesting is the optimal strategy especially when uncertainty in population estimates is large. For willow ptarmigan (*Lagopus lagopus*) in central Sweden, proportional harvest can give higher yields than the traditional proportional harvest and it reduces the variation of the annual bag (Aanes

*et al.* 2002). From these examples it becomes clear that investigating and testing the effect of different harvesting methods on the population may help to understand the dynamics and can inform management of harvested populations.

In density dependent populations, compensatory mortality or natality is often cited as the basis for sustainable harvesting and many examples in empirical and modelling studies have shown this (Boyce *et al.* 1999). Compensatory mortality has been shown in many grouse species, where parts of the harvest are compensated (Ellison 1991). The red grouse (*L. lagopus scoticus*) is an exception of this where full compensation has been shown in some populations (Ellison 1991). Despite intensive research on many populations, the mechanism for compensation is unclear. For example, it is not known whether harvesting is additive or compensatory in waterfowl management in the US (Johnson *et al.* 1997, 2002). Pedersen *et al.* (2004) have conducted an experimental study on willow grouse and found that only 33% of the loss due to harvesting was compensated for. The authors suggest that long distance juvenile dispersal explained the lack of compensation and stress the importance of scale in ecological studies. A similar explanation originates from fisheries where the compensating factor might be immigration from adjacent poorer habitats that restocks the number of animals in the exploited areas (Hutchings 1996). Immigration is therefore an important component when modelling the sustainability of shooting and population dynamics (Sutherland and Gill 2001). The timing of the harvesting might also be important as environmental variability introduced by seasonality results in fluctuations in abundance and demographic parameters (Xu *et al.* 2005).

## 1.2 Interactions of harvesting with parasites, territoriality and demography

Much insight has been gained about population dynamics from incorporating harvesting in models but studies on multiple interactions between harvest and other factors driving population fluctuations, such as parasites and behaviour, are few (but see Holmstad *et al.* 2006). It is known that parasites increase host susceptibility to predation (Murray *et al.* 1997, Joly and Messier 2004), and affect host behaviour (Thompson and Kavaliers 1994, Pelletier *et al.* 2005, Scantlebury *et al.* 2007) and population dynamics (Tompkins *et al.* 2002, Albon *et al.* 2002). Studies on the distribution of parasites within vertebrate hosts have shown differences in parasite burden of different host age- and sex-classes (Wilson *et al.* 2004, Irvine *et al.* 2000) but in many systems it is still unclear if and how parasites interact with demography and environmental stochasticity (but see Jolles *et al.* 2006).

Territoriality is a key feature of animal populations where individuals defend a certain area through aggressive behaviour towards competitors. Aggressiveness is driven by testosterone in many vertebrates and favours reproductive success but lowers immunocompetence (Folstad and Karter 1992). The immunocompetence handicap hypothesis has been applied to many populations and a trade-off between allocating recourses to immune function and growth or aggressiveness has been revealed in birds (Sheldon and Verhulst 1996, Møller *et al.* 1999) including grouse species (Isomursu *et al.* 2006). Aggressiveness increases with density in red grouse and has been shown to affect population dynamics by excluding young males from breeding in both the current year and the next year (Mougeot *et al.* 2005a,b; Matthiopoulos *et al.* 2003, 2005). The effect of exclusion of specific demographic groups from the breeding population is widespread in vertebrates and influences dynamics and harvesting of these populations (Coulson *et al.* 2004, Milner-Gulland *et al.* 2004, Clutton-Brock *et al.* 2002). Red grouse serve as an excellent case study where the interaction between harvesting, territoriality and parasites might influence population fluctuations.

The effect of age dependence in reproduction and its effects on population dynamics have been documented for mammals and birds (Solberg *et al.* 1999, Ezard *et al.* 2006). Decomposing the mean reproduction of the population into the contribution of different age-classes has revealed new insights into population growths rates and dynamics (Coulson *et al.* 2005, Ezard *et al.* 2006). Breeding success in many birds is influenced by female age, with younger birds laying smaller clutches, having lower nesting success and producing fewer fledglings (Curio 1983; Rockwell *et al.* 1983; Harvey *et al.* 1985). Senescent effects commonly occur in many bird species (review in Martin 1995) including both long-lived (Catry *et al.* 2006) and short-lived species (Møller and De Lope 1999). Age-related fecundity has also been demonstrated in grouse species: younger birds have lower reproductive potential than older birds (Sæther 1990, Martin 1995, Scherini *et al.* 2003). A recent study on willow and white-tailed ptarmigan (*L. leucurus*) by Sandercock *et al.* (2005) showed that egg production increased with age but that annual fecundity was not dependent on age, due to stochastic effects of brood and nest predation. Myrberget (1986) studied willow grouse and found no effect of hen age on breeding success. For red grouse a small study, based on measurements from 11-18 nests, by Moss *et al.* (1996) found no correlation between breeding success and hen age.

In complex natural systems, simulation modelling has helped to formulate and test hypotheses in a theoretical framework. Modelling has increasingly been recognised as a useful tool to understand and predict the dynamics of harvested populations (Milner-Gulland and Mace 1998, Hauser *et al.* 2006a). Age-structured models showed that harvesting strategies are more likely to be sustainable when the demography of the population is incorporated (Hauser *et al.* 2007). Modelling can inform management by incorporating uncertainty due to environmental stochasticity and variation in the harvest process itself (Milner-Gulland *et al.* 2001, Milner-Gulland *et al.* 2004, Nicholson and Possingham 2007). Therefore, modelling is a powerful tool to investigate and test the relative role of complex interactions observed in the field and to gain new insights into the dynamics of fluctuating populations.

## 1.3   The red grouse (*Lagopus lagopus scoticus*)

The red grouse, a subspecies of the widely distributed willow grouse, is a game bird restricted to the heather (*Calluna spp*) moorland of the British Isles. Shooting grouse is a sport for landowners but due to increased economic pressure and a general loss of heather, grouse shooting is now also leased for commercial gain and provides an important income for landowners (Hudson 1992). Early research on red grouse population dynamics started in Scotland in the 1960s (Jenkins *et al.* 1964) and in Northern England in the 1980s (Hudson 1986). It was when grouse numbers fell in Scotland in the mid 1970s and failed to show signs of recovery (Barnes 1987) that an increased interest in grouse research emerged (Hudson 1992). The aim of the early research was to explain the high mortality and the role of parasites but developed into a general interest in the mechanisms involved in population dynamics of fluctuating species.

Grouse shooting is an important source of income for landowners and enables them to employ gamekeepers in rural areas with otherwise poor employment opportunities. Therefore, it has a substantial impact on the rural economy and has always attracted much attention from different angles, including researchers, policy makers and landowners. Sustainable shooting is a key target of red grouse management to ensure income and employment. Therefore it is important to understand the drivers of sustainability of red grouse shooting. The results of this study will not only be beneficial for red grouse but also for the sustainable harvest of other fluctuating populations. The combination of long-term field data, detailed age- and sex-related data collection and advanced modelling will give a unique opportunity to study the dynamics of a harvested species.

Red grouse populations in the UK fluctuate over space and time (Hudson 1992) typically in a cyclic manner (Haydon *et al.* 2002). Research to explain the population cycles of red grouse has concentrated on the effect of parasites and territorial behaviour (e.g. Hudson *et al.* 1998; Moss *et al.* 1996; Mougeot *et al.* 2005a,b). Parasites have been shown to be a significant component driving red

grouse cycles, both empirically (Hudson *et al.* 1998; Newborn and Foster 2002) and theoretically (Dobson and Hudson 1992). However, this research has been criticised because it has concentrated on harvest data rather than actual population numbers and therefore overestimated the variance of the population size (Lambin *et al.* 1999). Further criticism pointed out that parasite reduction experiments reduced the extent of the crashes but a tendency to cycle was still visible (Tompkins and Begon 1999). Recent field experiments have shown that parasites alone cannot explain cycles in red grouse (Redpath *et al.* 2006a).

Another hypothesis has been proposed and studied in great detail to explain red grouse cycles; the kin facilitation and territoriality theory. The key component of this theory is that at low density aggression towards sons is low and allows them to establish an adjacent territory. At high densities aggression of old males towards their sons is high thereby preventing them from obtaining a territory. Family clusters break up and as space is still limited in the next year but unrelated males hold neighbouring territories, aggressiveness further increases and the population continues to decline. This has been followed up in field experiments where Mougeot *et al.* (2003a,b; 2005a,b) showed that aggression depends on the density of males in the population; at high density young males are excluded from next year's breeding population. Matthiopoulos *et al.* (2005) showed that an abrupt transition from tolerant to aggressive behaviour is needed to create cycles in a modelling environment. Recent work by Mougeot *et al.* (2006) and Redpath *et al.* (2006a,b) showed that aggressiveness and parasites are not exclusive theories. High aggressiveness and testosterone levels are followed by high parasite intensities and lower over-winter survival (Seivwright *et al.* 2005).

Few investigations have been carried out to understand the effect of shooting and its interaction with demography and parasites; shooting is implicitly assumed to have very little effect on grouse population dynamics. Jenkins *et al.* (1963) showed that harvesting mortality was compensated for by competition for territories, where non-territorial birds fill the territories made vacant by removing territorial males during

the shooting season. Watson *et al.* (1988) and Moss *et al.* (1996) stopped a red grouse population from further decline by removal of territorial males. Hudson and Dobson (2001) modelled the effect of shooting on fluctuating red grouse populations and showed that, in theory, shooting would dampen population oscillations. However, empirical data suggest that this is not the case (Shaw *et al.* 2004, Cattadori *et al.* 2005). It seems surprising and counterintuitive that shooting has no effect on population dynamics because a large proportion of the population is harvested, sometimes up to 50% (Hudson and Dobson 2001). The reason for the absence of a dampening effect remains unclear and Hudson and Dobson (2001) suggest that shooting happens after density dependent effects have already taken place. Shooting takes place from mid August throughout the autumn, whereas density dependent mortality, especially through parasites and predators, takes place in spring and early summer.

The demographic structure of populations has been proven widely to be important in understanding fluctuations (Hilborn and Mangel 1997, Leirs *et al.* 1997, Coulson *et al.* 2001) and to my best knowledge, studies of red grouse incorporating demographic information (both the age and sex structure) and harvesting remain to be conducted. Understanding the sustainability of red grouse shooting is a multi-dimensional task where density dependent effects, stochasticity and weather variables play an important role. In addition, research on the reproductive ecology and behaviour of a species contribute to the understanding of fluctuating populations and their sustainable management (Gosling 2003; Legendre *et al.* 1999). Harvesting an age and sex structured population sustainably requires in-depth knowledge on the underlying ecological mechanisms and detailed investigations of the shooting procedures and bag records. Kokko (2001) argues that lack of information often leads to suboptimal harvesting decisions and unfavourable management practices. The most obvious is overexploitation leading to extinction of the harvested species but also timing of harvesting can also reduce population size. Neglect of important factors like immigration, the age-sex structure of the population and timing of harvesting (Kokko and Lindström 1998, Boyce *et al.* 1999) might be reasons why

shooting is not detected as having an effect on the population dynamics of red grouse.

This thesis aims to assess the relative roles of age-related parasite burdens, fecundity and susceptibility to shooting in driving population dynamics in a fluctuating species, the red grouse. A combination of fieldwork and modelling was used to test the interactions of these factors in the light of red grouse population dynamics. The objectives are to:

- Quantify pre-breeding parasite burdens and fecundity for grouse of three age classes; 1year-old, 2-year-old and grouse of three years and older
- Evaluate susceptibility to shooting dependent on grouse age, sex and density and characteristics of grouse shooting events
- Develop an age- and sex-structured harvesting model to understand the effect of age- and sex-related aggressiveness, parasite burdens and susceptibility to shooting on red grouse population dynamics
- Make recommendations for sustainable shooting of red grouse, including testing the effect of moorland management and time and bag limits

## 1.4 Outline of the thesis

This thesis investigates the interaction between the demographic structure of red grouse populations and shooting, fecundity and parasites. Age-related parasite burdens were estimated from faecal egg counts of known-age grouse of 1 year, 2 years and 3 years and older before the breeding season (chapter 2). In the next chapter different aspects of age-related fecundity in red grouse were studied. For this study the age of the female and the interaction with nest habitat and yearly variation was investigated (chapter 3).

Harvesting is the predominant source of mortality for many grouse populations. The age and sex composition of shot grouse was determined on the smallest scale, the individual shooting event (drive). The young-to-old and sex ratios of the shooting bag were then compared with the ratios obtained by population counts before

shooting to investigate if harvest selectivity takes place and what factors might be involved (chapter 4). Findings from the chapters 2-4 were used to develop a sex- and age-structured population model of red grouse in discrete time steps to reflect the seasonality of the system. The model incorporates aggressiveness, parasites and harvesting. A deterministic model is first described and extended to a stochastic population model with three age classes and both sexes (chapter 5). Different harvesting rates and methods are applied to the model to investigate the effects of selective harvesting on population dynamics (chapter 6). Finally, management recommendations for sustainable harvesting of red grouse are made, and potential avenues for future research explored (chapter 7).

# Chapter 2

## Age-related parasite burdens in red grouse

## 2.1 Abstract

Population dynamics of fluctuating species have been studied in great detail and despite recent advances in the fields of wildlife diseases and demography their interaction is underrepresented in ecological studies. It is well known that parasites impair the survival and fecundity of the host. In vertebrates, parasite burdens commonly increase with age and age-intensity curves have been used to quantify parasite-induced mortality. The nematode *T. tenuis* and red grouse system is particularly well studied; it is known that old grouse (> 1 year) carry higher worm burdens than young grouse (<1 year). This study investigated the parasite burdens of old grouse by sampling faecal samples of known age grouse. Old grouse were split into two groups that consisted of two-year-old grouse and grouse of three years and older. The study showed that grouse three years and older had higher worm burdens than two-year-old grouse and that these carried more worms than one-year-old grouse. An increase of faecal egg output for individual grouse occurred during a short period of 54 days in February and March for all age classes. Two-year-old grouse showed the highest percentage of highly parasitized individuals and this might explain the high spring mortality observed in red grouse. Grouse in better condition carried fewer faecal eggs, but no interaction with age was detected. Combined with a detailed study of the demography of red grouse populations (chapter 3) this study highlights important interactions between parasites and demography for fluctuating species.

## 2.2   Introduction

The study of population dynamics has experienced rapid advances in recent years in two main areas: wildlife disease ecology (e.g. Hudson *et al.* 2002, Morgan *et al.* 2004) and demographic studies of large vertebrates (e.g. Clutton-Brock & Pemberton 2004). The demographic structure of populations has been widely proven to be important in understanding population fluctuations (Hilborn & Mangel 1997; Leirs *et al.* 1997). Density dependent and independent mechanisms influence the extent of the variation and can work at the same time in the same population (Leirs *et al.* 1997). Individual based data on Soay sheep (*Ovis aries*) showed that population crashes result from interactions between density and the age-sex structure of the population as well as weather variables and parasites (Coulson *et al.* 2001; Grenfell *et al.* 1998).

Parasites influence vertebrate population dynamics and host vital rates (Tompkins *et al.* 2002, Wilson *et al.* 2004). Studies on the distribution of parasites within vertebrate hosts have shown differences in parasite burden of different host age- and sex-classes (e.g. Soay sheep, Wilson *et al.* 2002, Svalbard reindeer (*Rangifer tarandus platyrhynchus*), Irvine *et al.* 2000). The relationship between the abundance and distribution of infection and host age has been used to quantify rates of transmission and parasite mortality (Anderson & May 1991, Rousset 1996).

The host parasite system of red grouse and *T. tenuis* has been well studied. Hudson *et al.* (1998) showed that the nematode reduces population growth rates and fecundity and plays a role in population cycles in red grouse. However, Redpath *et al.* (2006a) showed that a single trophic interaction between parasites and host did not explain the cyclic behaviour of the studied red grouse populations and more detailed investigations into the interactions between different processes are needed. For red grouse it is known that young individuals (< 1year) carry more parasites than older ones (>1 year; Shaw and Moss 1989, Hudson *et al.* 1992). The age-intensity curve has been estimated for red grouse, but this is done from post-mortem investigations of shot birds (Hudson 1992). Red grouse mortality induced by *T.*

*tenuis* peaks in March and April (Hudson *et al.* 1997), the interaction between demography and parasite intensity is unknown for this period. This study aims to further enhance knowledge on how age and parasite intensity interact in early spring by estimating individual-based parasite burdens of three red grouse age classes.

## 2.3   Methods

### 2.3.1   Data collection

Red grouse were recaptured between 2004 and 2006 in the North Pennines, UK as part of a longer-term mark-recapture study. Individual metal rings (British Trust for Ornithology) were attached to birds and their age and sex recorded. Young birds were distinguished from old birds according to toenail scars (no scars in young birds) and the shape and colour of their second and third primary (round and pale in old birds: Cramp & Simmons 1980). The sex was determined by plumage colour and comb size (Hudson & Newborn 1995).

Red grouse were recaptured during a 54-day period in February and March 2006. The mark-recapture study allowed allocating fifty-three individual red grouse to three age classes: one-year-old, two-year-old and grouse three years and older. The condition of the individual grouse was assessed by the size of their flight muscles: (1) poor, (2) medium and (3) good. Grouse were caught between 21.00 and 24.00 with a net and by dazzling them with a headlamp. They were then placed in individual cages overnight and released not later than one hour after sunrise the next morning to minimise food deprivation. Faecal samples were collected and transported to the laboratory, where they were processed the same day or stored at a constant temperature of 5 degrees Celsius to inhibit parasite egg development. All samples were processed within 2 days of collection, which is within the storage recommendation (< 2 weeks) of Seivwright *et al.* (2004) to ensure reliable estimates. From each sample 1 g was extracted and diluted in saturated NaCL solution. A sub-sample was placed in a McMaster counting slide. The number of nematode eggs in the slide was counted and the number of eggs per gram faeces was calculated.

Recent scientific work has shown that *T. tenuis* fecundity is not density dependent and that faecal egg counts (FEC) provide a reliable measure of *T. tenuis* intensities in red grouse (Hudson *et al.* 1997, Moss *et al.* 1990, Seivwright *et al.* 2004). Therefore from the number of faecal eggs the number of worms inside the host can be calculated.

A subset of eleven red grouse were fitted with a 15g necklace radio transmitter provided by Biotrack Ltd. Roosting locations of individual grouse were pin-pointed at night and faecal material was collected the next morning from these locations (Hudson 1992). There was no significant effect of necklace radio transmitters on survival or breeding success of red grouse in an earlier study (Thirgood *et al.* 1995).

Red grouse density was estimated on the study area in the North Pennines using standard methods of 1 km$^2$ block counts (Jenkins *et al.* 1963, Mougeot *et al.* 2005b, Redpath *et al.* 2006a) between 1987 and 2007.

### 2.3.2   Statistical analysis

Parasite data are highly skewed with a small proportion of hosts carrying a large proportion of the parasites (Wilson *et al.* 2002). The data set was analysed using a generalised linear model with a log link and a quasi-Poisson error distribution for overdispersed data. Most parasite studies have been shown to follow a negative binomial distribution (Shaw *et al.* 1998) but recent advances in statistical computing allow fitting data where the variance exceeds the mean in a flexible way where the overdispersion parameter is estimated by the variance to mean ratio (McCulloch & Searle 2001, Crawley 2007). In the sample of 53 grouse held overnight, one random sample was drawn from individuals with more than one data point to avoid pseudo-replication. This resulted in a data set for the analysis of 47 grouse with one measurement each. Significance was assessed using an F test instead of a Chi-square test for overdispersed data (Crawley 2007). Orthogonal contrasts were built to compare different classes of age and condition (Crawley 2007).

The inverse aggregation parameter $k$ was estimated for three age classes separately by

$$k = \frac{m^2 - \dfrac{v}{n}}{v - m} \tag{2.1}$$

where $m$ is the mean, $v$ the variance and $n$ is the sample size (Smith & Guerrero 1993, Morgan *et al.* 2005).

A generalised linear mixed effects model with quasi-Poisson error structure was applied to the data set of eleven individuals using lmer in package lme4 (R ver 2.4.1 R Development Core Team 2007). The response variable was number of eggs from FEC, Julian date was added as a fixed effect while individual was added as a random effect. Generalised linear mixed effects models are under development and many different opinions are expressed. The R Development Core Team is followed in not giving p-values for this type of model. This is because the purpose of this analysis is to show trends in individual grouse.

Bootstrapping was carried out to estimate 95% confidence intervals of the model parameters as described in Crawley (2007). The residuals and the fitted values were extracted from the model. The residuals were shuffled 2000 times and added to the fitted values in different permutations. Then the model was fitted to the new data sets to obtain the distribution of parameter values.

The time series was assessed with an Ljung-Box test (Ljung and Box 1978) to test whether the cycles were distinguishable from white noise.

## 2.4 Results

Red grouse showed no clear pattern of cycles in the study area and were not distinguishable from white noise (Ljung-Box test, $X^2=0.02$, df=1, p=0.9). Fluctuations show a clear population low in 2005 and an increase in 2006 and 2007 (Fig 2.1).
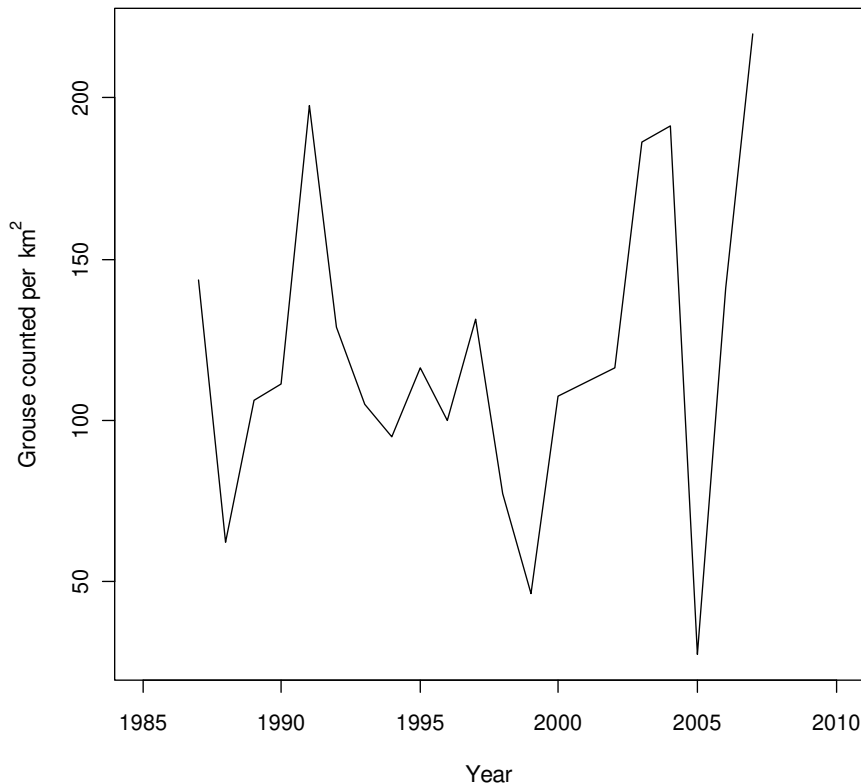


Figure 2.1: July counts of red grouse from 1987 until 2007 on the study moor in the North Pennines.

The generalised linear model for the full dataset (Table 2.1) showed that age with three levels ($F_{2,44}=62.3$, p<0.0001) and condition with three levels were significant ($F_{2,42}=9.8$, p<0.001). FEC increased significantly with date in February and March ($F_{1,41}=63.5$, p<0.0001). Grouse of three years and older showed higher FEC than 2-

year-old grouse (t=-6.6, df=41, p<0.001) and these showed higher FEC than 1-year-old grouse (t=-4.4, df=41, p<0.001). Grouse in poor condition had higher FEC than grouse in medium condition (t=3.8, df=41, p<0.001) and these excreted more faecal eggs than grouse in good condition (t=4.2, df=41, p<0.001). Although condition and age were correlated, with older grouse being in worse condition than younger grouse (Pearson's correlation cor=-0.33, t=-2.35, df=45, p=0.02) the interaction between age and condition ($F_{4,37}$=0.4, p=0.8) was not significant. The interaction between age and date ($F_{2,35}$=2.7, p=0.08) and condition and date were also not significant ($F_{2,33}$=0.2, p=0.8).

Table 2.1: Faecal egg counts (n=47) were conducted in February and March 2006 for three age classes: (1) one-year-old, (2) two-year-old and (3) three-year-old and older grouse in three conditions: (1) poor, (2) medium and (3) good. The values were drawn from a generalised linear model with a log-link and a quasi-Poisson error structure for overdispersed count data. 95% confidence intervals were calculated by bootstrapping (n=2000).

|  | Estimate | SE | t | P | 95% CI (boot) |
|---|---|---|---|---|---|
| Intercept | 1.687 | 1.01 | 1.7 | 0.1 | 1.674 -1.728 |
| Age2 | 1.135 | 0.4 | 3.0 | <0.005 | 1.123 - 1.142 |
| Age3 | 2.01 | 0.4 | 5.6 | <0.001 | 2.00 - 2.015 |
| Con2 | -0.495 | 0.2 | -2.5 | <0.02 | -0.499 - -0.492 |
| Con3 | -1.205 | 0.3 | -4.3 | <0.001 | -1.208 - -1.194 |
| Date | 0.103 | 0.01 | 7.3 | <0.001 | 0.1026 - 0.1035 |
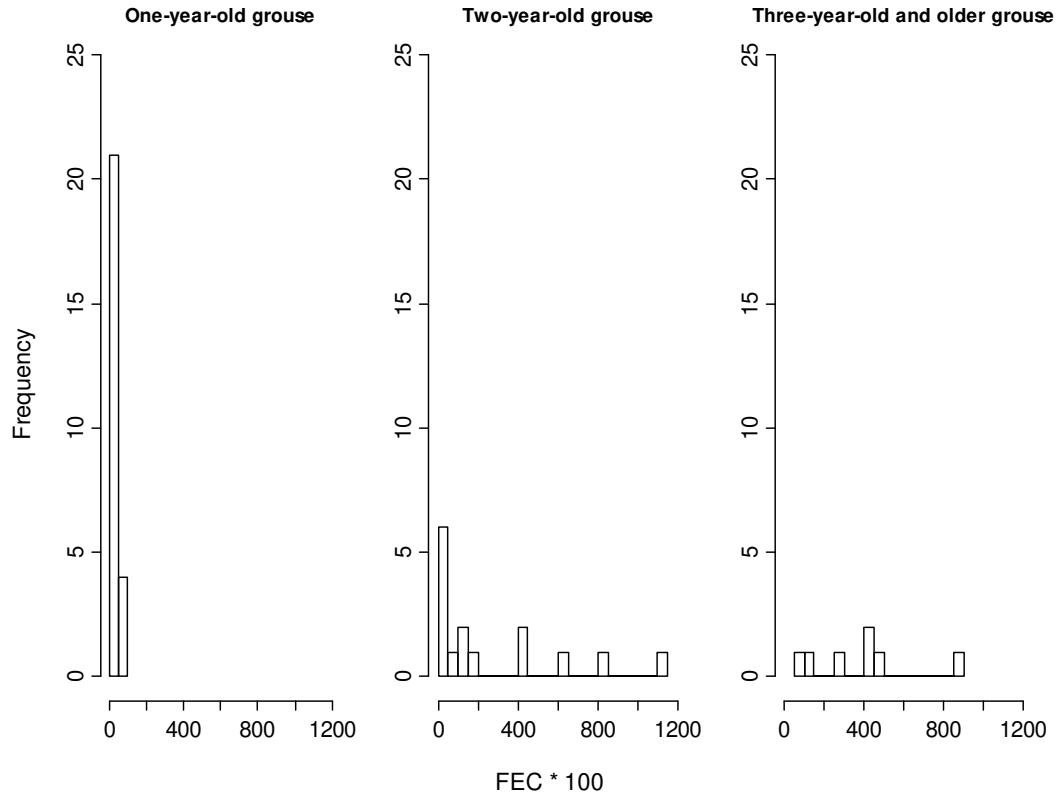
Figure 2.2: Histogram for faecal egg counts for three age classes of grouse: (1) one-year-old, (2) two-year-old and (3) three-year-old grouse and older (total n=47).

Three out of 15 and 1 out of 7 of the second and third age class, respectively, faced high parasite burdens of more than 50 thousand eggs per gram, which would be more than 5 thousand worms per bird (calculated after Seivwright et al. 2004). None of the one-year-old grouse in this study showed such high worm burdens. The data are highly aggregated and the FEC of two-year old grouse (k=0.52) showed the highest degree of aggregation. One-year-old grouse (k=1.22) showed an intermediate degree of aggregation whereas grouse of three years and older (k=2.02) showed the lowest degree of aggregation (Fig 2.2).

Faecal egg count data from eleven individual grouse showed that the faecal egg output increased with time (estimate=0.04 log worms per bird ± 0.008 (SE), t=5.4; Fig 2.3).
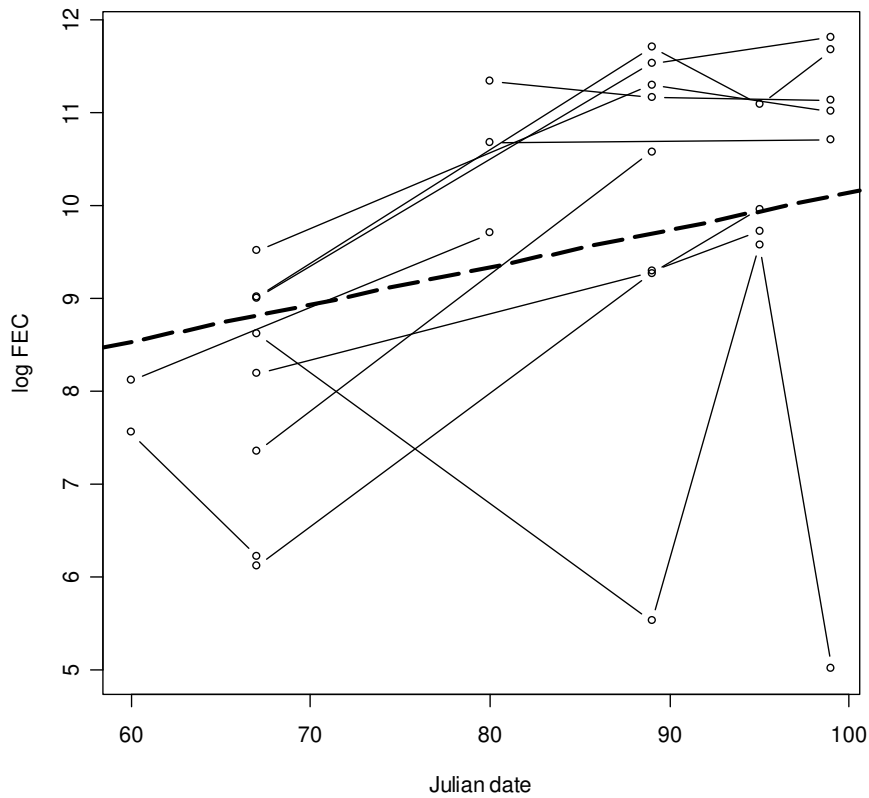
Figure 2.3: Faecal egg counts (n=31) of eleven individual grouse in February and March 2006. The dashed line is estimated by fitting a generalised linear mixed model with a log-link function and quasi-Poisson error structure to correct for overdispersion.

## 2.5 Discussion

This study estimated the parasite burden at the transition period between winter and spring and how this interacts with age classes. Results show that there was an increase in faecal egg output for all age classes during February and March and that worm burden increased with age. Grouse in better condition have lower worm burdens but the interaction between condition and age was not significant. *T. tenuis* larvae are picked up by red grouse during the first few months of their lives, until the first autumn (Potts *et al.* 1984). There is no output of eggs that could develop into infective larvae during the winter (Shaw 1988, Shaw *et al.* 1989, Shaw & Moss

1989) so there is no further increase in faecal egg output or worm burden in either young or old grouse during winter. A second period of infection starts in spring (Hudson & Dobson 1997).

The decrease of the inverse aggregation parameter $k$ at old age suggested that grouse between two and three years experienced further acquisition of parasites and probably high mortality rates, resulting in old grouse ($\geq$ 3 years) showing high mean parasite burdens but a more normal distribution with no extremely highly parasitized individuals. Hudson (1992) showed that the age-intensity curve for *T. tenuis* in red grouse reached its asymptote after 10-15 months. This study showed that parasite burdens can further increase from 10 to 22 and 34 months of age, with the increase being most pronounced between 10 and 22 months (Fig 2.3) and reaching its asymptote at 34 months.

The frequency distribution of parasite burdens of dead red grouse found during regular corpse searches peaked at circa 5000 worms per bird (Hudson *et al.* 1992). However, no information is available on the age-structure of the grouse killed by parasites. Anderson and Gordon (1982) showed that density-dependent parasite-induced mortality reduces the variance to mean ratio of the parasite distribution with host age. The aggregation parameter has been used with field data to indicate parasite-induced mortality without the need to find dead hosts (e.g. Rousset 1996). Krasnov *et al.* (2006) found a similar aggregation in their study on flea parasites on rodents showing a convex aggregation curve among host age; middle-aged individuals showed the most aggregated distribution of parasites. In this study, conducted in late winter and early spring, when red grouse mortality is at its highest (Hudson *et al.* 1997), between 20 and 14 percent of the second and third age class respectively showed worm burdens exceeding 5000 worms per bird. This suggests that the increased spring mortality detected on managed grouse moors came mainly from two-year-old grouse, because once grouse have reached three years or more, most highly parasitized birds have died. Old grouse ($\geq$ 3 years) showed a less

aggregated distribution and therefore the population consisted of fewer grouse but with more evenly distributed high parasite burdens.

FEC increases in spring in red grouse (Shaw & Moss 1989, Moss *et al.* 1990). Data collection for this study took place during a short time span of 54 days during this period. Studies of parasites and FEC suffer from small sample sizes because of the high degree of aggregation of the parasites within the hosts; a small number of hosts carrying a large percentage of the total parasite burden of the population (Wilson *et al.* 2002). Morgan *et al.* (2005) demonstrated that there is a high probability of underestimating the mean parasite burdens of samples rather than overestimating it and that this error is largely reduced when sample size increases and the distribution becomes less aggregated. The smallest sample sizes in this study were for the oldest age class, but the sample of the oldest age class was least aggregated and therefore reliability of the results increased. The individual-based data strongly support the hypothesis that faecal egg output in red grouse increases with date in late winter and early spring and that the effect found was due to this increase and not due to sample size. This is also in line with Shaw & Moss (1989) who found an increase in *T. tenuis* egg output in March in red grouse.

In an ideal world, age-intensity curves should be drawn from individual-based data, where the parasite burden of the same animal is estimated at different ages over the entire life span. So far this has been difficult because sampling endoparasites involves removing the sampled individuals from the population. Since more research has been conducted to validate the relationship between FEC and parasite burdens in vertebrates (red grouse - Seivwright *et al.* 2004, Soay sheep - Wilson *et al.* 2002), individual-based data is more feasible to collect. This type of data will increase our knowledge about the interaction between parasites, demography and vital rates.

Modelling has increasingly been recognised as a useful tool to understand and predict population dynamics affected by parasites (e.g. Stone *et al.* 2007) and human harvest (e.g. Milner *et al.* 2007). The age-structure of the host and the distribution of

parasites between age-classes have been shown to be important to understand epidemics in a modelling approach (Patel *et al.* 2005). Combined with data from the current study, further age-structured modelling studies will enhance our knowledge about fluctuating species and their interaction with parasites and human intervention.

# Chapter 3

## The influence of age, habitat and yearly variation on fecundity in red grouse

## 3.1 Abstract

Age-related fecundity has been the interest of many avian studies and a general pattern shows an increase in breeding performance with age. However, senescent effects have also been observed, mostly in long-lived species, but also in short lived species. Extrinsic effects like yearly variation in weather variables might further affect fecundity in birds. Different aspects of fecundity (clutch size, hatchling and fledgling success) were studied over three years in red grouse, and the interaction with age was investigated for three age classes; one-year-old, two-year-old and three-year and older grouse. No simple pattern was detected but the study showed that three-year and older females hatched fewer chicks when nesting in location with less vegetation cover. Also the same age class hatched fewer chicks with later hatch date. Young females (1-year-old) were accompanied by more fledglings in July than older females whereas there was a trend that young males were less successful. Yearly variation in survival was estimated using a mark-recapture study; the females abandoning the nest or being predated coincided with years of low survival during the breeding season. This study showed that age-related fecundity might play a role in red grouse but that the interaction of yearly variation in survival and fecundity and the age structure of the population might interact in a way that needs more long-term individual-based data. This hypothesis is in line with other long-term studies that found age-related fecundity only in some years and with some aspects of fecundity due to stochastic environmental effects.

## 3.2   Introduction

It is widely accepted that breeding performance in birds increases with age (Curio 1983, Sæther 1990, Forslund and Pärt 1995) but variation in the shape of age-dependent performance curves occurs between and within bird taxa (Martin 1995). Stochastic and deterministic processes affect the performance of individuals in different ways, depending on their age and sex (Leirs *et al.* 1997, Coulson *et al.* 2001). Due to stochastic effects of brood and nest predation, annual fecundity was not age-dependent despite egg production increasing with age in two ptarmigan species (*Lagopus lagopus* and *L. leucurus*; Sandercock *et al.* 2005). Yearly differences in recruitment of broods were observed in a study of individual great tits (*Parus major*; Pettifor *et al.* 2001) and annual environmental fluctuations have been shown to influence the recruitment of large clutches to a greater extent than smaller clutches in the same species (Boyce and Perrins 1987).

While performance increases at young age, senescence commonly occurs in many bird species (e.g. sparrowhawk *Accipiter nisus*; Newton and Rothery 1997, Newton and Rothery 2002, review in Martin 1995). Long-lived birds are primarily affected (Catry *et al.* 2006), but senescent effects have been observed in short-lived species (e.g. barn swallows *Hirtundo rustica*; Møller and de Lope 1999).

Predator presence and abundance can have a significant effect on the breeding performance of ground- and tree-nesting birds, with losses up to 50% or more (reviews in Martin 1992, Caro 2005). Nesting habitat influences the success of nesting attempts in many birds, for example mallards (*Anas platyrhynchos*; Albrecht and Klvana 2004) and northern bobwhite (*Colinus virginianus*; Taylor *et al.* 1999), but the optimal amount of concealment and type of habitat varies across species (Smith *et al.* 2007), latitude and season (Wiebe and Martin 1998a). Differences between years can interact with nesting habitat, such that favourable vegetation cover increased nest success in one year but not in another in red grouse (Campbell *et al.* 2002). Studies on the interactions between nest habitat and experience showed

that nest habitat choice changed over the season and depended on whether predation occurred at an earlier nesting attempt (Wiebe and Martin 1998a).

General theory on the relationship between age and mate quality suggests that older age in males might signal genetic quality because individuals have proven longevity. Kokko and Lindström (1996) have shown in a simulation model that female choice for old males is favourable in a mutation-selection balance. Old males have fewer disadvantageous mutations that would have decreased their viability and these traits are also inherited by their offspring. Choosing older males as mates is evolutionarily plausible in resource-based breeding systems where increased age represents experience that helps males to provide resources to the female. Older males might invest more in current offspring and be better parents because of their greater experience. On the other hand, older males might be less able to produce high-quality ejaculates, e.g. because of higher parasite burdens at old age. In a rapidly changing environment older males might be out-of-date and younger males present a better-adapted gene pool (for review see Brooks and Kemps 2001). Red grouse are monogamous birds and males defend territories they have taken up in autumn (Watson and Jenkins 1964). Males contribute to breeding success by defending territories and guarding their females while foraging, accompanying the brood and defending young.

It is well known that parasite intensity increases with age in red grouse (Shaw and Moss 1989, Hudson *et al.* 1992, chapter 2) and that high parasite burdens decrease fecundity (Hudson *et al.* 1998). As fecundity increases with age in many species this chapter investigates the interaction between three age classes in red grouse, 1-year-old, two-year-old and 3-year-old and older grouse, habitat and yearly variation in breeding success and survival in a fluctuating short-lived species. This study aims to give a first insight into interactions between demography and extrinsic factors affecting reproductive performance in this species.

## 3.3   Methods

### 3.3.1   Catching and marking grouse

Red grouse were caught between 2004 and 2006 in Northern England. Individuals were dazzled with a headlamp and caught with a net. Metal rings and coloured wing tags were attached to distinguish yearlings and adults in the field. Mark-recapture was carried out in February 2004, February/March 2005, September 2005, Febuary/March 2006 and September 2006. In 2006, sixteen red grouse were fitted with a 15g necklace radio transmitter provided by Biotrack Ltd. There was no significant effect of necklace radio transmitters on survival or breeding success of red grouse in an earlier study (Thirgood *et al.* 1995).

### 3.3.2   Fecundity

Eighty-two nests were found by radio-tracking and following wing-tagged females back to the nest after feeding periods in 2005, 2006 and 2007. Time series of counts for the study area are shown in Fig 2.1. For 43 nests the age of the female was known as one-year-old, two-year-old and three-year-old and older. The nests were only marked with a GPS to minimise disturbance. All nests were checked every fourth day to minimise disturbance of the hen on the nest. All hens were only disturbed once to count the number of eggs. Hatching success was determined after females had left by investigating how many eggs remained unhatched or were destroyed in the nest. Nests were classified as abandoned when the female was absent, the eggs intact (not predated) but cold on at least two visits.

Detailed habitat measurements of all nests between 2005 and 2007 were conducted following a protocol developed by Campbell *et al.* (2002). Habitat measurements were taken not longer than one week after hatching and vegetation height, lateral nest cover and canopy concealment were measured in centimetres.

Line transect counts were conducted in July using trained dogs and observations from a car to estimate the number of chicks per adult female and male. The age of

the adult birds was determined from the coloured wing-tags. Individuals older than 1 year were classified as old instead of splitting them in 2-year-old and 3+-year-old birds because of small sample size. The number of fledglings was determined for 89 females and 82 males.

### 3.3.3   Statistical analysis

The data set was analysed in R (R Development Core Team 2007) using fecundity parameters as the dependent variables. Fecundity was measured as the number of eggs laid (clutch size), number of chicks leaving the nest (number of hatchlings) and number of chicks accompanying the female and males in July (number of fledglings).

A generalised linear model (GLM) with a Poisson error structure was used to analyse the number of eggs laid. The number of eggs hatched was analysed with a linear model after testing for normality with a Shapiro-Wilk test (Crawley 2007). Explanatory variables for both analyses included female age, year, vegetation height, lateral cover and canopy cover.

Fledgling success was analysed with a generalised linear mixed effects model using lmer in the lme4 package (R ver 2.4.1 R Development Core Team 2007). The response variable fledgling success, number of chicks accompanied by males and females, were nested within year and method (dog or car observation) and these were added to the model as nested random effects. The number of fledglings were analysed with a log-link and a Poisson error structure. The success rates, where a 1 indicates a success and a zero a failure, were analysed with a logit-link and a binomial error structure.

All models were started with all variables added and each term was dropped from the model and its significance assessed. The best model was selected on the basis of a deviance test and significant variables were reinstated in the model. The deviance test for generalised linear models follows a Chi-square distribution. For linear

models an F test was used to assess significance of variables (Crawley 2007, Venables and Ripley 2002).

### 3.3.4 Mark-recapture analysis

In total 755 individuals were marked and there were 895 captures. A Cormack-Jolly-Seber model for live recaptures was run in programme MARK (White and Burnham 1999). The encounter history file was created by assigning a "1" if a grouse was caught on an occasion and a "0" if it is was not caught. The model structure follows the Cormack-Jolly-Seber model and it starts with both survival and recapture as time dependent. The age structure was added to the model by grouping every individual as young female, old female, young male or old male. These were added using parameter index matrices (PIMs).

To select for the most parsimonious model a full time variant and age sex structured model is fitted and then reduced by fitting one parameter for time and the age sex classes. The most parsimonious model was selected on the basis of Akaike's information criterion (AIC).

The goodness-of-fit is estimated first by calculating ĉ, the variance inflation factor and adjusted in MARK if larger than "1". The new model, correcting for overdispersion is then tested for goodness-of-fit using the RELEASE GOF implanted in MARK (Lebreton *et al.* 1992).

## 3.4 Results

### 3.4.1 Clutch size and number of hatchlings

Clutch size was not influenced by female age ($\chi^2$=2.5, df=2, p=0.3), cover ($\chi^2$=0.01, df=1, p=0.9), canopy ($\chi^2$=0.01, df=1, p=0.9), height ($\chi^2$=1.2, df=1, p=0.3), year ($\chi^2$=0.2, df=2, p=0.9) or date ($\chi^2$=0.2, df=1, p=0.6).

The number of hatchlings of successful nests was not influenced by the vegetation height ($F_{1,27}$=0.76, p=0.4), the canopy cover ($F_{1,27}$=1.03, p=0.3), the hatching date ($F_{1,27}$=0.8, p=0.4) or the year ($F_{2,27}$=0.4, p=0.6). In the final model, the interaction between female age and lateral cover had a significant influence on the number of hatchlings ($F_{2,32}$=3.9, p=0.03). While the trends for one-year-old and two-year-old grouse were not significant, three-year-old grouse showed a significant decrease in hatching success with less lateral cover (t=2.4, df=32, p=0.02, Fig 3.1). Further analysis showed that the lateral cover of the nest decreased for three-year-old grouse as the breeding season progressed (t=-3.2, df=32, p=0.003, Fig 3.2).
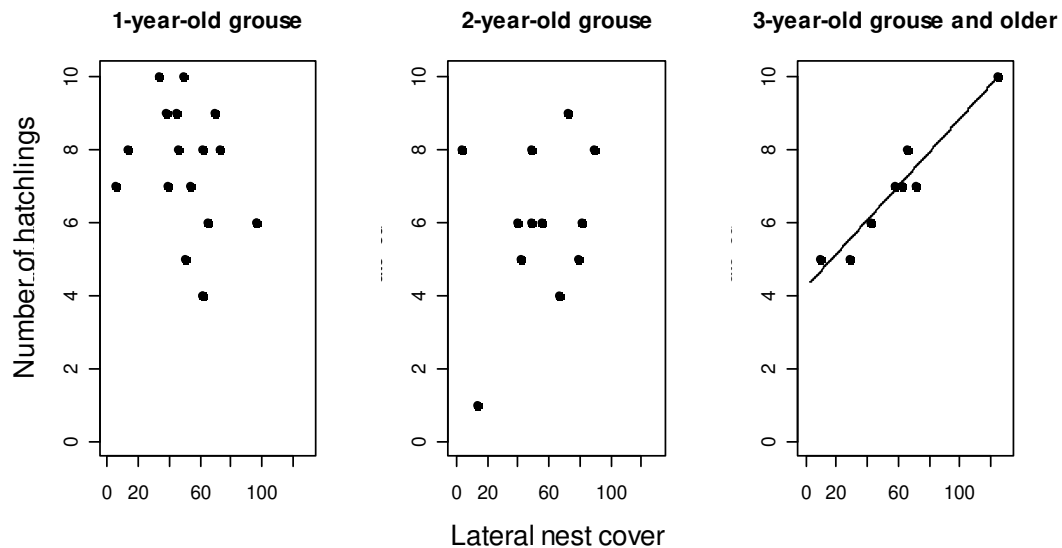


Figure 3.1: The number of grouse chicks hatched as a function of lateral vegetation cover for 1-year-old, two-year-old and three years and older females as predicted from the most parsimonious generalised linear model with Poisson error structure and a log-link function.
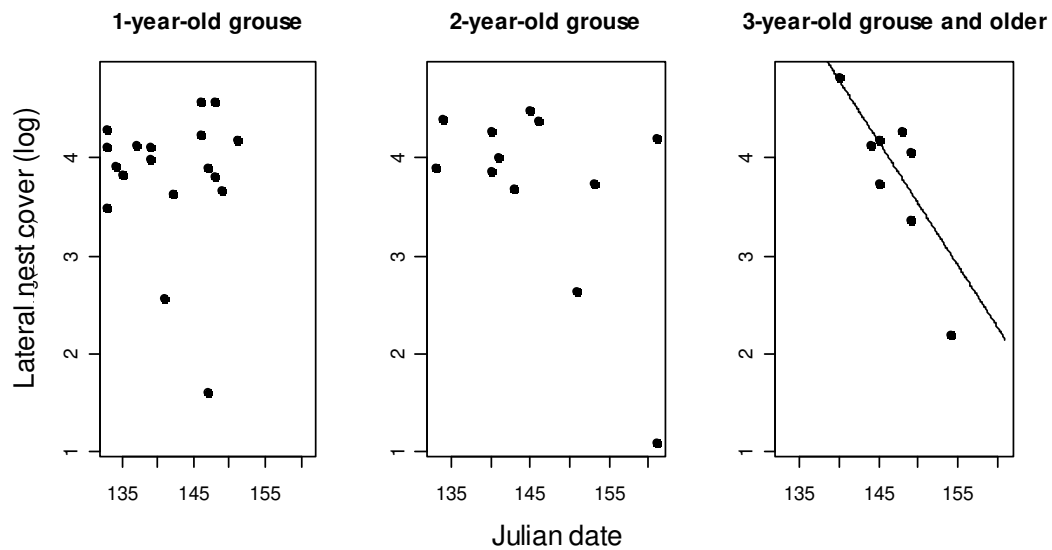
Figure 3.2: The lateral vegetation cover of the nest (log-transformed) as a function of Julian date for 1-year-old, two-year-old and three years and older females as predicted from the most parsimonious generalised linear model with Poisson error structure and a log-link function.

If a nest was successful or not was influenced by the interaction between female age and lateral cover ($\chi^2$=8.4, df=2, p=0.01). However, this effect was not clear for any of the age classes because only 4 out of 43 nests were not successful, therefore a full analysis of nest success rate with all explanatory variables was not possible. Lateral cover ($\chi^2$=0.4, df=1, p=0.5), height ($\chi^2$=2.9, df=1, p=0.09) and canopy cover ($\chi^2$=1.1, df=1, p=0.3) had no significant effect on the success rate of the nest.

### 3.4.2  Number of fledglings

The number of fledglings in July was not influenced by differences between years (females: $\chi^2$=3.5, df=2, p=0.2; males: $\chi^2$=3.9, df=2, p=0.15). The age of the parent, when taking into account only females and males accompanied by at least one young, was not significant (females: $\chi^2$=0.05, df=1, p=0.8, males: $\chi^2$=0.3, df=1, p=0.6).

The probability of having reared at least one chick was not significantly different between years (females: $\chi^2$=2.5, df=2, p=0.3; males: $\chi^2$=3.0, df=2, p=0.2) or between young and old parents (females: $\chi^2$=2.4, df=1, p=0.1; males: $\chi^2$=1.1, df=1, p=0.3). However, analysing the number of chicks per female and male with unsuccessful broods included, showed almost significant differences between years (females: $\chi^2$=4.9, df=2, p=0.08; males: $\chi^2$=5.8, df=2, p=0.06). Young females had a higher success than old females (old: 2.5, young: 3.3 chicks per female, $\chi^2$=5.0, df=1, p=0.025) whereas for males the opposite trend was observed; young males had a lower success than old males, although this effect was not significant (old: 2.9, young: 2.2 chicks per male, $\chi^2$=3.3, df=1, p=0.07).

### 3.4.3 Survival and Year-to-year variation

The initial mark recapture model was adjusted for overdispersion as measured by ĉ=2.5. Once adjusted the model gave a reasonable fit to the data ($\chi^2$=16.79, df=26, p=0.9). The survival estimates of red grouse in the study area showed a significant drop in 2005 when survival was only 7% (± 2 SE) between March 2005 and September 2005. After the crash, survival of the remaining population was 73% (± 24 SE) between September 2005 and March 2006. Survival was in between these two extremes before and after the crash (Table 3.2).

Table 3.1: Summary for mark-recapture model selection for a full time variant model for survival and recapture for all four age-sex classes, and a time variant model with different parameters for males and females and a recapture model with one parameter for the second recapture period and one parameter for all other periods. The best model was found for time variant survival without distinction for age or sex and the two parameters for recapture as explained above.

| Model | QAIC | ΔQAIC | No. Parameters | Deviance |
|---|---|---|---|---|
| Survival, recapture (2 par) | 334.9 | 0 | 6 | 38.8 |
| Survival (sex), recapture (2 par.) | 336.6 | 1.7 | 9 | 34.3 |
| Survival and recapture (time and age-sex) | 360.9 | 26 | 25 | 24.8 |

Table 3.2: Survival and recapture estimates from the most parsimonious model estimated from a mark-recapture model. Recaptures were conducted in March 2004, 2005 and 2006 and also in September 2005 and 2006.

|  | Period | Estimate | SE |
|---|---|---|---|
| Survival | Mar04-Mar05 | 0.36 | 0.07 |
|  | Mar05-Sept05 | 0.07 | 0.02 |
|  | Sept05-Mar06 | 0.73 | 0.24 |
|  | Mar06-Sept06 | 0.40 | 0.13 |
| Recapture | All periods except Mar05-Sept05 | 0.40 | 0.06 |
|  | Mar05-Sept05 | 0.22 | 0.06 |

The summer 2005 saw a large-scale crash of the red grouse population in the study area (Fig 2.1). The total loss of broods due to predation and the female abandoning the nest was significantly higher in 2005 than in 2006 (t=1.99, df=78, p=0.046). In particular, the percentage of females abandoning the nest was high in 2005 (Table 3.3). All nests in 2007 produced at least one hatchling.

Table 3.3: Overview of yearly differences in reproductive success. The number of hatchlings include only successful nests. July counts are total number obtained from sample transects in an area of approximately 1 km$^2$.

|  | 2005 n=26 | 2006 n=39 | 2007 n=17 |
|---|---|---|---|
| Predated nests | 3 | 3 | 0 |
| Abandoned nests | 4 | 0 | 0 |
| Hatchlings | 7.8 | 6.8 | 7.4 |

## 3.5  Discussion

This study found a decrease in reproductive performance at older ages, but only in the number of hatchlings and fledglings for females. Interaction with nest cover, and the fact that this interaction was only significant in three-year-olds and older grouse, might explain why other studies on *Lagopus* species did not find any effect of age on breeding success. The study also found a tendency of older males being accompanied by more fledglings in July, which could have an effect on the fecundity of their female mate. Due to small sample size the interaction effect of female and male age could not be studied. Moss *et al.* (1996) found no correlation between breeding success and hen age in red grouse in a study based on measurements from 11-18 nests when considering young grouse (< 1 year) and old grouse (> 1 year) and Mougeot *et al.* (2006) did not find an effect of male age on the number of young fledged. Wiebe and Martin (1998b) showed that younger ptarmigan had larger clutches, earlier laying dates and better spring body condition. However, reproductive performance was not significantly better than in old ptarmigan because they fledged a higher proportion of the clutch. The interaction with year in a fluctuating species like the red grouse is important as fecundity and survival are substantially reduced in some years. However, these interactions could not be investigated to a full extent due to small sample size and a limited number of years. Therefore this study points out the importance of long-term studies, especially when interactions are complex and single trophic interactions fail to explain observed population dynamics (Redpath *et al.* 2006a).

This study showed that females of different age nested in different degree of nest cover and that this influenced the number of hatchlings. The nest cover was also influenced by the date, with less nest cover for nests having started later in the season. There was no direct support for the hypothesis that later breeders were less successful, but the interaction of later breeders having less nest concealment, which then decreases hatching success suggests that there are multiple interactions of nest concealment, time of season, age and possibly condition of the female.

One explanation for the variation in the interaction between nest success and cover might be that there are costs and benefits associated with nest concealment. Nests with more cover provide the female with shelter and create a favourable microclimate. Wiebe and Martin (1998a) showed that concealed nests suffered less from egg depredation but increased the risk of females being killed because of difficulties in escaping. Grouse in the latter study suffered from high predation (40-70%) whereas predation of nests in the current study is low (0-11%), due to predator control on English grouse moors (Hudson 1992). It could be hypothesised that old females that have had experience with low risk of predation in previous years benefit from high lateral cover and an energy saving microclimate. Therefore, females choosing a high degree of nest concealment might save energy and spend more time incubating.

This study suggests that changes in reproductive output are driven by complex interactions between years, habitat and age. Campbell *et al.*'s (2002) study on red grouse nest success in Scotland found a relationship between nest success and vegetation height in one year but not in the other year. Age-independent mechanisms in survival before and during the nesting period, shown by the high variation in nest abandonment in one year, could explain population changes. Weather and parasites could not be directly linked to age and reproductive performance in this study but are known to influence population dynamics (Cattadori *et al.* 2005). Therefore, variation between years in weather variables and parasites might clarify population dynamics in red grouse.

The interaction between age, breeding experience and female quality is important when disentangling age-specific breeding success in birds (Forslund and Pårt 1995). Individual-based data incorporating age, condition and parasite burden of the bird would increase the understanding of fluctuating populations and is needed to understand population fluctuations. Individual-based data on Soay sheep (*Ovis aries*) showed that population crashes result from interactions between density and the age-sex structure of the population as well as weather variables (Coulson *et al.* 2001;

Grenfell *et al.* 1998). Additionally, long-term data on these measurements are needed since stochastic environmental processes interact with demographic processes to create complex dynamics in population behaviour (Falls *et al.* 2007). Therefore, only demographic data on red grouse collected over a longer period would be able to tease apart the factors of age-related breeding success and survival, influenced by parasites, territoriality, density and weather variables.

# Chapter 4

# The interaction between demography and shooting in red grouse

## 4.1 Abstract

Harvest records of animals are commonly used to describe population processes assuming a random off-take. However, selective harvesting has important implications for population dynamics. This study compared age and sex ratios in the bag with those in the population before shooting for red grouse. Although hunters cannot consciously select for a specific sex or age class during the shooting process, more young than old grouse were shot at large bag sizes and vice versa for small bag sizes than would be expected from the population composition before shooting. The susceptibility of old males to shooting increased with bag size and was high early in the season but decreased with the number of times an area was shot. This has important implications for understanding red grouse population dynamics since recent research has found that parasites alone do not explain cycles in red grouse. Shooting and parasites might interact at high density such that old highly parasitized grouse remain in the population after shooting. These findings are not only relevant for red grouse but apply to systems showing interactions between selective harvesting and wider ecological processes, such as parasites, which may drive population fluctuations. The study also stresses that the assumption made in many studies that harvest records reflect the age and sex ratio of the population and therefore reflect productivity can be misleading.

## 4.2   Introduction

Population fluctuations of animals are explained by temporal variation in survival and fecundity, and the demographic structure of populations is important in understanding these fluctuations (Leirs *et al.* 1997, Coulson *et al.* 2001). Variation in vital rates has been studied widely in birds and age related survival, fecundity and dispersal is a common feature in avian populations (Arcese 1989, Curio 1983, Sæther 1990, Martin 1995, Paradis *et al.* 1998, Møller and de Lope 1999, Warren and Baines 2002 & 2007, Hatch and Westneat 2007). Decomposing the contribution of an age class to population growth rates and the effect on bird population dynamics has received increased attention (Ezard *et al.* 2006). Many bird populations face high anthropogenic threats (IUCN Red List 2007) and the effect of selective harvesting of a certain age or sex class on the demographic structure, and therefore on the growth rate, of a population can be significant (Ginsberg and Milner-Gulland 1994, Kokko *et al.* 2001, Milner *et al.* 2007).

Hunters often purposely target a specific age or sex class, but this is not always the case. In non-dimorphic bird species, it is assumed that shooting is unselective, as hunters cannot consciously select during shooting (Hudson and Newborn 1995). However, Hörnell-Willebrand *et al.* (2006) showed that unintentional selection took place in willow grouse (*Lagopus lagopus*), as juveniles were under-represented in the bag when compared with counts before the hunting season. This study made the assumption that the population consisted of equal numbers of adults and made no further investigation of harvest selectivity for adult grouse. Hudson (1986) showed that during shoots in the North of England, old red grouse males were more frequently shot than would be expected from the age-sex composition of the population estimated before shooting but did not link this to any other covariates, e.g. density. In contrary to the studies mentioned so far, DeStefano and Rusch (1986) found no age or sex bias in the harvest for ruffed grouse (*Bonasa umbellus*). Given the uncertainty in shooting selectivity and the unresolved question of which factors create cycles in red grouse (Redpath *et al.* 2006a) further work linking

shooting selectivity, grouse density and demography could generate new hypotheses for understanding red grouse population dynamics.

Red grouse populations in the UK typically fluctuate in a cyclic manner (Haydon *et al.* 2002). Hudson and Dobson (2001) modelled the effect of shooting on fluctuating red grouse populations and showed that in theory shooting should dampen population oscillations. However, empirical data suggest that this is not the case (Shaw *et al.* 2004, Cattadori *et al.* 2005) and the reason for the absence of a dampening effect remains unclear. It seems surprising and counterintuitive that shooting has no effect on population dynamics of red grouse because a large proportion of the population is harvested every year, sometimes up to 50% (Hudson 1985, 1986). Moreover, Jonzén *et al.* (2003) showed in a modelling study that shooting creates rather than dampen cycles in willow grouse when stochasticity of the environment and uncertainty of the harvest rate itself are taken into account. Most studies on hunting selectivity compare different hunting strategies (Martinez *et al.* 2005, Mysterud *et al.* 2006) or harvested and non-harvested areas (Coltman *et al.* 2003) but are not able to compare the age and sex structure of the bag with the population before harvesting to assess susceptibility to shooting according to age, sex and density. Red grouse populations in the North of England provide an excellent system to study these mechanisms as they have been well studied regarding social interactions (territoriality) and age-related differences in parasite load effects on population dynamics, they are hunted, and can be closely monitored regarding their population structure. This allows to derive clear predictions based on their biology and to collect the appropriate data to test those predictions.

The territorial behaviour of red grouse is well studied and it has been demonstrated that old males begin to establish territories during the shooting season (Jenkins *et al.* 1967). Aggressiveness and territorial activity increase with population density (Moss *et al.* 1996) and young males are mostly excluded from the breeding population (Mougeot *et al.* 2003a,b). High aggressiveness and elevated testosterone levels produce two main effects in grouse: an increase in parasite intensity (Mougeot *et al.*

2006) and a decrease in recruitment of young grouse (Mougeot *et al.* 2005a,b). It is also well known that old grouse carry more parasites than young grouse (Mougeot *et al.* 2005a, Hudson *et al.* 1992) and that parasites reduce mobility, although this has only been demonstrated in willow grouse (Holmstad *et al.* 2006). Therefore at high grouse densities we predict that during driven shooting old males will return to their territories rather than flying over the line of hunters due to territoriality or high parasite load, both consequences of increased density and aggressiveness. In contrast, we expect that young males are more likely to cross the line of hunters at high grouse densities because they have not been able to secure a territory and do not suffer from high parasite loads (reduced mobility). Therefore, we predict that with increasing grouse numbers more young grouse are shot than expected from the counts. We also expect that shooting selectivity will become more biased towards females later in the season when males have invested heavily in territorial behaviour and may be more reluctant to leave their territory.

In this study we test the above predictions by comparing the age-sex ratios of birds shot at different points in the season with the population composition estimated from counts just prior to shooting.

## 4.3  Methods

### 4.3.1  Data collection

Data on shooting selectivity were collected in 2005 and 2006 between mid August and the end of September on nine moors in Northern England. All data come from driven grouse shooting days where beaters drive grouse in the direction of a line of hunters. A day of grouse shooting usually consists of 4-5 separate shooting locations (drives) and the data presented here reflect drives rather than shooting days. An individual drive is usually shot several times during the season, at intervals ranging from a few hours to several weeks. For a more detailed description on shooting grouse see Hudson (1986). Forty-five drives were attended, and the total number of shot grouse, broken down by age and sex, was determined for each drive (Table 4.1).

The length of the drive was calculated using GIS (MapInfo Professional v8.0, MapInfo Corporation, New York, USA). This was based on the estimated drive area drawn on a map by the head keeper of the estate, who organised the drive and located the beaters. Drive length was consistent for particular drives on different days and in both years because it is mainly determined by landscape features (e.g. rivers, valleys). The number of beaters involved in each drive was also noted.

To compare the age- and sex-ratios of shot birds with the age and sex ratio of the population before shooting, counts were conducted in July 2005 and 2006 in the same areas where shooting data were collected. For all 45 drives visited during the shooting season the age structure was known but only for 33 drives the sex-ratio of the old birds was available. The counts were part of the long term data collection conducted by the Game and Wildlife Conservation Trust to determine the ratio of old birds to young of the year and the sex ratio of the old birds (Figure 4.1, Hudson and Newborn 1995). For a subset of 30 drives, grouse density was estimated using standard methods of 1 km$^2$ block counts (Jenkins *et al.* 1963, Mougeot *et al.* 2005b, Redpath *et al.* 2006a) and distance sampling. The density estimates from distance sampling were taken from Warren (2006) following the method by Buckland *et al.* 1993).
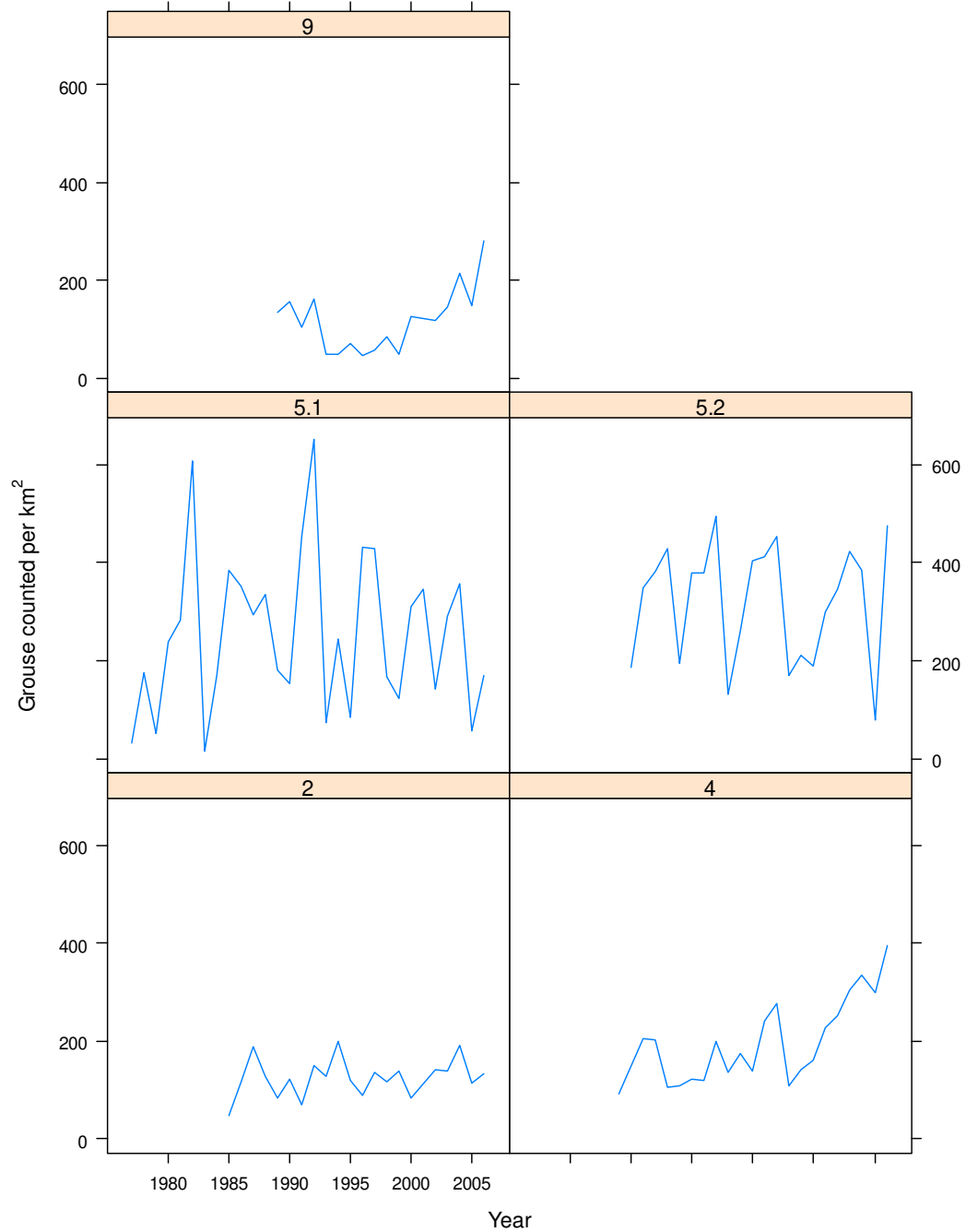
Figure 4.1: Time series of July counts standardised as grouse counted per 1 km$^2$, for areas where counts are available for more than the years of 2005 and 2006 when the detailed study was conducted. The number above the panel relate to the moors in Table 4.1. Moor 5 has two different areas as indicated by 5.1 and 5.2.

### 4.3.2  Statistical analysis

All analysis was carried out using R (R Development Core Team 2007). Separate linear mixed effects models (lme, package nlme ver. 3.1-79, Pinheiro and Bates 2000) were fitted to the response variables 'number of grouse shot', 'relative young-to-old ratio' and 'relative sex-ratio'. The 'number of grouse shot' was determined as all grouse in the bag from a single drive rather than from the whole day of shooting. To obtain the relative ratios, the sex- and age-ratio of the bag was divided by the sex- and age-ratio of the July count. The July counts and bag data derive from the same areas. The number of grouse shot and all ratios were log transformed. The models were fitted with a constant intercept and nested random terms. Data were collected over two years (2005 and 2006) but only two moors were nested in both years (Table 4.1), therefore moor and drive within moor were inserted as random effects but year could not be included in the analysis. Wald tests were used to test the significance of fixed effects (Pinheiro and Bates 2000). The explanatory variables were the number of beaters per square kilometre, the length of the drive, the total number of grouse shot, a code indicating whether the data came from the first, second or the third/fourth shooting event (the third and fourth events were pooled together because of small sample sizes). Orthogonal contrasts were designed to compare first, second and third category of shooting event. This model structure, nesting drive within moor, and analysing each shooting event separately within drive, enables us to correctly represent the non-independent nature of shooting events.

Table 4.1: The nested structure of the data is shown: sample size (n=number of shooting events) is broken down by moors, drives within moors and the year when the data were collected. Drives can be shot more than once a year and therefore the number of drives is not equal to the sum of the number of shooting events in both years.

| moor | drives | 2005 (n) | 2006 (n) |
|-------|--------|----------|----------|
| 1 | 3 | - | 3 |
| 2 | 1 | 1 | - |
| 3 | 2 | 2 | - |
| 4 | 3 | - | 3 |
| 5 | 1 | 2 | 1 |
| 6 | 2 | - | 5 |
| 7 | 5 | - | 11 |
| 8 | 7 | 9 | - |
| 9 | 2 | 2 | 6 |
| Total | 26 | 16 | 29 |

A variance components analysis of the mixed effects models described above was carried out (Pinheiro and Bates 2000, Crawley 2007) in order to estimate the variation explained by the nesting factors moor and drive within moor. Variance components analysis is a useful tool to decompose the total variation into different spatial scales (Börger *et al.* 2006a,b; Sims *et al.* 2006).

## 4.4   Results

### 4.4.1   *Correlation of bag numbers with population size*

The number of grouse shot in a single drive was correlated with the grouse density estimated in July (Fig 4.2). The intercept depended on the shooting event, with the second shooting event having fewer grouse in the bag compared to the counts than the first shooting event (Table 4.2). There was no significant interaction between July counts and shooting event, which suggests that bag data provide a consistent estimate of density over the shooting season. The model including July density as

explanatory variable explained with 88% a high proportion of the variation of the total number of grouse shot on a single shooting event (drive).
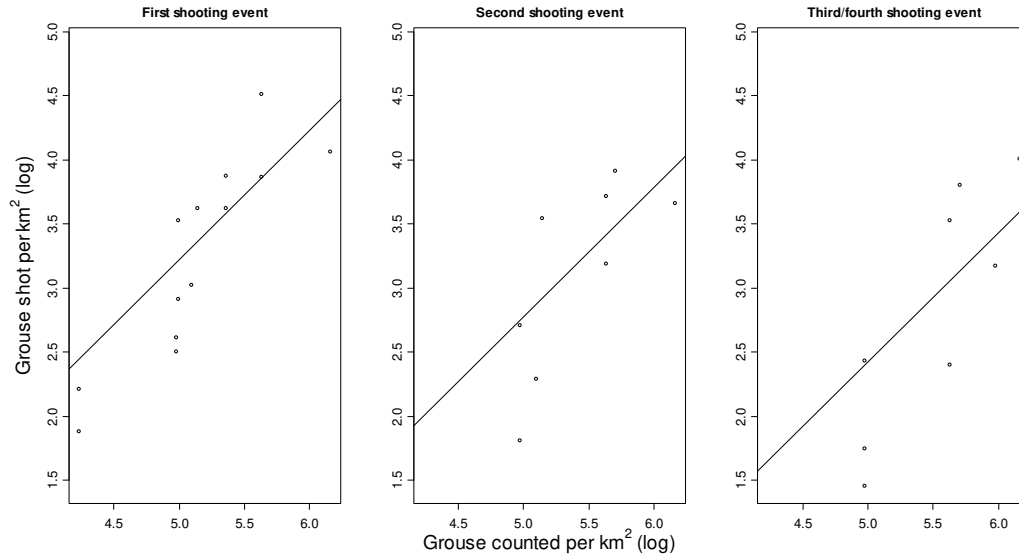


Figure 4.2: The relationship between the number of grouse shot in a single drive and the estimated population density (grouse km$^{-2}$) in July for the first, second and third/fourth shooting event. The slope is the same for shooting events one, two and three/four, but the intercept is significantly lower in the second shooting event compared to the first one (Table 4.2). There is an almost significant decrease in intercept from the second to the third/fourth shooting event.

Table 4.2: Fixed effects of the mixed effects model for number of grouse shot (on log scale) with drive nested within moor. The total number of grouse shot is explained by the shooting event (three levels) and grouse density estimated in July before the shooting season.

| Fixed effects | Estimate | S.E. | t-value (df=15) | p-value |
|---|---|---|---|---|
| Intercept (1$^{st}$ shooting event) | -1.50 | 1.48 | -1.02 | 0.3 |
| Second shooting event | -0.46 | 0.18 | -2.55 | 0.02 |
| Third/fourth shooting event | -0.80 | 0.19 | -4.11 | <0.001 |
| July count (log) | 0.999 | 0.28 | 3.56 | 0.003 |

*4.4.2 Age ratio*

The relative age ratio increased with the total number of grouse shot per drive (t=2.2, df=20, p<0.04), so with increasing numbers of grouse shot, relatively more young grouse were found in the bag (Fig 4.2). There was no influence of how many times the area was shot ($F_{2,15}$=0.03, p=0.9), the number of beaters per square kilometre ($F_{1,15}$=0.1, p=0.7) or the length of the drive ($F_{1,15}$=0.8, p=0.4) on the relative age ratio. The final model represented a good fit to the relative age ratio data with 31% of the variation explained.
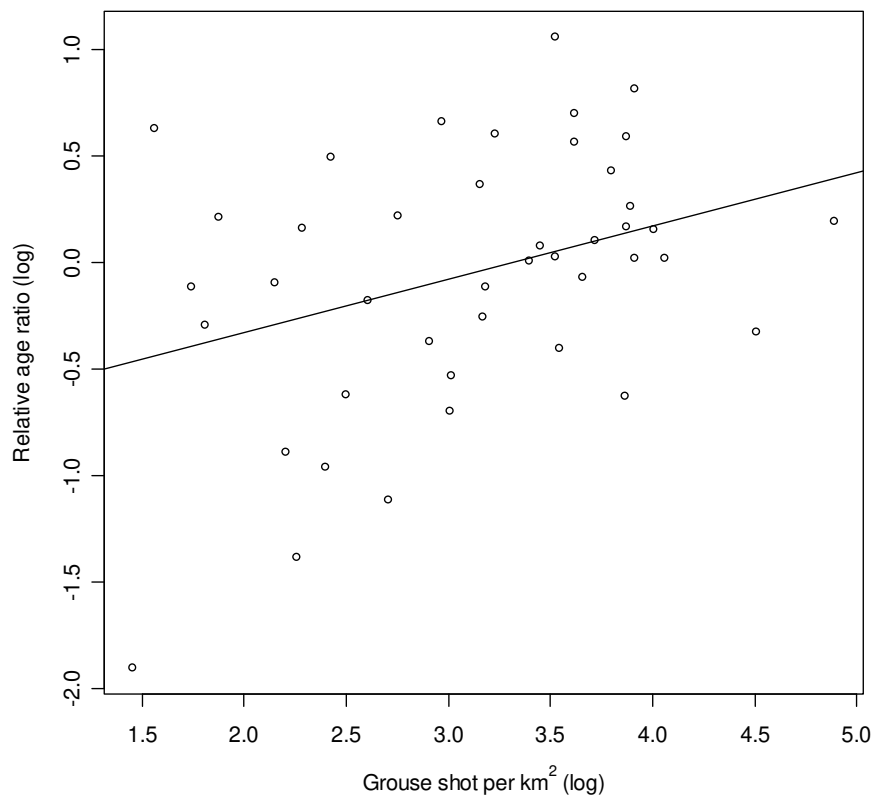
Figure 4.3: The young-to-old ratio of the bag divided by the July count (log transformed) for different bag sizes. A log bag/count ratio>0 for young/old means a higher proportion of young birds were shot than occurred in the population before shooting.

### 4.4.3   Sex ratio

The sex ratio analysis was only applied to old grouse because of the difficulty of sexing young grouse during counts in July. The number of beaters per square kilometre ($F_{1,10}$=0.5, p=0.5), the length of the drive ($F_{1,10}$=2.3, p=0.2) and the year ($F_{1,10}$=0.8, p=0.4) had no significant effect on the relative sex ratio. Old females showed a decreasing susceptibility to shooting with increasing bag size (t=2.5, df=15, p=0.03; Fig 4.4). A competing model substituting bag size with the number of shooting events showed that relatively more females were shot the third/fourth time an area was shot than at the first time (t=2.4, df=14, p=0.03; Fig 4.5). The final model with shooting event added explained 60% and with bag size added explained 68% of the variation of the relative sex ratio in the bag. The model with bag size as explanatory variable had a lower AIC than the shooting event model (Table 4.3).

Table 4.3: Log-likelihood, Akaike Information Criterion (AIC) and ΔAIC for general mixed effects models with (a) bag (Fig 4.4) and (b) shooting event (Fig 4.5) as explanatory variable and the log relative sex ratio as response variable. The model (a) would be preferable to model (b) because the log-likelihood and the AIC is lower.

| Model (explanatory variable) | Log-Likel. | AIC | ΔAIC |
|---|---|---|---|
| (a) Bag | -31.671 | 73.343 | 0 |
| (b) Shooting event | -31.999 | 75.998 | 2.66 |
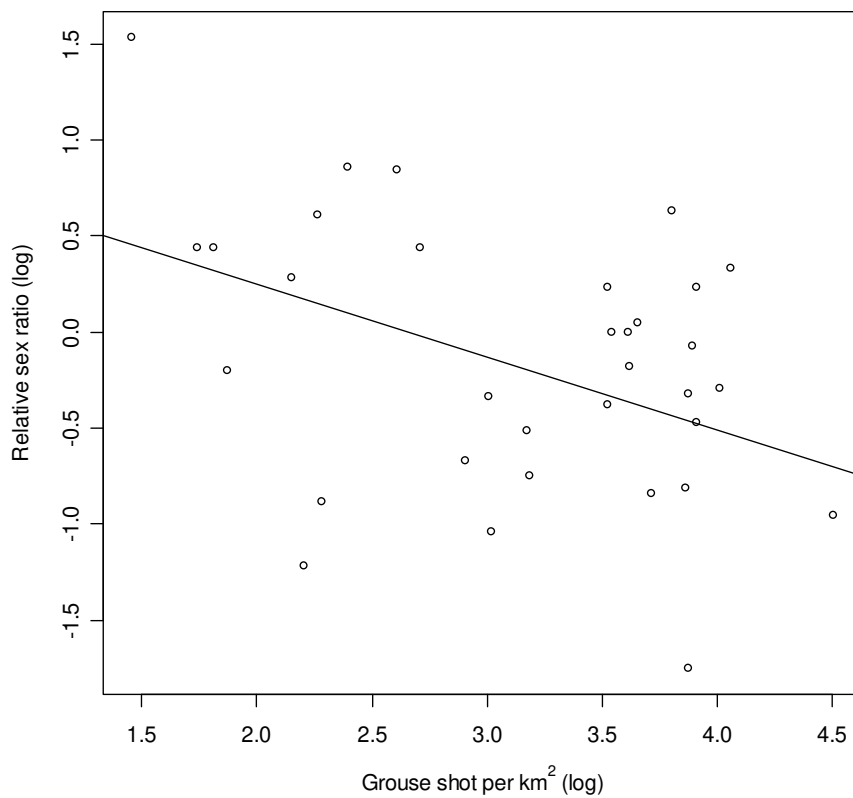
Figure 4.4: The female-to-male ratio of the bag divided by the July count (log transformed) for different bag sizes. A log bag/count ratio>0 for females/males means a higher proportion of females were shot than occurred in the population before shooting. The regression line was predicted from a mixed effect model.
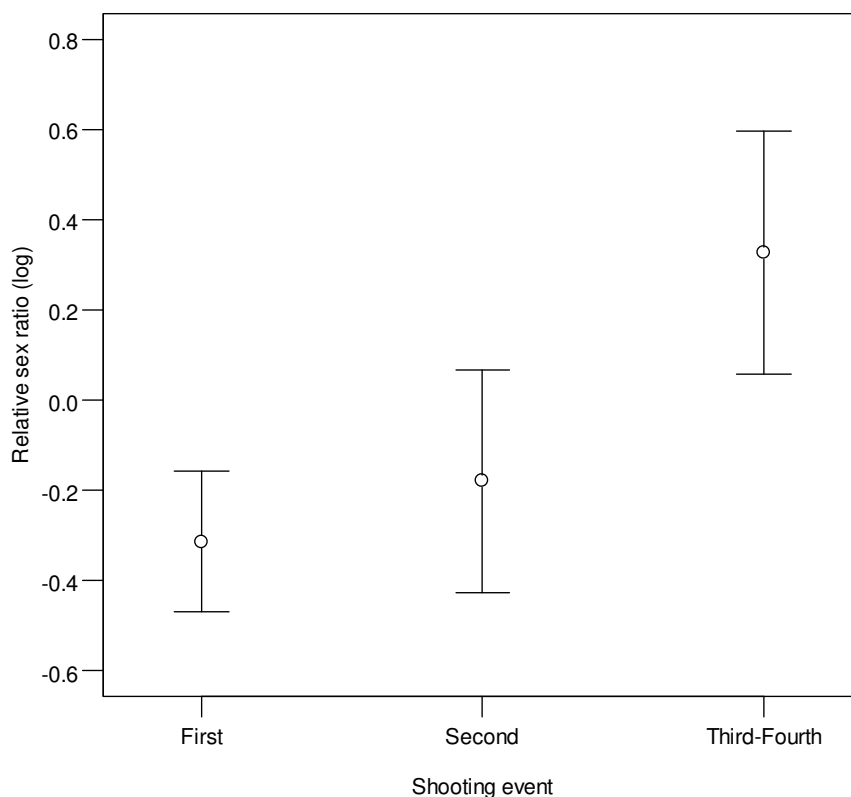
Figure 4.5: Predicted values from the mixed effects models are presented with ±1 standard error for the female-to-male ratio of the bag divided by the July count (log transformed) for different shooting events. A log bag/count ratio>0 for the female-to-male ratio means a higher proportion of females were shot than occurred in the population before shooting.

### 4.4.4 Variance components analysis

Differences between moors explained between 28% and 9% of the total variance explained in the number of grouse shot, whereas drive within moor explained between 16% and 37% of the total variance (Table 4.4). Both random effects (moor and drive) were less important in the analysis of relative age ratio; they only explained 23% and 5% of the variance respectively. With the number of grouse shot inserted as fixed effect, moor (12%) explained little of the variance and drive no measurable proportion (Table 4.4). For the analysis of relative sex ratio the random effect of moor had no measurable effect on the variance component and drive within

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moor explained 37%. Adding the shooting event to the model as fixed effect changed the variation explained to 29% whereas adding the bag size changed the variation explained to 42% (Table 4.4).

Table 4.4: The percentage of total variance explained by the nesting factors moor and drive within moor for models with response variable total number of grouse shot (bag), relative age ratio (age) and relative sex ratio (sex). Model A contains only random effects, model B also fixed effects. For the sex ratio model one model with shooting event and a second one with bag size as explanatory variable is given in brackets.

| | *Variance components (%)* | | | | | |
|---|---|---|---|---|---|---|
| | Moor | | Drive/moor | | Residual variance | |
| | A | B | A | B | A | B |
| Bag | 28 | 9 | 16 | 37 | 56 | 54 |
| Age | 23 | 12 | 5 | - | 72 | 88 |
| Sex | - | - (-) | 37 | 29 (42) | 63 | 71 (58) |

## 4.5 Discussion

The study showed that susceptibility of old grouse to shooting decreased with bag size, which is in agreement with our first hypothesis. At high bag numbers the relative young-old-ratio was above zero indicating that more young grouse were shot than expected from the counts before shooting. Our second hypothesis that among old grouse the males are shot early in the season and that the proportion of old males declines as the shooting season progresses could be verified. A second possible model showed that old males relative to old females decrease in their susceptibility to shooting with bag size. Males come through as singletons while females tend to come through in groups and single birds are more likely to be shot (Hudson 1986). It could be hypothesised that old males establish territories earlier than young males that still follow family groups (Hudson 1986) and this might be more pronounced at high densities when aggressiveness and territorial behaviour is high (Moss *et al.* 1996). At high densities old males are expected to be more motivated to separate

from families groups to establish territories. This might explain the finding that old birds are less likely to be shot at high densities. Furthermore, the few males that pass the line of guns, do so as singletons and are therefore more susceptible to shooting than old females particularly at high density when territorial behaviour is likely to be more important. However, this should not be confused with the finding that old birds in general are less susceptible to shooting at high density. High off-takes of old males and increased territorial behaviour might explain the low proportion of old males and the higher proportion of females in the bag later in the shooting season. Detailed observations of marked animals during the shooting events are required to clarify behavioural mechanisms behind the observed results.

Cattadori *et al.* (2003) showed that total bag numbers for a whole moor for one season correlate well with actual population numbers. This trend was also shown on a smaller scale for the current data set where the number of grouse shot in a single shooting event (drive) correlated consistently with grouse numbers obtained by counts in the same area before shooting (Fig 4.2).

The results of this study encourage further hypotheses regarding the effects of shooting on red grouse population fluctuations. The study showed that at high bag numbers, used as a proxy for population density, young grouse are more susceptible to shooting than old grouse. Consequently, shooting can bias the population structure towards old males when population density is high. Given that old grouse harbour more parasites (Hudson *et al.* 1998), that parasites are accumulated at high grouse densities, that parasites reduce over winter survival (Hudson *et al.* 1992, Moss *et al.* 1993) and can generate population fluctuations, shooting might therefore add to population crashes by leaving old, highly parasitized birds in the population at peak density. Thus shooting might be a factor in creating rather than dampening red grouse cycles. Theoretically, in a highly fluctuating species with high off-takes like red grouse, harvesting might be expected to dampen cycles. Hudson and Dobson (2001), however, found that harvesting apparently did not dampen cycles, and our findings may now provide an explanation for this contrast between theory and

empirical data. Indeed, that harvesting can create cycles has been shown also in an empirical study on moose (*Alces alces*). The mean age of adult females increased because of selective harvest of young moose. This led to an increase in productivity, which is closely related to age in moose. The mean age then decreased after years of high recruitment, and so productivity dropped, thus generating cycles (Solberg *et al.* 1999).

It could be hypothesised that the age composition of the bag would not be expected to reflect the composition of the population at the July count due to differential mortality rates of young and old grouse between the time of counting and the shooting season. However, the time period between counts (throughout July) and the data collection (mid August-end of September) was short and mortality in red grouse during this period has been shown to be low for both young and old birds (Hudson *et al.* 1997).

This study applied mixed effects models to the data to investigate the variation of spatial scale on the shooting data. The analysis of count and bag data showed considerable variation at the moor and drive level. Much of the observed variation might be due to the hunter quality with significant more grouse shot at a given density than with inexperienced hunters. Less variation due to moor and drive was found when fitting mixed effects models to the relative age and sex ratio. This indicates that the smallest scale possible (individual drives) was appropriate for the analysis. Ratio of young-to-old and female-to-male ratio where collected from counts in the same areas as the shooting took place and this allowed for a direct comparison of the structure of the population with the age- and sex-ratio of the bag.

The ratio of juveniles to adults in the bag is a common and cost-effective method for estimating productivity in a given year. Flanders-Wanner *et al.* (2004) found no trend in age ratio with time in the shooting season in a study on sharp-tailed grouse (*Tympanuchus phasianellus jamesi*) and greater prairie chicken (*T. cupido pinnatus)*, validating the use of the age-ratio method. However, Hörnell-Willebrand *et al.*

(2006) showed that this method is not useful for willow grouse in Sweden and Norway, because the proportion of juveniles is underestimated in the bag. This study on red grouse demonstrates differences between the age-ratio in the count and in the bag, an interaction with density, and an increase within the shooting season of the ratio of old females in the bag. Therefore, harvest data need to be treated with great caution as a proxy for the underlying population structure. Age ratios obtained from harvest data need to be checked against count data collected prior to the harvesting season at a range of population densities before considering them as proxies for population productivity.

# Chapter 5

# An age- and sex-structured population model for red grouse: Model exploration

## 5.1 Abstract

Animal populations face increasing pressure from human exploitation and modelling has been a useful tool to understand and predict population dynamics of harvested species. In this chapter an age- and sex-structured population model for red grouse is constructed incorporating aggressiveness, parasites and harvesting. Sensitivity analysis of the model showed that the simulated population is in line with field observations under a range of parameter values. Mean, minimum and maximum population size as well as cycle length are comparable to studies carried out on natural populations. Furthermore, the sensitivity analysis showed that the model outcome is most sensitive to the function that describes the parasite accumulation in relation to grouse density. This model lays the foundation for the next chapter where the effect of harvesting selectivity on population dynamics is explored.

## 5.2 Introduction

Modelling has proved useful when aiming to understand and predict population fluctuations under the influence of harvesting (Lande *et al.* 1997, Jonzén *et al.* 2002, Lande *et al.* 2003). Different harvesting methods, their advantages and limitations have been explored using simulation modelling. Traditionally, fixed-quota harvesting, where a constant number of individuals is removed, has been used for many populations, especially in fisheries (e.g. Rosenberg *et al.* 1993). However, this method has been shown to increase the risk of population collapse (Lande *et al.* 1995, Fryxell *et al.* 2005). Proportional and threshold harvesting have been suggested (Lande *et al.* 1995, 1997) to account for variation in the population, but both strategies come at the cost of monitoring populations reliably (Hauser 2006b) and informatively (Katzner *et al.* 2006). Even under the best efforts, uncertainty is still introduced by stochasticity in the environment and in the harvest rate itself. These processes have been shown to influence fluctuating populations under human pressure, especially when harvesting rates are high and variable (Mangel 2000, Jonzén *et al.* 2002).

Climatic events have been shown to synchronise population fluctuations on a large-scale (Grenfell *et al.* 1998, Post and Forchhammer 2002, Jenouvrier 2005). Stochastic weather may have particularly pronounced effects for populations that are influenced by interactions between climate and parasites; the survival and availability of infective stages depends on a favourable climate if the parasite cycle includes free-living phases (Anderson 2000). Strong seasonal variation in temperature and rainfall may further amplify the influence of parasite-climate interactions on population dynamics (Altizer *et al.* 2006, Stone *et al.* 2007). This study uses red grouse to explore the dynamics of a system that is under heavy anthropogenic harvest pressure, monitored regularly and where both stochastic weather and parasites have been shown to significantly influence population fluctuations (Hudson *et al.* 1992, Moss *et al.* 1993, Cattadori *et al.* 2005).

Red grouse modelling efforts have concentrated on parasite-host models and more recently on territorial and aggressiveness models to understand the factors creating cycles in red grouse populations. The parasitic nematode *T. tenuis* affects survival and breeding success of red grouse (Hudson *et al.* 1998) and the model by Dobson and Hudson (1992) extended the general host-parasite model developed by Anderson and May (1978) and May and Anderson (1978). Dobson and Hudson (1992) showed that parasites are an important factor in red grouse cycles and this was also observed in a later field experiment (Hudson *et al.* 1998).

Empirical studies have shown that aggressive behaviour plays a role in red grouse cycles. This has been supported by field experiments (Moss *et al.* 1996, Mougeot *et al.* 2003a,b, 2005a,b) and by theoretical modelling (Matthiopoulos *et al.* 1998, 2000, 2002, 2003). In an age-structured model, Matthiopoulos *et al.* (2003, 2005) created interactions between aggressiveness and density and found that an abrupt transition from tolerant to intolerant behaviour was needed to create cycles. These models are based on density dependent aggressiveness of old males towards young males and lead to exclusion from next year's breeding population.

Harvesting has not been included explicitly in the aggressiveness and parasite-host models mentioned above, even though harvesting influences population dynamics and introduces a significant degree of uncertainty (Milner-Gulland *et al.* 2001, Milner-Gulland *et al.* 2004). This is surprising given that up to 50% of the population is harvested every year (Hudson 1985, 1986). To my best knowledge, only two theoretical studies on red grouse have taken harvesting into account. Potts *et al.* (1984) showed that a harvesting model captured the dynamics of the red grouse population when stochasticity was added to the fecundity rate and to the rate at which parasites where accumulated. However, density dependent effects were related to bag numbers, not to actual grouse numbers. This approach has led to criticism because of the error introduced by overestimating the variance of the actual population size when using harvest data (Lambin *et al.* 1999). In a second harvesting model, Hudson and Dobson (2001) used the Hassell equation (Hassell 1975, Hassell

*et al.* 1976) and reduced the survival rate by the harvesting rate to show that theoretically harvesting should dampen the oscillations in red grouse populations. However, the effects of aggressiveness and parasites and their interaction with harvesting were not included in this model.

Understanding the population fluctuations of red grouse is a multi-dimensional task where density dependent effects, such as parasites and aggressiveness, but also density independent effects, such as stochastic weather variables, play an important role in a harvested population. This chapter aims to develop and test a deterministic age- and sex-structured model of the population dynamics of red grouse incorporating parasites, age- and density-related aggressiveness and harvesting and to extend this to a stochastic model. The next chapter will then test the effect of age- and sex-related susceptibility to harvesting under uncertainty.

## 5.3  Methods

Red grouse population dynamics are modelled with an age- and sex-structured model in discrete time to reflect the seasonality of events (Matthiopoulos *et al.* 2003). The demography of the model reflects current knowledge of grouse age structure where the population consists mostly of young grouse (< 1 year), 2-year-old grouse and 3-year-old grouse (chapter 2). The dynamics were modelled in three time steps identified to be important for grouse (Fig 5.1b).
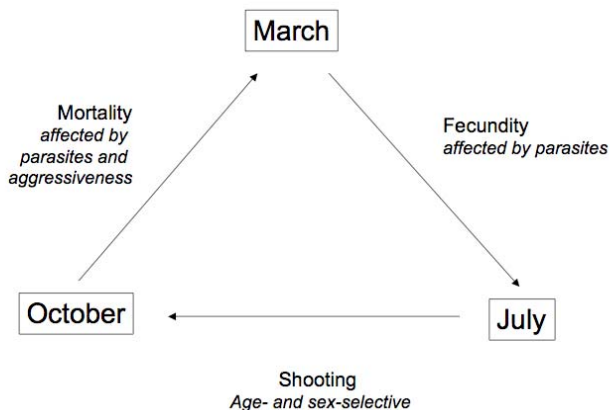
Figure 5.1a: Overview of the seasonality of the red grouse model
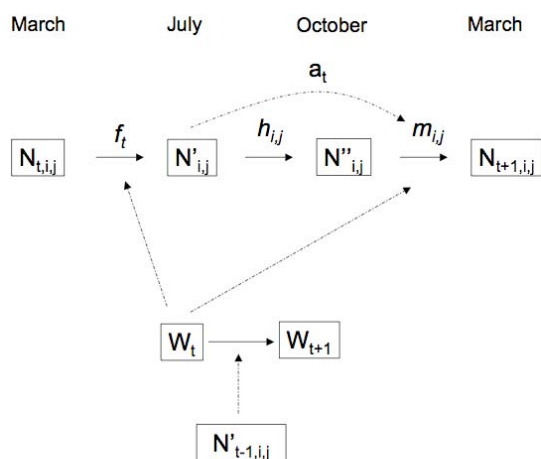


Figure 5.1b: Representation of the red grouse model. The subscripts $i,j$ represent the age and sex classes respectively with 3 age classes (1-year-old, 2-year-old and 3 years and older) and males and females in each sex class. The parameters $f, h, m$ describe the fecundity, harvest rate and over-winter mortality respectively in a given year $t$. Aggressiveness $a$ depends on the number of grouse in July $N'_t$ and affects the mortality of young grouse of the year. Parasites $W$ depend on the population size in the preceding July $N'_{t-1}$ and affect fecundity of all ages and survival of old grouse (2 years and more).

### 5.3.1 *Parasites and grouse density*

Moss *et al.* (1993) and Hudson *et al.* (1992) agreed that grouse densities have a significant influence on the *T. tenuis* parasite intensities in the following year but both studies point out that weather explains a significant part of the year-to-year variation in parasite intensity. *T. tenuis* has a simple life cycle with no intermediate host and free-living larval stages that depend on favourable climatic condition to develop (Shaw *et al.* 1989). Rainfall in the preceding July (Moss *et al.* 1993) and preceding minimum July temperature (Hudson *et al.* 1992) explains a considerable amount of variation in spring and autumn parasite intensities respectively. Cattadori *et al.* (2005) show that climate interacts with parasites in red grouse and thereby synchronizes population fluctuations in areas subject to similar climatic conditions. In this model the worm burden of grouse in year *t* depends on the grouse population density in year *t-1* according to the following equation:

$$w_t = pN'_{t-1} + c \tag{5.1}$$

where $w_t$ is the number of worms in year *t* depending on the population in the preceding July $N'_{t-1}$ and two constants *p* and *c*. The equation is estimated from a regression by Hudson *et al.* (1992) whereby the data points were extracted from the publication and a regression line was fitted and the estimates extracted.

The model was first run without stochastic weather effects and then stochasticity was added to the values of *p* and *c* to reflect the effect of weather on parasite accumulation due to grouse density. Stochasticity was added as a normal distribution around *p* and *c*.

### 5.3.2 *Fecundity*

The most frequently used fecundity measure in field studies is July young-old ratio (Newborn and Foster 2002, Hudson *et al.* 1992, Redpath *et al.* 2006a); hence this is used as an output measure in the model. Parasite burdens in early spring (March)

have been shown to affect fecundity in a number of studies (e.g. Hudson *et al.* 1992, Moss *et al.* 1993, Newborn and Foster 2002). Fecundity $f_t$ in the model depends on the worm burden $w$ in a given year $t$ and two constants $s$ and $u$ (Hudson *et al.* 1992).

$$f_t = e^{(sw_t + u)} \tag{5.2}$$

The population size in spring $N_t$ multiplied by the fecundity $f_t$ produces the young of the year $t$, which are added to $N_t$ to get the July population $N'_t$.

$$N'_{t,i,j} = N_{t,i,j} + f_t N_{t,i,j} \tag{5.3}$$

### 5.3.3   Shooting mortality

The main shooting season for grouse ranges from mid August until mid October (Hudson and Newborn 1995). After mid October, most of the grouse shooting has stopped and between then and March the following year grouse are subjected to winter mortality (Hudson *et al.* 1992). Shooting mortality in the model is fixed and added as proportional mortality.

$$N''_{t,i,j} = N'_{t,i,j}(1 - h) \tag{5.4}$$

where $N'_{t,i,j}$ is the population size in July of age $i$ and sex $j$; and $h$ is the harvest rate.

### 5.3.4   Parasite-related mortality

Parasites have been shown to affect over-winter survival of grouse, with the proportion of grouse dying dependent on parasite intensity (Hudson *et al.* 1992). Parasite burdens in a grouse population show a negative binomial distribution (chapter 2). Given the mean parasite burden $w$ from equation (5.1), the distribution is simulated as follows:

$$v_{t,i} = nbinom(N''_{t,i}, w_t, k_i)$$ (5.5)

where $v$ is a vector of parasite intensity for 2-year-old and 3+-old grouse with size $N''_{t,i}$ after shooting, drawn from the negative binomial distribution of worms among grouse $N''_{t,i}$ with mean worm burden $w_t$ and inverse aggregation parameter $k_i$. The parameter $k_i$ differs between age classes $i$ (chapter 2, Table 5.1).

Parasite-induced mortality for two- and three-year-old grouse was modelled such that the mortality is the proportion of grouse harbouring more parasites than the threshold parasite load.

$$m_{2+,t,i} = \frac{\sum_{N''_{t,i}} z_{t,i}}{N''_{t,i}} \qquad z = \begin{cases} 1 & if \quad v > w_{max} \\ 0 & otherwise \end{cases}$$ (5.6)

where $m_{2+,t,i}$ is the mortality rate of two-year-old grouse and 3+-year-old grouse as the fraction of the total grouse in the specific age group carrying more parasites than a certain threshold $w_{max}$.

### 5.3.5 Exclusion by aggressiveness

It has also been shown that territoriality and parasite-induced mortality interact such that aggressiveness increases with high grouse density in the same year and that this increases parasite burdens next year (Mougeot *et al.* 2005a,b, 2006). Young grouse (<1 year-old) seldom die from parasites but are instead excluded from breeding by older males through aggressiveness (Matthiopoulos *et al.* 2003, Mougeot *et al.* 2003a). Aggressiveness affects the recruitment of both males and females (Mougeot *et al.* 2005a, Moss *et al.* 1996). For the simplicity of the model testosterone-driven aggressiveness was not modelled directly. Matthiopoulos *et al.* (2005) showed that abrupt transition between tolerance and aggression is needed to drive red grouse population cycles. Thus, density-dependent aggressiveness towards young grouse

(<1-year-old) is introduced as a threshold grouse density $e$ above which young grouse of both sexes have a lower survival rate $r$.

$$m_{1,t,i} = \begin{cases} r & if \quad N'_{t,i} > e \\ 1 & otherwise \end{cases} \qquad (5.7)$$

where $m_{1,t,i}$ is the survival rate of one-year-old grouse if grouse density $N'_{t,i}$ in July is above a threshold $e$. This is assumed to represent permanent exclusion from breeding through mortality or dispersal to other areas. The exclusion parameter is directly density dependent. Thus the delayed density dependence of the parasites in the model is needed to create cycles.

Table 5.1: Parameters used for the base case model. The units for *max density exclusion* is population size $N'_t$ in July and for the *mortality threshold parasites* the unit is worms per bird. All other parameters are unitless.

| Parameter | Symbol | Value | Source | Permutation for sensitivity analysis |
|---|---|---|---|---|
| Harvest rate | h | 0.3 | Hudson 1985, 1986 | - |
| Slope (fecundity) | s | -0.41 | Hudson *et al.* 1992 | -0.31- (-0.51) |
| Intercept (fecundity) | u | 2.32 | Hudson *et al.* 1992 | 2.12-2.52 |
| Slope (parasites) | p | 10.85 | Hudson *et al.* 1992 | 2-15 |
| Intercept (parasites) | c | -149.05 | Hudson *et al.* 1992 | -100-(-200) |
| Mortality threshold, | wmax | 5000 | Hudson *et al.* | 3000-7000 |

| | | | | |
|---|---|---|---|---|
| parasites | | | 1992 | |
| Parasite aggregation 2-y-old grouse | k2 | 0.5 | Chapter 2 | 0.2-6.0 |
| Parasite aggregation 3+-y-old grouse | k3 | 2.0 | Chapter 2 | 0.2-6.0 |
| Max density exclusion | e | 150 | Moss *et al.* 1996, Mougeot *et al.* 2005b | 120-180 |
| Exclusion proportion | r | 0.6 | Moss *et al.* 1996, Mougeot *et al.* 2005b | 0.4-0.8 |

### 5.3.6   *Sensitivity Analysis*

Sensitivity analysis is a useful tool for model understanding, verifying parameters and exploring uncertainty. Especially when there is a clear conservation or management aim, sensitivity analysis can inform decision making (Milner-Gulland and Rowcliffe 2007).

The sensitivity analysis involved model perturbations by varying all key parameters of the model simultaneously within the observed range from the literature and from this study (Table 1). Values were generated from a uniform normal distribution. In non-cyclic species, equilibrium population size (Nilsen *et al.* 2007) and population growth rate (Katzner *et al.* 2006) are often used to estimate the influence of perturbations on the model outcome. However, for a cyclic species (e.g. voles) the cycle length and maximum population size are more informative (Ylönen *et al.* 2003). For this study, the cycle length, mean population size and maximum and minimum population size were used to test the effect of parameter perturbations on the population model. The cycle length is an important measurement for red grouse management because longer cycles mean fewer population crashes and fewer years

of economic loss. Driven grouse shooting only takes place in years when population size is above a threshold, usually of 30 birds km$^{-2}$ (Hudson *et al.* 1998). Therefore, minimum population size is a valuable outcome of the model. The maximum population size and mean population size determine the income generated from grouse shooting and therefore are interesting measurements that inform landowners about the outcome of different management options. One hundred sets of parameters values were generated and the model was run for 100 years; model output was included in the analysis after transients (20 years). Cycle length, mean population size and minimum and maximum population size were determined for 80 years in each run. Each perturbed parameter value was then log transformed to account for non-linearity and individually plotted against the outcome metrics of the population model to check for linearity (McCarthy *et al.* 1995). Regression models were fitted to the data. These were scaled to have a mean of zero and a standard deviation of unity (Saltelli *et al.* 2000). This technique gives unit-less coefficients and gives information on the relative importance of parameters (Fieberg and Jenkins 2005)

### 5.3.7  Spectral analysis and cycle length

The time series generated by the model was assessed with an Ljung-Box test (Ljung and Box 1978) to test whether the cycles were distinguishable from white noise. A spectral analysis was conducted to estimate the frequency of the cycles (Haydon *et al.* 2002, Matthiopoulos *et al.* 2003). Spectral analysis was bounded between 2 and 15 years (Haydon *et al.* 2002).

## 5.4  Results

### 5.4.1  Model outcome

The baseline age and sex structured population model for red grouse shows fluctuations that are significantly distinguishable from white noise (Fig 5.2, $\chi^2$=10.74, df=1, p=0.001) and a clear age structure in the population; 1-year-old grouse are most abundant, followed by 2-year-old grouse and lowest numbers for grouse three years and older. (Fig 5.3).
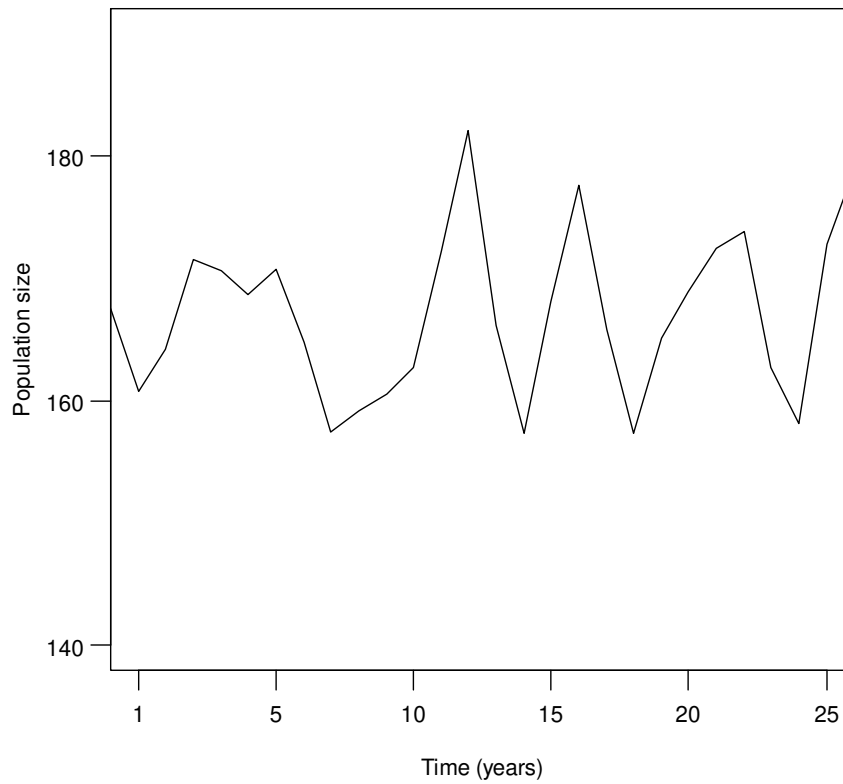
Figure 5.2: Population fluctuations of 1-year-old grouse, 2-year-old grouse and grouse of three years and older in a single run of the deterministic model, starting after transients have passed.
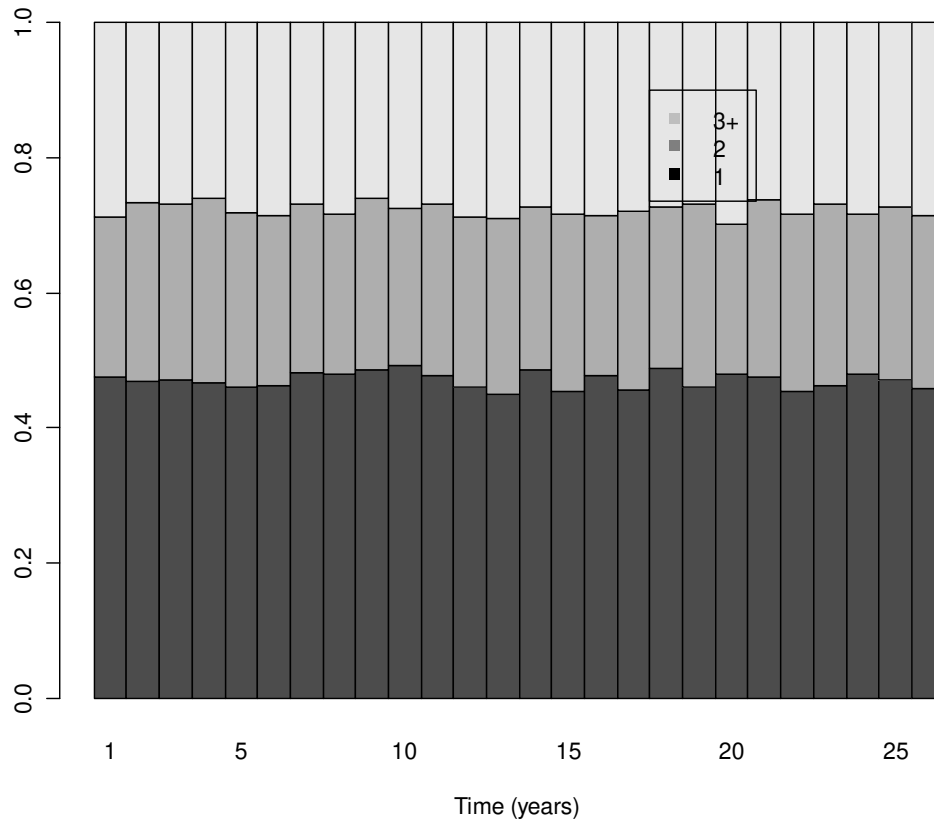
Figure 5.3: Age structure from a single run of the deterministic model, showing 1-year-old, 2-year-old and 3+-year-old grouse. The figure shows the proportion of grouse of different age classes in different years.

### 5.4.2   Sensitivity Analysis

The sensitivity analysis showed that the parameter with the most influence on the model outcome was the slope of the function describing the effect of grouse density on the accumulation of parasites (Table 5.2). The number of worms at which grouse mortality occurs ($w_{max}$) was also important for population size. The parameters linking fecundity to parasite intensity influenced the maximum and mean population size. Notably, the cycle length was robust to parameter variation. The cycle length shows a mean of 6 years for the deterministic model (Table 5.3). Grouse abundance (mean population size) in the model is 272 grouse per km$^2$. The mean fecundity rate is 2.4 young-of-the-year per old grouse or 4.8 chicks per hen.

Table 5.2: Sensitivity analysis was conducted for mean population size, cycle length, maximum population size and minimum populations size for a range of parameters. The standardized β are gained by scaled linear regression. All β>0.50 are given in bold. For parameter description see Table 5.1.

| Parameter | Description | Outcome | Deterministic model | |
|---|---|---|---|---|
| | | | β | p-value |
| wmax | Max parasites | Mean pop size | 0.2 | <0.001 |
| | | Cycle length | 0.04 | <0.001 |
| | | Max pop size | 0.21 | <0.001 |
| | | Min pop size | 0.26 | <0.001 |
| p | Slope parasites | Mean pop size | **-0.90** | **<0.001** |
| | | Cycle length | -0.23 | <0.001 |
| | | Max pop size | **-0.89** | **<0.001** |
| | | Min pop size | **-0.90** | **<0.001** |
| c | Intercept parasites | Mean pop size | 0.002 | 0.5 |
| | | Cycle length | 0.007 | 0.5 |
| | | Max pop size | 0.001 | 0.6 |
| | | Min pop size | 0.004 | 0.1 |
| s | Slope fecundity | Mean pop size | -0.11 | <0.001 |
| | | Cycle length | 0.07 | <0.001 |
| | | Max pop size | 0.12 | <0.001 |
| | | Min pop size | 0.10 | <0.001 |
| u | Intercept fecundity | Mean pop size | 0.07 | <0.001 |
| | | Cycle length | 0.02 | 0.09 |
| | | Max pop size | 0.08 | <0.001 |
| | | Min pop size | 0.06 | <0.001 |
| k2 | Aggregation age 2 | Mean pop size | -0.02 | <0.001 |
| | | Cycle length | -0.03 | <0.001 |
| | | Max pop size | -0.01 | <0.001 |
| | | Min pop size | -0.02 | <0.001 |
| k3 | Aggregation age 3 | Mean pop size | 0.05 | <0.001 |

| | | | | |
|---|---|---|---|---|
| | | Cycle length | -0.03 | 0.005 |
| | | Max pop size | -0.06 | 0.2 |
| | | Min pop size | 0.05 | <0.001 |
| e | Max density | Mean pop size | 0.02 | <0.001 |
| | | Cycle length | -0.02 | 0.1 |
| | | Max pop size | 0.02 | <0.001 |
| | | Min pop size | 0.02 | <0.001 |
| r | Exclusion proportion | Mean pop size | 0.30 | <0.001 |
| | | Cycle length | -0.3 | <0.001 |
| | | Max pop size | 0.31 | <0.001 |
| | | Min pop size | 0.27 | <0.001 |
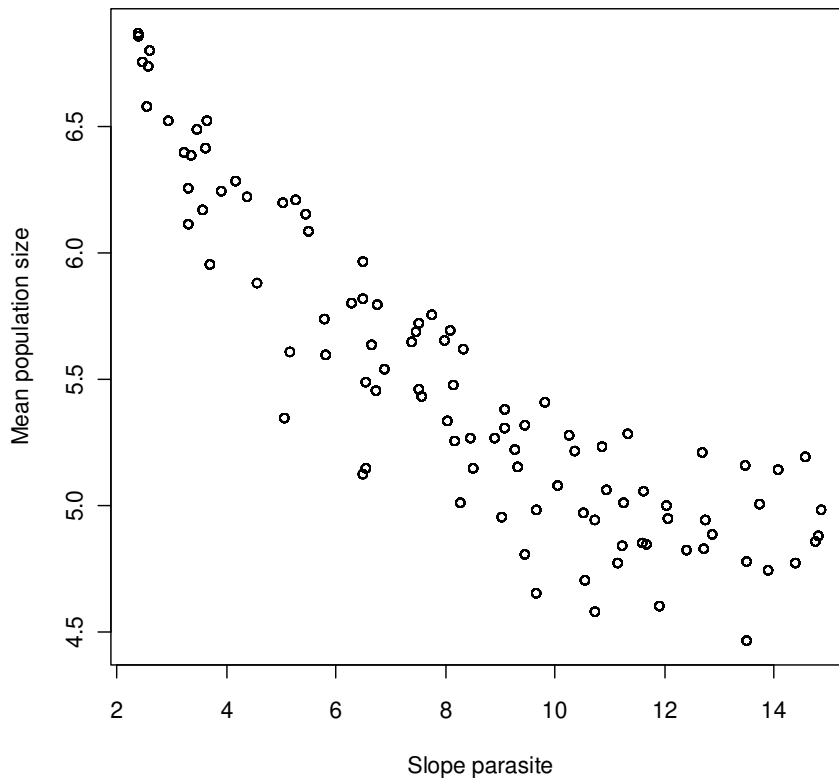
Figure 5.4: Sensitivity analysis of the deterministic model. The effect of perturbing the slope of the parasite accumulation function $p$ on the mean population size (log-transformed). The effects on minimum and maximum population size show the same pattern.

Table 5.3: Model outcome measured from the sensitivity analysis of the deterministic model, showing mean (range) of total grouse abundance km$^{-2}$, of one-, two- and 3+-year-old grouse and cycle length, young/old ratio in July and mean number of worms per bird. The unit of the reference to field studies depends on the available data and reports the mean, range or standard error (SE).

| Population measure | Deterministic model | Field studies | Source |
|---|---|---|---|
| Mean pop size | 272 (82-928) | Range: 17-252 | Redpath *et al.* 2006a |
| 1-year-old | 138 (36-546) | - | - |
| 2-year-old | 66 (20-238) | Breeding females | |
| 3+-year-old | 68 (12-288) | range: 20-70 | Dobson and Hudson 1992 |
| Cycle length (years) | 6 (3.5-13) | Mean: 6-7 | Watson and Moss 1979, |
| | | Range: 3-13 | Haydon *et al.* 2002, |
| | | Range: 5-10 | Dobson and Hudson 1992 |
| July young/old | 2.4 (1.5-3.6) | Mean: 2.2 | Newborn and Foster 2002 |
| | | Range: 0.9-3.4 | |
| No. worms | 3757 (2645-5358) | Mean: 3041 | Redpath *et al.* 2006a |
| | | SE: 2041 | |

### 5.4.3   Stochastic population model

The sensitivity analysis of the deterministic model showed that the slope that links parasite intensity to population density is the most influential parameter in the population model. Stochasticity added to this rate did not affect the cycle length or the mean population size, but the minimum and maximum population size reached more extreme numbers with an increasing degree of stochasticity (Table 5.4).

Table 5.4: The effect of the stochasticity added to the slope $p$ and intercept $c$ (eqn 5.1) is shown. The standard deviation for the intercept was held constant at sd=100 and the standard deviation for the slope was changed according to the value given in the table (SD). The mean (standard deviation) outcome of 100 runs is shown.

| SD | Cycle length | Mean pop size | Max pop size | Min pop size |
|---|---|---|---|---|
| 1 | 8 (2) | 167 (2) | 209 (10) | 132 (7) |
| 2 | 8 (2) | 170 (4) | 261 (27) | 112 (9) |
| 3 | 9 (2) | 174 (7) | 343 (61) | 88 (18) |
| 4 | 8 (2) | 180 (9) | 500 (172) | 45 (32) |
| 5 | 8 (2) | 180 (13) | 886 (570) | 19 (26) |
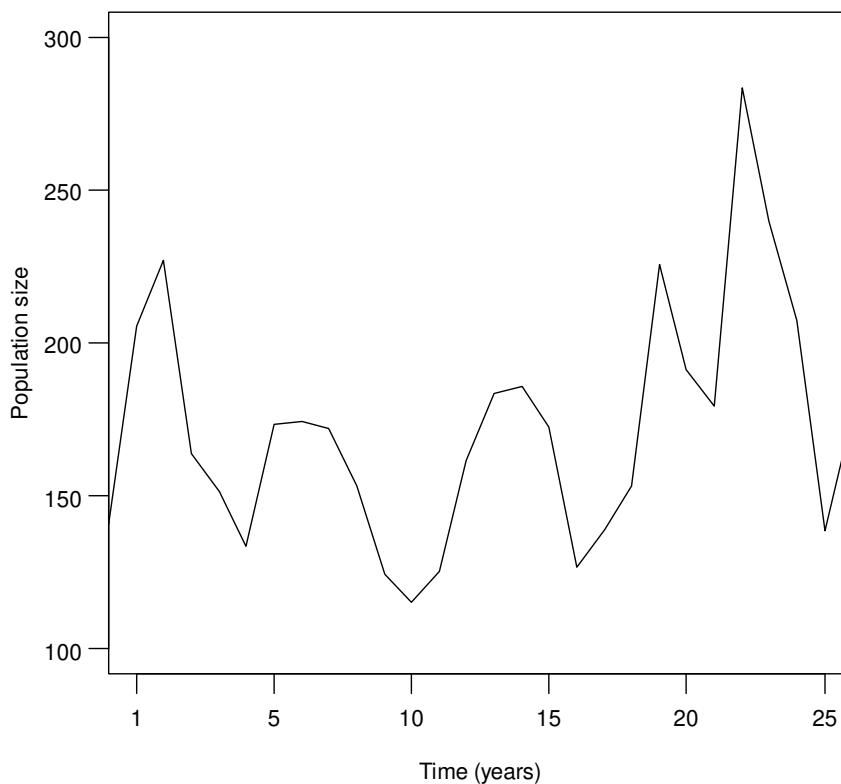


Figure 5.5: Population fluctuations of the total grouse population in a single run of the stochastic model, starting after transients have passed. Stochasticity is added to the slope $p$ (sd=2) and intercept $c$ (sd=100) from equation 5.1.
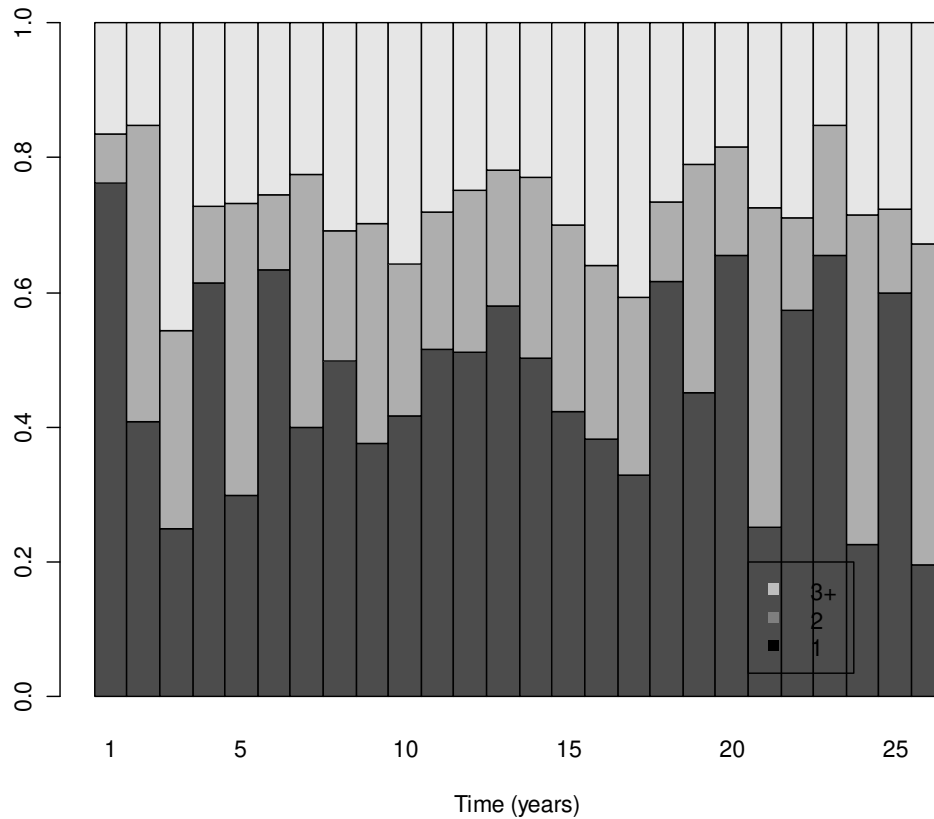
Figure 5.6: Age structure from a single run of the stochastic model, showing 1-year-old, 2-year-old and 3+-year-old grouse. The standard deviation for the slope $p$ and intercept $c$ is 3 and 100 respectively. The figure shows the proportion of grouse of different age classes in different years.

## 5.5  Discussion

The parameters of the model used here are based on data from a number of red grouse field studies. The outputs are within observed ranges. For example, the mean cycle length of 6 years (varying between 3 and 13 years as the parameters are varied) is close to empirical observations (6 years Watson and Moss 1979, 7 (3-13) years Haydon *et al.* 2002). Empirical data (Hudson *et al.* 1992) and modelling output (Dobson and Hudson 1992) found cycle lengths of about 5 years and this is in line with the model in this chapter. Grouse abundance, the young-to-old ratio in July and

the worm burden in the model are also in line with earlier field studies and the model output by Dobson and Hudson (1992). See Table 5.3 for details.

This chapter showed that the behaviour of the model is most sensitive to the slope of the relationship between grouse density and the worm burden of the population. The worm burden then influences both mortality of grouse older than one year and fecundity of all age classes and is therefore an influential parameter in the model. Stochasticity was introduced to this rate reflecting the importance of climate for the biology of the grouse parasite. The parasitic nematode *T. tenuis* has a direct life cycle with free-living larval stages and no intermediate hosts. The survival of free-living stages depend on climatic variables such as temperature of the surface (Shaw *et al.* 1989) and humidity on the ground measured as rainfall (Moss et al 1993, Hudson et al 1992). The importance of climatic events on the small scale of parasites and individual grouse has been linked to large-scale population dynamics; Cattadori *et al.* (2005) showed that climate synchronises red grouse population fluctuations.

Another factor in the model, the threshold of parasite-induced mortality ($w_{max}$) influences the outcome of the model. The parasite intensity of the model population is linked to grouse density in the preceding July. There is still uncertainty about the mortality rate of grouse due to parasites. Hudson *et al.* (1992) showed that mortality rate varies with the mean parasite intensity. In the current study, grouse mortality is modelled as a percentage of grouse above a given parasite threshold and is therefore in line with results from field studies. The significant effect of this threshold in the sensitivity analysis of the model shows that more work is needed to clarify drivers of red grouse mortality.

Modelling studies showed that aggressiveness can create cycles in red grouse (Matthiopoulos *et al.* 2003, 2005). Old males hold territories and exclude young males form breeding the next year (Mougeot *et al.* 2005a). Additionally, larger dispersal distances were reported for young grouse in the decline phase than in the increase phase, with a 2-year time lag (Watson *et al.* 1994) and density dependent

dispersal has been observed in willow grouse (Rørvik *et al.* 1998). Therefore, at high density young grouse are lost to the local population due to aggressiveness and dispersal and this is reflected in the current model by a threshold density where young grouse are excluded from the population. Thus the model uses a simplified representation of the exclusion of young grouse from next year's population at high density by aggressiveness and dispersal.

Mortality of young and old grouse is included into the model in different ways. Young grouse are excluded from establishing a territory and most non-territorial males are lost over winter, whereas old grouse show higher worm burdens than young grouse and therefore suffer parasite-related mortality. Recent work has shown that modelling density dependence in red grouse population dynamics through parasites is not exclusive to territoriality since high aggressiveness regulated by high testosterone levels increases parasite intensity in red grouse (Mougeot *et al.* 2006). In this simplified model, instead of including detailed interactions between density, aggressiveness and parasites for old grouse, aggressiveness is dropped from the model for old grouse and instead density directly governs parasite levels and hence mortality in old grouse. However, the fundamentals of the process are still captured.

The behaviour of the model reflects crucial components of the red grouse population dynamics. Harvesting in this model is introduced as a proportional off-take and is kept at a constant rate. The next chapter will explore the effect of varying harvesting strategies on the population dynamics of red grouse using the model presented here.

# Chapter 6

## A stochastic age- and sex-structured population model for red grouse: Harvesting and management

## 6.1 Abstract

In this chapter the effect of a range of harvest rates and methods on red grouse population dynamics is tested in a deterministic and stochastic age- and sex-structured population model. The model showed that at a harvest rate of 0.48 the maximum yield was reached. However, above 0.5 the yield decreased dramatically and the probability of extirpation was high above a harvest rate of 0.8. The relative susceptibility of old males to harvesting affects the population sex ratio and productivity as well as population size and yield. Adding uncertainty in the harvest rate increases the probability of extirpation, even when harvest takes place only above a threshold population size. Harvesting earlier in the season increases the yield because population size is partly reduced before infective stages of the parasite are available. The chapter explores the interaction of parasite-induced mortality, exclusion by aggressiveness and harvesting. The exclusion of young grouse can shift the harvest rate at which the yield is maximised whereas the aggregation of parasites of old grouse does not have an effect on this measure. Based on the results, the current management strategy of hunting 20-50% of the population appears a good precautionary approach under uncertainty.

## 6.2 Introduction

There is an increasing need to understand how animal populations behave in human dominated landscapes and how they react to alterations of natural systems by human use such as harvesting. To actively manage natural populations, a detailed understanding of ecology, demographic rates and human harvesting behaviour is needed (Bro *et al.* 2000, Marboutin *et al.* 2003).

For a sustainable harvest of natural populations the impact of the off-take on future population dynamics needs to be investigated. Modelling has been recognised as a useful tool to understand and predict population dynamics of species affected by human harvest (Milner-Gulland and Mace 1998, Hauser *et al.* 2006b). Modelling also has great potential to inform management of exploited populations because it can take different types of uncertainty into account (Milner-Gulland *et al.* 2001, Milner-Gulland *et al.* 2004, Nicholson and Possingham 2007).

Altering the age- and sex-ratio of a population by harvesting can have a great influence on productivity of the population because different age- and sex-classes have different mortality rates and reproductive outputs (Milner *et al.* 2007, Festa-Bianchet 2003). Hauser *et al.* (2006b, 2007) showed in a recent modelling study that harvesting strategies are more likely to be sustainable when the age structure of the population is incorporated. They used a sex- and age-structured model for harvesting Canada geese (*Branta canadensis*) because field observations have shown that geese of different age classes have different fecundity and survival rates, including differential vulnerability to harvesting (Hardy and Tacha 1989, Mowbray *et al.* 2002). This structure might also be relevant to red grouse, since different age- and sex-classes in red grouse show different susceptibility to shooting (chapter 4). Most studies on sex-related hunting selectivity are conducted on polygynous species where one male can inseminate more than one female (Mysterud *et al.* 2006, Milner *et al.* 2007). In monogamous species, like red grouse, the effect of sex-selective harvesting might be stronger because the reproductive output of the population

depends on an equal number of both sexes. An example comes from a study on the monogamous beaver (*Castor fiber*) where male-biased harvesting delayed parturition in females, which is considered crucial for reproductive success and fitness of the offspring (Parker *et al.* 2007).

Hudson and Dobson (2001) showed in a model that harvesting stabilises overcompensation and dampens the cycles in red grouse. However, empirical data on red grouse show that cycles occur on moors with regular red grouse shooting (Cattadori *et al.* 2005). In contrast to earlier assumptions drawn from red grouse studies, it has been demonstrated for other vertebrates that harvesting can create cycles; for example in an empirical study on moose (Solberg *et al.* 1999) and freshwater fish (Huusko and Hyvärinen 2005) and in a modelling study on willow grouse (Jonzén *et al.* 2003).

The red grouse is a monogamous species where male numbers mainly govern female numbers (Watson and Jenkins 1968, Moss *et al.* 1996, Mougeot *et al.* 2003b). The species is harvested regularly and sex- and age- selective harvesting has been found in two different studies (Hudson 1985; chapter 4).

This chapter aims to test the effect of (1) a range of harvest rates, (2) timing of harvesting, (3) stochasticity of the environment and the harvest rate itself and (4) age- and sex-selective harvesting on the population dynamics of red grouse.

## 6.3 Methods

### 6.3.1 Harvesting strategies

Two harvesting strategies were investigated, proportional and threshold proportional harvesting. Proportional harvesting was introduced in equation (5.3) as a fixed rate of 0.3. In this chapter the effect of different harvesting rates (0.1 to 0.9) on the yield and on the population size is determined, with yield defined as the mean number of grouse shot per year over a time span of 80 years.

Grouse shooting tends to be stopped when July density $N'_t$ falls below 30 grouse km$^{-2}$ (Hudson *et al*. 1998). Grouse shooting was simulated in the model with proportional harvesting and a threshold below which shooting does not take place:

$$h = \begin{cases} h & if \quad N' > d \\ 0 & otherwise \end{cases} \qquad (6.1)$$

where $h$ is the proportional harvesting if the July population size $N'_t$ is above the threshold of $d$. The threshold is chosen to vary between 0 and 100 grouse km$^{-2}$.

In order to vary timing of harvesting the following adjustments were made to equation (5.1):

$$w_t = p\left(N'_{t-1} - \frac{hN'_{t-1}}{z}\right) + c \qquad (6.2)$$

where the number of worms $w_t$ in the next year depends on two constants $p, c$ and the number of grouse in the preceding July $N'_{t-1}$. To test the effect of timing of harvesting on the accumulation of parasites, the number of grouse in July $N'_{t-1}$ is reduced by a proportion $z$ of the number of grouse harvested.

### 6.3.2   Stochasticity

Stochasticity is introduced to equation (5.1) with a standard deviation between 1 and 4 on the slope and a standard deviation of 100 on the intercept (Table 5.3). Values are drawn from a Normal distribution. Uncertainty in harvesting rate is modelled by varying the harvest rate by a standard deviation of 0.1-0.3. Values are drawn from a Normal distribution.

### 6.3.3   Age and sex selective harvesting

Selectivity in the harvesting process is introduced by allowing *h* in eqn 6.3 to become age- and sex-specific:

$$N''_{i,j} = N'_{i,j}(1 - h_{i,j}) \qquad\qquad (6.3)$$

The breeding success of females depends on males establishing territories and although a few males have two females and some have none, male numbers largely govern the number of breeding females (Watson and Jenkins 1968, Moss *et al.* 1996, Mougeot *et al.* 2003b). When shooting is biased, a shortfall of one sex may appear. In the model the sex class that is less abundant in the population before breeding determines the number of breeding pairs.

From field studies it is known that grouse are shot at rates between 0.2 and 0.4 (Hudson 1985). Therefore it is highly likely that the data in chapter 4 are collected from populations experiencing these harvest rates. The model uses harvest rates of 0.2 and 0.4 and examines the consequences of the hypothesis that at high harvest rates and high density old males are less likely to get shot whereas at low density and low harvest rates shooting selectively takes a higher proportion of old males. The variation around the regression line describing age-selective harvesting (chapter 4, reproduced in Fig 6.11) is large and *a priori* it is not clear cut that older males are selected for, rather than against, at high density. To test this, an equal harvest rate of 0.2 and 0.4 for all age- and sex-classes is compared with male-biased harvest

selectivity 2.5 x lower or higher. Old males are defined as all males older than 1 year and therefore belonging to the second and third age class.

## 6.4   Results

### *6.4.1   Proportional harvesting*

Testing the effect of proportional harvesting between 0.1 and 0.9 in the deterministic model shows that the maximum yield is reached at an annual harvest rate of 0.48 (Fig 6.1). The yield increases up to the maximum yield and shows a steep decline thereafter in one-year-old grouse. In 3+-year-old grouse the opposite is the case; a steep increase and a gradual decline. The population goes extinct at a harvest rate above 0.8.

The variability in the harvest yield shows a gradual decline from zero to 0.7, then shows high variability around 0.7 and decreases as the population dynamics stabilise (Fig 6.2). As this is a deterministic model, this variation is due to the cyclic nature of the population dynamics rather than stochasticity. The cycle length shows an increase with the harvest rate. Around a harvest rate of 0.7 the cycles are less predictable and above 0.8 no cycles take place (Fig 6.3 & 6.4).
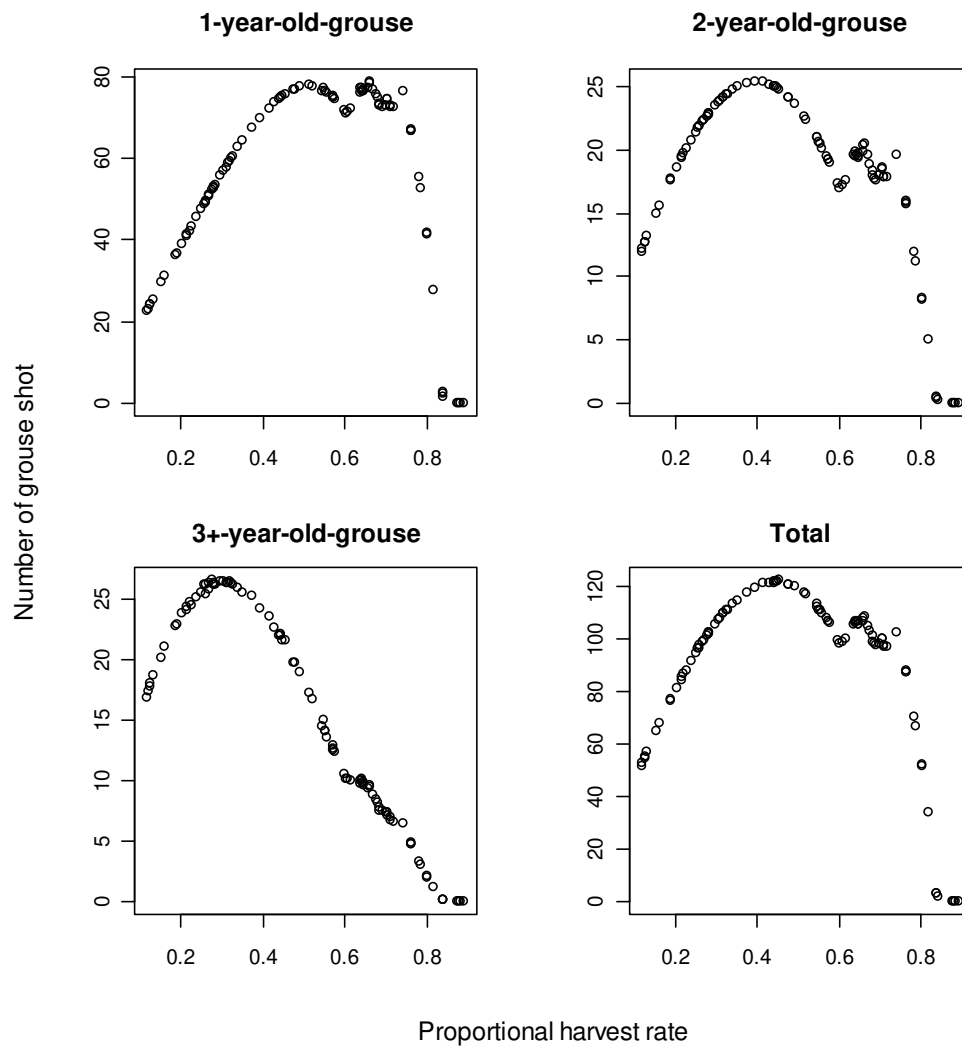
Figure 6.1: The yield at different proportional harvest rates are presented for a deterministic model.
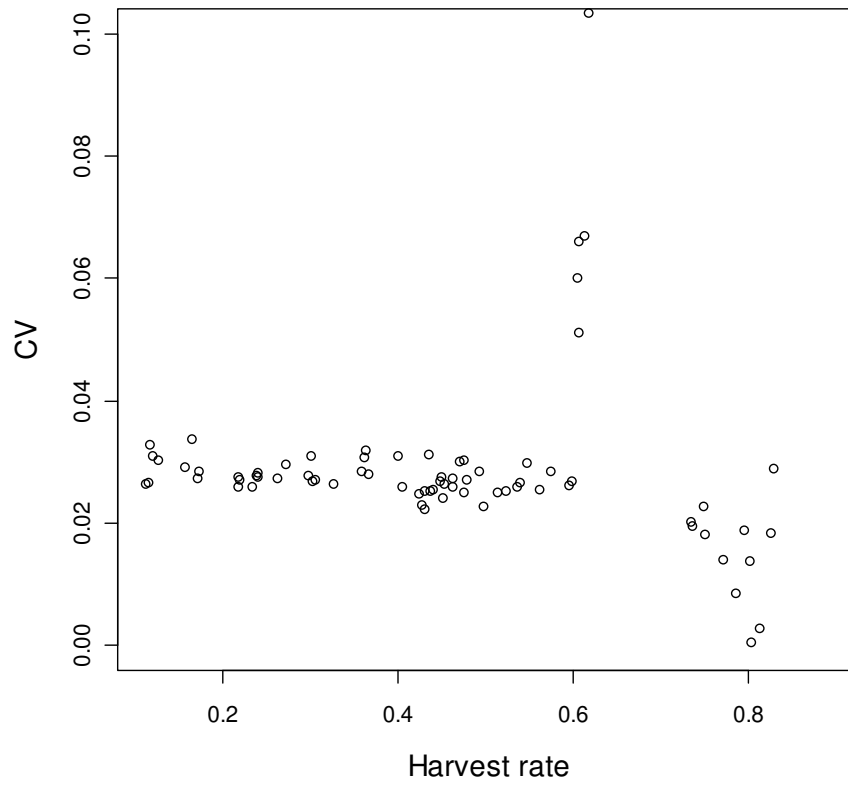
Figure 6.2: Coefficient of variation of the total yield for harvest rates between 0.1 and 0.8. At a harvest rate of 0.9 the population has gone extinct.
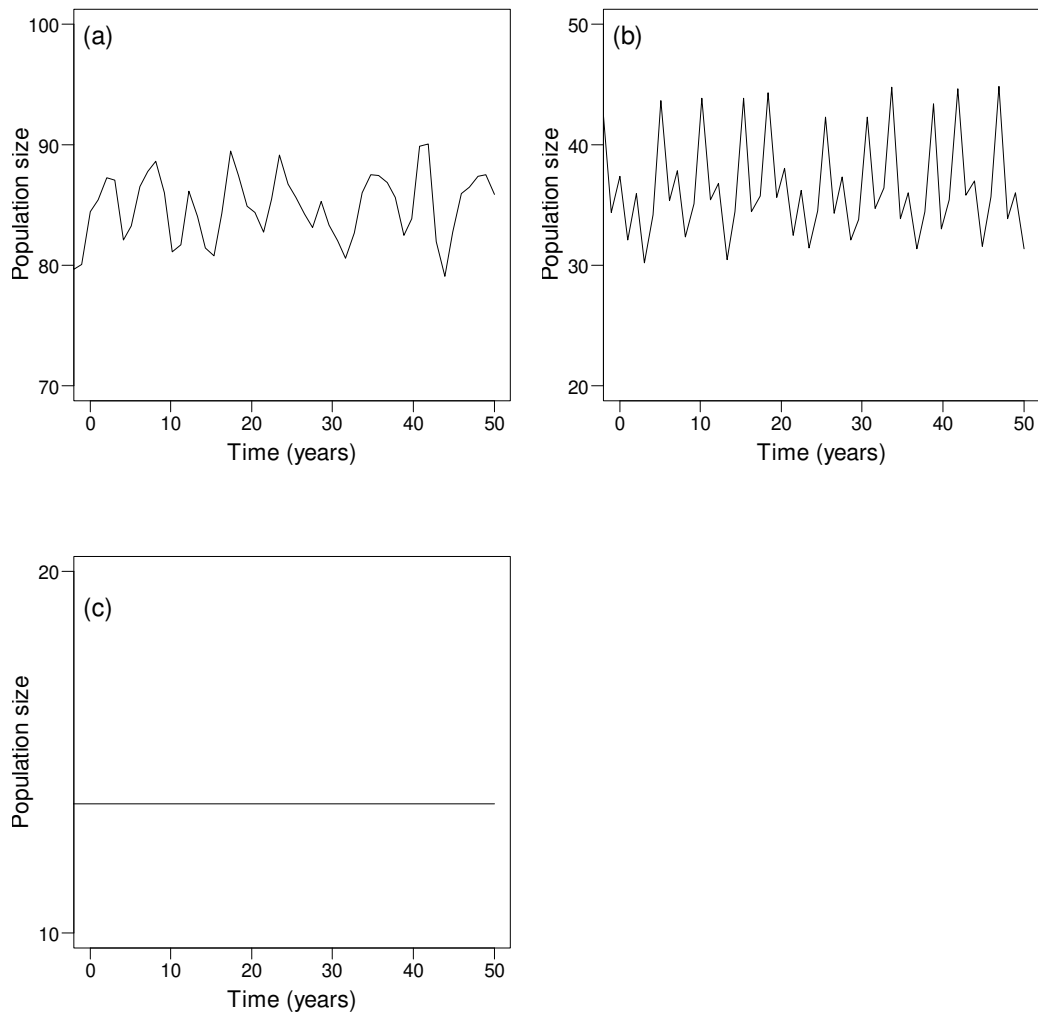
Figure 6.3: Population dynamics at a harvest rate of (a) 0.5, (b) 0.7 and (c) 0.8 for a single run of the deterministic model. The total population size is shown for 50 years after transients.
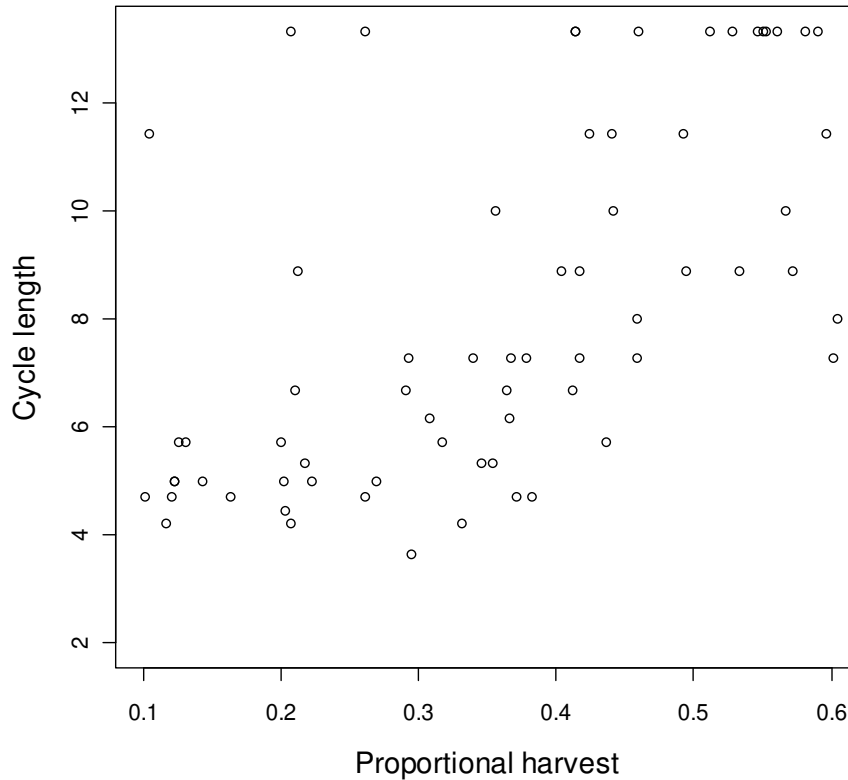
Figure 6.4: The cycle length for a range of proportional harvest rates from a deterministic model for 80 years after transients of 20 years have passed. At a harvest rate of 0.7 short cycles are visible and at 0.8, cycle lengths are simply the length of the run, showing no cycles are taking place. See also Fig 6.3.

The outcome of the model shows a slow increase in fecundity at low harvest rates and this keeps the population size of young of the year stable before the number of young decreases dramatically as harvest pressure continues to rise (Fig 6.5 & Fig 6.8). Fecundity increases exponentially with the harvest pressure because it is a function of density (Fig 6.5). The survival rate of one-year-old grouse is driven by the threshold density of exclusion governed by the grouse density in July. There is a slow decline in survival with harvesting, when survival is taken as natural mortality and harvesting combined and this is lower for one-year-old grouse than for the older age classes (Fig 6.7). With increasing harvest pressure the harvest mortality increases for all age classes but only the first age class benefits from high fecundity

(Fig 6.8) whereas at low harvest rates population density is high, fecundity low (Fig 6.5) and survival high at all age classes (Fig 6.7). The proportion of young birds in the population increases with harvest rates because of low population size, therefore low worm burdens and high fecundity characterise high harvest rates (Fig 6.6). The interaction of exponentially increasing fecundity and linear decrease in survival explains the slow increase and the right skew of the yield of the first age class (Fig 6.1).
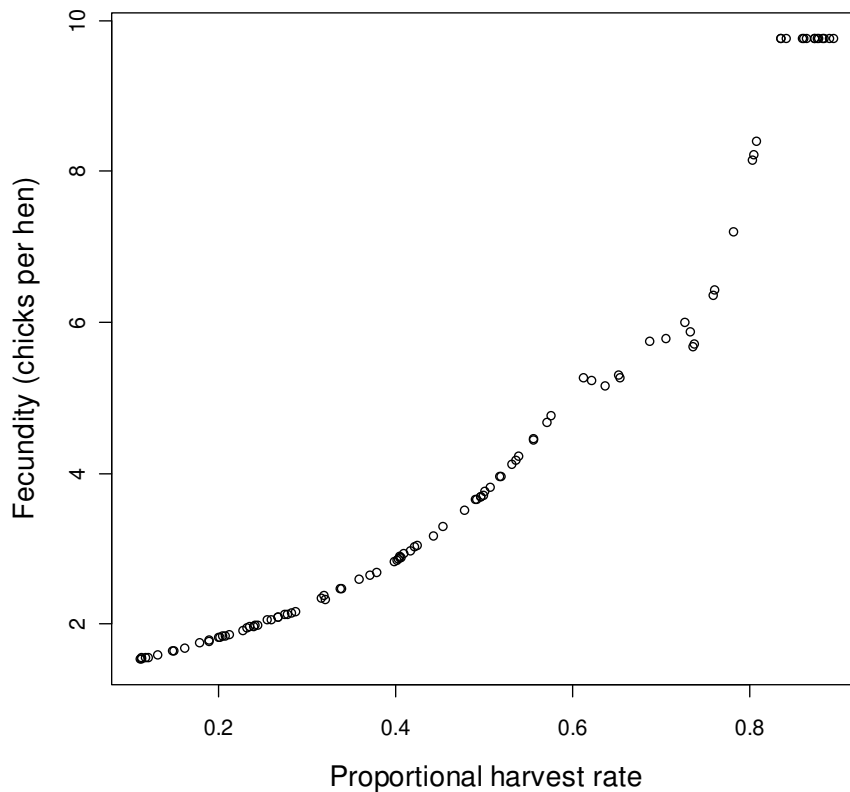


Figure 6.5: Fecundity, measured as chicks per hen, for a range of proportional harvest rates. Every data point represents the mean fecundity for 80 years of the deterministic model after 20 years of transients have passed.
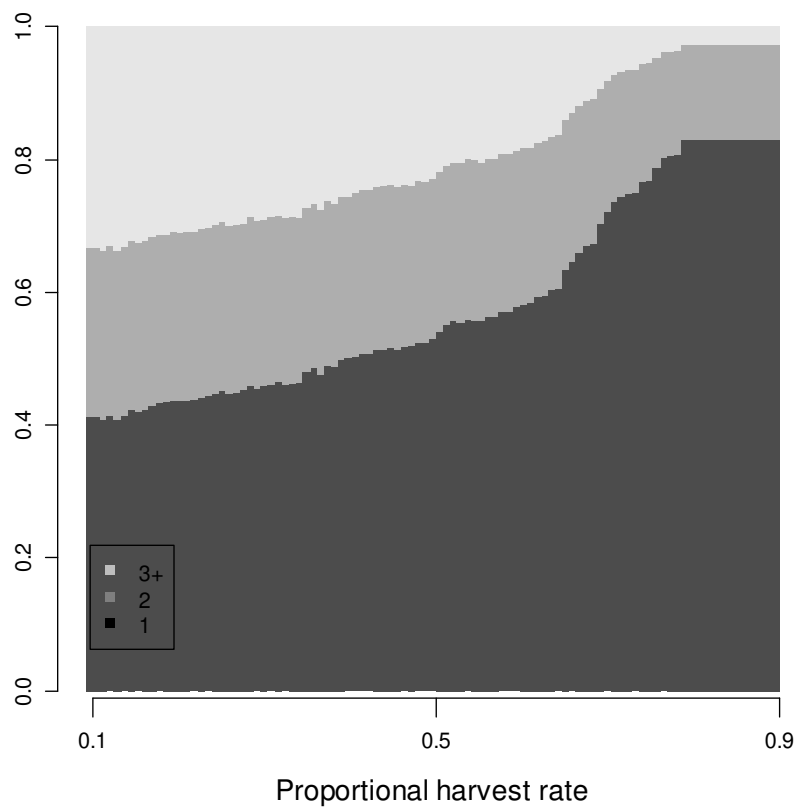
Figure 6.6: Decomposition of the total population into proportion of age classes (1, 2, 3+-year-old grouse). Mean proportion is shown for 80 years of a deterministic model after transients have passed.
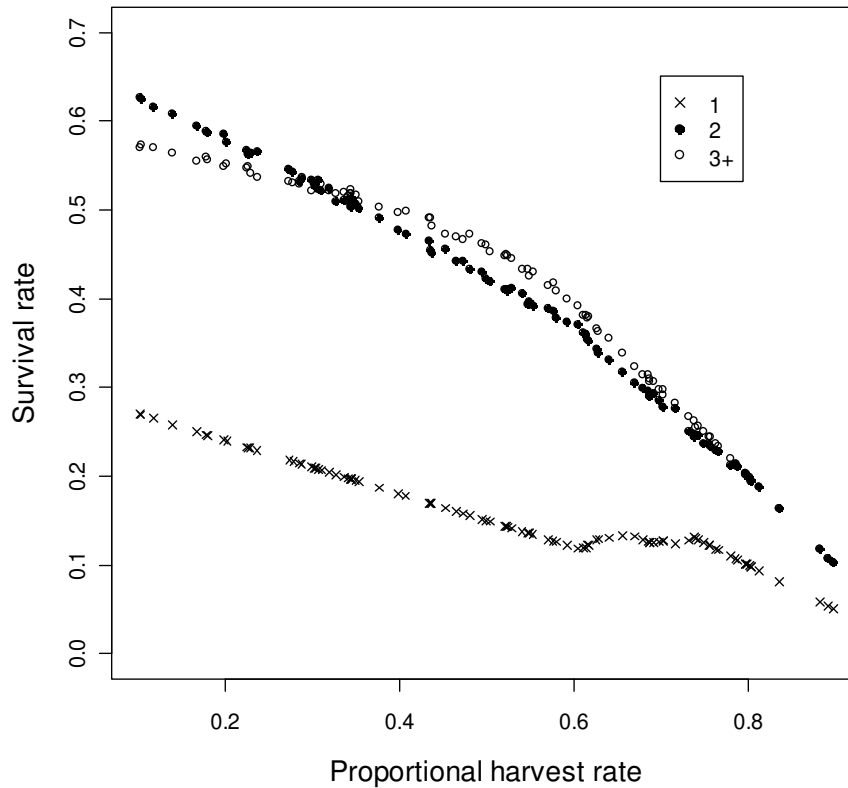
Figure 6.7: Mean survival rate of 1-, 2- and 3+-year-old grouse over-winter (harvesting and natural mortality) for a deterministic model for 80 years after transients have passed.

The effect of harvesting on survival rates varies with age classes. The survival rates of older birds (2 & 3+) are driven by mean parasite intensity of the population. Fecundity and survival combine to produce a nonlinear effect of harvesting on the number of grouse in each age class (Fig 6.8). Harvesting and parasites interact to produce nonlinear changes in vital rates as the aggregation parameter $k$ increases. Increasing the aggregation parameter $k$ leads to a more even distribution of the parasites within the host. High values of $k$ (less aggregated parasites) lead to an initial drop in survival but as harvest pressure increases, survival remains high for longer but declines more steeply as harvest, population size and parasite burden continues to increase. This pattern is illustrated in Fig 6.7 where parasites in 2-year-old grouse are more aggregated ($k=0.5$) than in 3+-year-old grouse ($k=2.0$). The

combination of the aggregation parameter and the number of grouse from the second age class feeding into the third age class generates the left skew of the yield curve for 3+-year-old grouse.
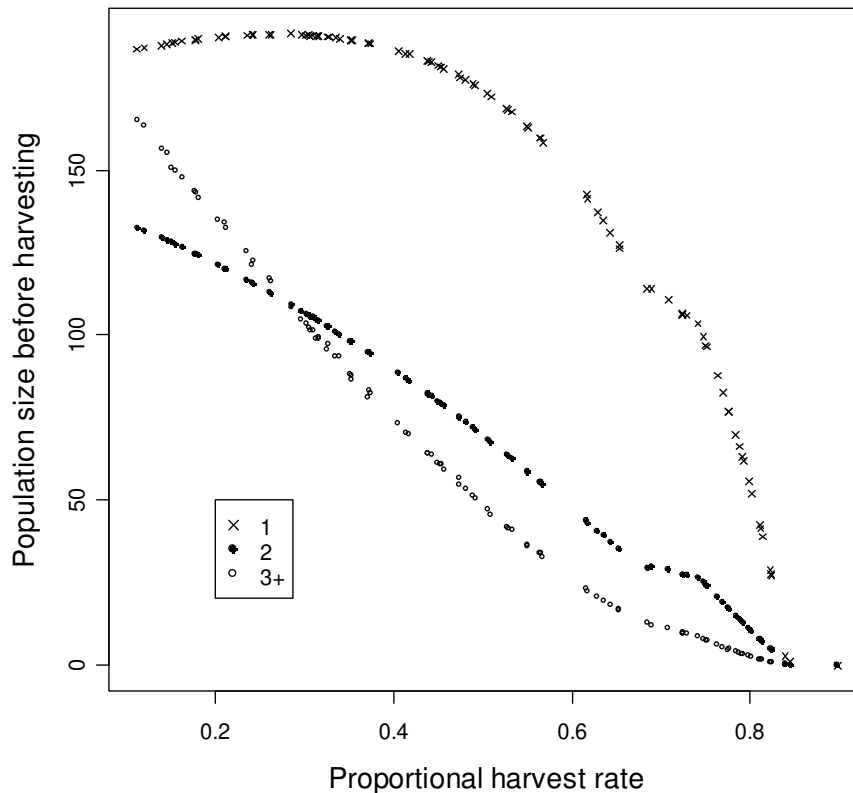


Figure 6.8: Population size before harvesting for three age classes (1, 2 and 3+-year-old grouse) for harvest rates between 0.1 and 0.9 for 80 years after transients have passed.

In order to explore the effect of the underlying processes of parasite infection and aggression on the outcome of harvesting, the exclusion proportion and aggregation parameter were varied. The effect on the skewness of the yield-effort curve for different age-classes was examined (Fig 6.1). Decreasing the proportion of one-year-old grouse excluded from breeding at high densities shifts the maximum sustainable yield (MSY) to lower harvest rates and this affects all age classes (Fig 6.9). However, there is no effect of the threshold grouse density at which young grouse are excluded and also no effect of the aggregation parameter on the relative skew of the yield-effort curve.
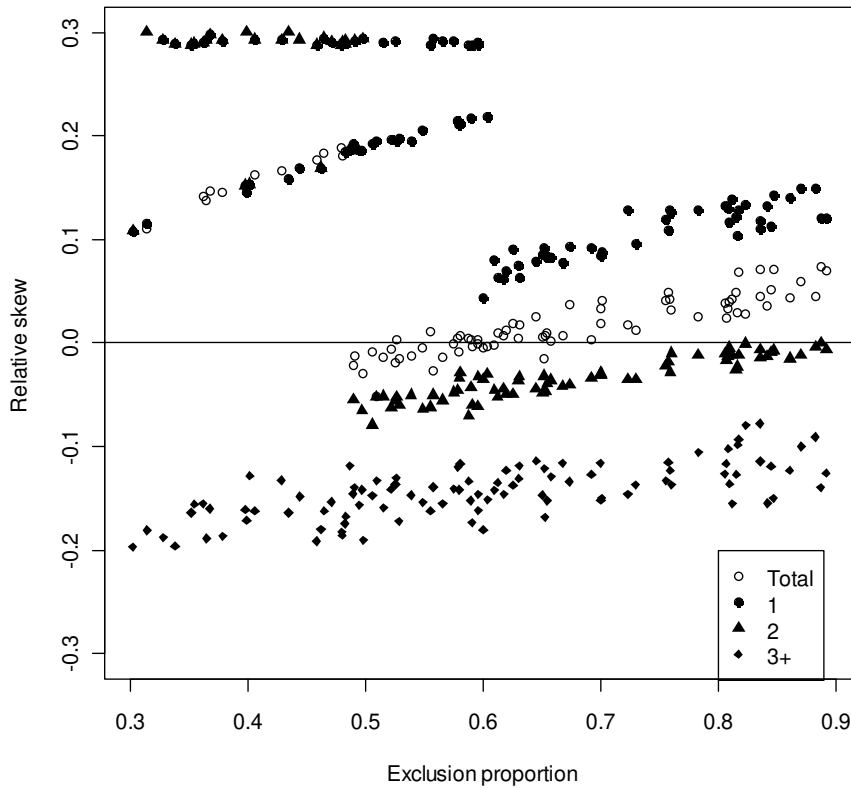
Figure 6.9: The relative skew of the maximum sustainable yield (MSY) relative to the baseline model is shown for the exclusion parameter. The horizontal line at zero indicates the MSY at a harvest rate of 0.48 (the baseline model for all age classes combined); negative values represent a lower harvest rate at which MSY is reached and positive values a higher harvest rate for MSY, compared to the baseline model. Below a harvest rate of 0.6, two different maxima for MSY are found and the model is sensitive to these small changes. The baseline model has an exclusion proportion of 0.6.

## 6.4.2 Timing of harvesting

The effect of harvesting grouse at different times in the season was tested. Harvesting grouse earlier in the season decreases the number of grouse contributing to the availability and accumulation of infective stages of the parasite. Moving the first shooting event to before infective stages are available increases the yield at all harvest rates compared to the baseline model. It also increases the right-skew of the

yield-effect curve, by increasing the parasite-dependent fecundity and the production of young grouse due to high numbers of grouse in the older age classes at low to intermediate harvest rates. Thus, the population available for harvest is increased when shooting earlier in the season (Table 6.1).

Table 6.1: The maximum sustainable yield (MSY) and the harvest rate at which it is reached for different timings of harvesting. A zero for the parameter $z$ indicates that all harvesting happens after infective stages of the parasite are available and 1 that all harvesting is before parasites are available.

| Proportion harvesting ($z$) before parasites available | MSY | Harvest rate |
|---|---|---|
| 0 | 122 | 0.44 |
| 0.2 | 145 | 0.46 |
| 0.4 | 150 | 0.49 |
| 0.6 | 171 | 0.49 |
| 0.8 | 200 | 0.55 |
| 1 | 250 | 0.58 |

### 6.4.3   Stochasticity of the environment and the harvest rate

Introducing uncertainty to the harvesting by varying the harvest rate with a standard deviation between 0.1 and 0.3 increases the chance of extirpation of the local grouse population (Fig 6.10). Then a threshold population density, below which no harvest takes place, varying between 1 and 200 grouse is added to the same model. However, this decreases the extirpation probability only marginally.

In a separate run the effect of environmental stochasticity added to the model was tested without uncertainty in the harvest rate and threshold harvesting. Environmental stochasticity was added by varying the slope of the parasite accumulation curve with a standard deviation between 1 and 4. Environmental stochasticity does not affect the extirpation probability.
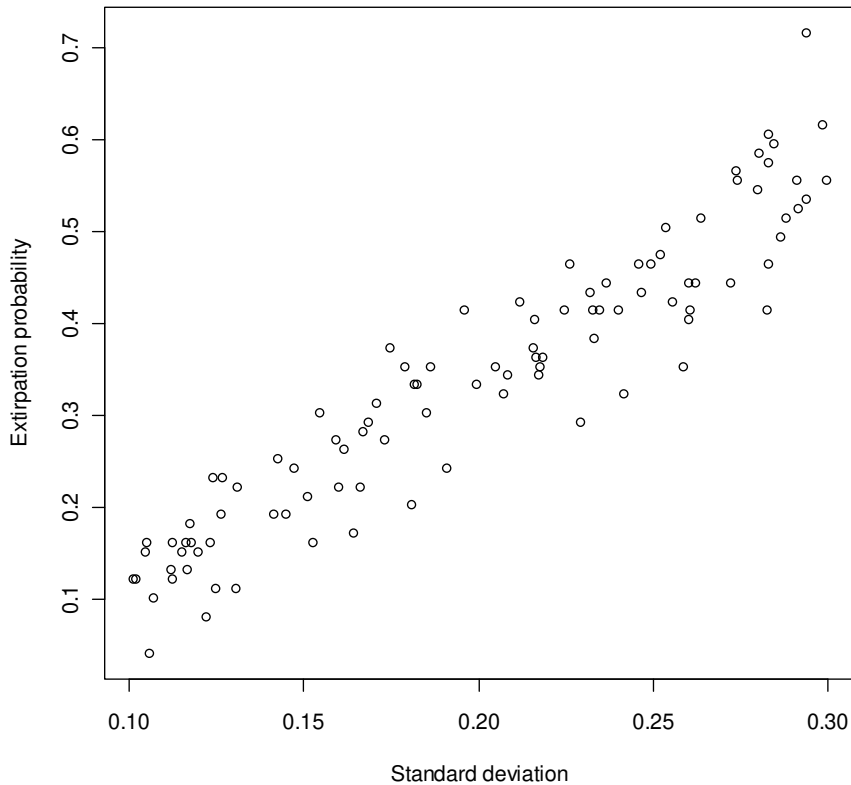
Figure 6.10: The extirpation probability, ranging from 0 to 1, is shown for uncertainty added to the harvest rate by sampling from a Normal distribution with a standard deviation ranging from 0.1 to 0.3. The harvest ranges from 0.1 to 0.9.

### *6.4.4   Age and sex selective harvesting*

Age- and sex-selective harvesting was tested in the deterministic model. Altering the harvesting selectivity of old males (>1 year) such that they are selected for compared to all other age and sex classes produces a similar output to the empirical data analysed in chapter 4, with more young grouse in the bag than expected from the counts when old males are selectively harvested and vice versa (Fig. 6.11).

The effect of both selection for, or selection against, old males is a skewed sex ratio in the population. This affects the number of fledglings in a monogamous bird, where the less abundant sex determines the number of breeding pairs. The drop in

population size decreases parasite burdens and therefore increases fecundity but this effect is not able to compensate for the skewed sex ratio and the loss of breeding birds, and thus the reduction in number of fledglings. The effect of a skewed sex ratio is a reduced population size and reduced yield and this is true whichever sex is being selected for (Table 6.2).
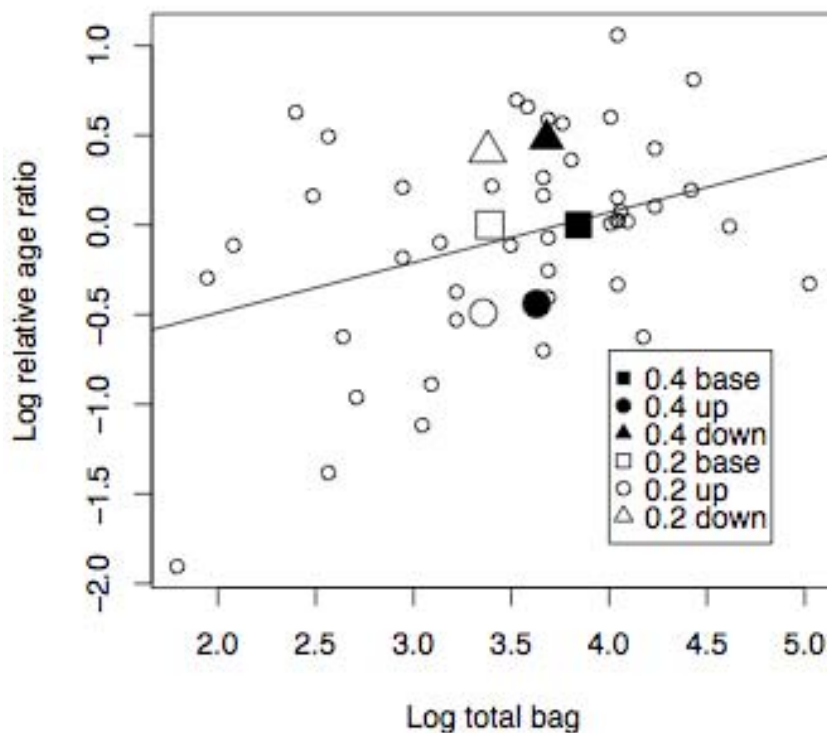


Figure 6.11: The log-transformed total number of grouse shot (log total bag) and the age ratio of the bag divided by the age ratio of the count (log relative age ratio) is taken from chapter 4. The log relative age ratios obtained by selective harvesting in the model are added. More details on selectivity levels tested can be found in Table 6.2.

Table 6.2: The selectivity for old males was tested at two different harvesting rates: 0.4 and 0.2. The index *up* represents a 2.5 times higher probability of being shot for old males (>1 year) than all other age classes in the model. The index *down* represents the inverse where old males are 2.5 times less likely to be shot. The outcome of the model is shown as mean, maximum and minimum population size, worms per bird, number of grouse shot (bag), number of fledglings, number of chicks per female (fecundity), cycle length and percentage of each age class in the population. The values of *up* and *down* are percent change compared to the *no selection* model, where negative values represent a decrease and positive values an increase. All values are means from 100 runs of each 100 years measured after 20 years of transients.

| Measure | Harvest rate 0.4 | | | Harvest rate 0.2 | | |
| | No selection | Old male bias (%) | | No selection | Old male bias (%) | |
| | | up | down | | up | down |
|---|---|---|---|---|---|---|
| Mean pop | 124 | -24 | -15 | 210 | -5 | -5 |
| Max pop | 135 | -26 | -15 | 230 | -6 | -5 |
| Min pop | 112 | -22 | -14 | 190 | -5 | -5 |
| Mean worms | 3107 | -29 | -22 | 4196 | -8 | -7 |
| Bag | 120 | -29 | -18 | 80 | -9 | -2 |
| Fledglings | 176 | -31 | -25 | 191 | -11 | -8 |
| Fecundity | 2.8 | +48 | +34 | 1.8 | +17 | +14 |
| Cycle length | 7.6 | +0.9 | +19 | 6.0 | +2 | +10 |
| 1-y-old males (%) | 26 | 0 | -27 | 22 | 0 | -9 |
| 1-y-old females (%) | 26 | 0 | -27 | 22 | 0 | -9 |
| 2-y-old males (%) | 12 | -67 | +8 | 14 | -29 | +7 |
| 2-y-old females (%) | 12 | +25 | -33 | 14 | 0 | -21 |
| 3+-y-old males (%) | 12 | -93 | +192 | 14 | -36 | +71 |
| 3+-y-old females (%) | 12 | +125 | -42 | 14 | +64 | -7 |

## 6.5   Discussion

This chapter shows how different harvesting rates and strategies influence the population abundance, harvest yield and dynamics of a red grouse population. In this modelling study selective harvesting altered the age and sex ratio of the population and this has consequences for the demographic structure, population size and yield. A bias in the sex-ratio in either direction by sex-selective harvesting results in a decrease in recruitment and population size. The current study is not the first that demonstrates the hampering of populations by sex-biased harvesting. Trophy and sex-biased hunting has been discussed as a cause for population decline and crashes (Ginsberg and Milner-Gulland 1994, Milner-Gulland *et al.* 2003, McLoughlin *et al.* 2005). However, this study is a first example of how unintentional harvesting selectivity decreases yield in a monogamous species and it is unusual in considering both directions of selectivity.

In the model a steep decline in the yield occurs above a 50% harvest rate. This increases the risk of overexploitation and local extinction. This might explain why estates rarely harvest more than 40% of the population (Hudson 1985). After adding stochasticity to the harvest rate, the risk of local extinction is apparent even when a threshold density is introduced, below which harvesting is halted. Interestingly, the uncertainty in harvest rates is the most important factor influencing the probability of extirpation whereas increasing the threshold had only minimal effect. Environmental stochasticity increases the amplitude in population fluctuations (chapter 5) but the tested range of stochasticity does not increase the probability of extirpation.

An earlier modelling study on red grouse predicted a dampening effect on the population cycles due to harvesting (Hudson and Dobson 2001). However, the study did not incorporate stochasticity like weather effects or uncertainty in the harvest rate, even though these have been widely demonstrated to affect population dynamics (Lande *et al.* 2003). In particular, the uncertainty introduced by the

harvesting itself can be crucial to incorporate when aiming to understand population dynamics (Jonzén *et al.* 2002). In a modelling study on Finnish grouse, Jonzén *et al.* (2003) showed that adding environmental stochasticity and uncertainty to the harvesting rate increased the amplitude of the fluctuations. The effect of uncertainty in the harvesting process has also been demonstrated in red deer (*Cervus elaphus*). The study showed that poor knowledge of the demography and density of the population can lead to suboptimal harvesting strategies because the actual harvest rate differs from the target (Milner-Gulland *et al.* 2004).

Timing of harvesting is important because young grouse pick up infected stages of the parasite during feeding in July and August (Hudson and Dobson 1997) and shooting starts on 12th August. So far it has been assumed that shooting has no effect on the population dynamics of red grouse, because the density dependent infective stages of the parasites are already on the ground by the time reduction of the population size by shooting takes place (Hudson and Dobson 2001). It might be realistic to assume that accumulation and availability of infective stages of the parasite carries on in August since temperatures are still favourable. Shooting early in the season might help to reduce the extent of the accumulation and this modelling study shows that removing parts of the grouse population before infective stages are picked up increases the sustainable yield. It also shows that timing of harvesting alters the population dynamics and shifts the MSY to a higher harvest rate. Therefore, shooting earlier in the season might contribute to the stability to harvest grouse at a higher rate.

The degree of aggregation of the distribution of parasites within the host determines the stability of parasite-host population dynamics (May and Anderson 1978, Rosa and Pugliese 2002). Parasite-induced mortality increases with a less aggregated distribution, leading to declines in host density (Tompkins *et al.* 2002). This insight is invaluable especially when considering the effect of harvesting. At low harvest rates and high population density the survival is lower for 3+-year-old than for two-year-old grouse because 3+-year-old grouse have a less aggregated parasite

aggregation than two-year-old grouse. However, intermediate harvest rates decrease population size and parasite intensity and a random distribution of parasites leads to higher survival because fewer hosts harbour parasite intensities that are above the threshold at which they face increased mortality. This study shows that when the parasite distribution is more aggregated lower harvest rates maximise yield and vice versa if it is less aggregated. This stresses the importance of the distribution of parasites within hosts and shows that parasite aggregation and parasite-induced mortality interact with harvest rate. The degree of aggregation is an important parameter to estimate and should be estimated for different age classes of the population separately (Shaw *et al.* 1998), which is further supported by the results of this study.

The red grouse system is highly complex with density-dependent effects of testosterone-driven aggressive behaviour, parasites and harvesting as well as climatic effects influencing population dynamics. There is an increasing tendency towards complex models to reflect reality, but the strength of models in ecological research is their conceptual clarity (Kokko 2005). Identifying the key processes driving population dynamics from parameter-rich simulation models can be extremely difficult given the variability in the estimates of input parameters. These can be caused by low precision of parameter estimates or by models with exceedingly large numbers of parameter combinations (Bunnefeld *et al.* 2007). Thus, this modelling exercise aims to build a simple model by focussing on the interacting effects of harvesting and the two key factors of parasites and aggressiveness on population dynamics and on capturing the essential behaviour of the study system.

### 6.5.1   *Red grouse management*
The results of this study might be useful for red grouse management. The highest physical yield is reached around a harvest rate of 50%. Reducing the uncertainty in the proportion of the population represented by a given shooting quota might allow higher harvest rates. Detailed population counts including accurate information on

the sex ratio in spring might allow estimation of the breeding success and thus the harvestable population more reliably. This modelling study shows that only at very high harvest rates population cycles are dampened. Such high harvest rates increase the risk of extirpation of the local population and are therefore unlikely to be a sustainable strategy.

This study has shown that by removing grouse early in the season, managers might be able to increase the yield by reducing the availability of infective stages of the parasitic nematode *T. tenuis.* Grouse managers are concerned by disease control and gamekeepers apply anthelmintic drugs to prevent disease outbreaks and population crashes (Newborn and Foster 2002). Harvesting may remove susceptible and infected hosts by targeting old males.

Aggressive interactions have been found to affect grouse population fluctuations and experimental removal of old males has been shown to be able to prevent population crashes (Moss *et al.* 1996). Selective harvesting of old males might allow young males to establish territories. The interaction of aggressiveness and parasites has only recently been studied (Seivwright 2005, Redpath *et al.* 2006a,b) and the effect of removing old males by harvesting on the aggressiveness and parasite burden of the population by harvesting remains to be tested in field studies. This model gives an insight into how harvesting might interact with other processes in determining the population dynamics of red grouse in the light of aggressiveness and parasites.

# Chapter 7

## General Discussion

### 7.1   Harvesting and ecological studies

The dynamics of natural populations are driven by dispersal, recruitment and survival. The effects of intrinsic and extrinsic factors such as density and climate on population dynamics have been the focus of numerous studies. However, many populations inhabit human dominated landscapes where the main source of mortality is of anthropogenic origin, such as hunting or shooting. Thus, drivers of population dynamics of harvested species differ considerably from non-harvested species, but hunting and shooting are often considered simply as another source of mortality.

Studying exploited species is logistically difficult because many wild populations are not easily accessible or they have decreased to such low numbers that detailed ecological research is impossible due to small sample sizes. Red grouse are a fascinating and especially suitable study species because of the relatively high abundance of the species, the high harvest pressure and the available scientific knowledge. Furthermore, studies on red grouse might be transferable to other species of the grouse family (*Tetraonidae*) that occur throughout most of the northern hemisphere, many of which are under severe harvest pressure and some of which are threatened with extinction (Storch 2000). Thus, scientific studies of red grouse harvesting are highly relevant to management of species with similar harvesting pressure and life histories.

The effect of the interaction between the demographic structure of a population and harvesting pressure on red grouse population dynamics was investigated in this thesis. The study showed that shooting in red grouse is selective and that this selectivity interacts with the number of grouse shot and with the number of shooting events (chapter 4). Most scientific projects studying population dynamics of

vertebrates have assumed that harvesting does not affect population dynamics. This is based on the assumption that harvesting is unselective and does not interact with other factors driving the dynamics of the population. The modelling part of this thesis has shown that harvesting affects the dynamics and the demographic structure of the population. Furthermore, aggressiveness, parasites and harvesting interact in a complex way that affects the yield and the harvest rate at which the maximum sustainable yield is reached. The interaction differs between age-classes and is affected by the mating system of the species. It also showed that this has consequences for the management of red grouse because age- and sex-selective harvesting resulted in a decrease of the population and the bag size (chapter 6).

## 7.2   Parasite aggregation parameter and population dynamics

The aggregation parameter describing the distribution of parasites within their host has important implications for host population dynamics (Anderson and May 1978, May and Anderson 1978). Since these early studies, researchers have described the aggregation parameter for various vertebrates and discussed the implications for population dynamics (Tompkins *et al.* 2001, Newey *et al.* 2005). Anderson and Gordon (1982) and Rousset (1996) showed that the aggregation parameter can be used to detect parasite-induced mortality in the host. A recent study on rodents demonstrated a convex pattern of the aggregation of flea parasites among their hosts; the middle age classes showed the most aggregated distribution. A similar convex shape was found for the three age classes in this study. Furthermore, the field study for this thesis investigated the effect of age differences in parasite aggregation on the population dynamics (chapter 2 & 6). Further field studies into the aggregation of *T. tenuis* parasites within red grouse might show variability in the age dependence of the aggregation parameter over the season and with the phase of the population cycle. This might feed into models where the aggregation parameter is not fixed for each age class but changes according to the season and phase of the cycle. This thesis showed that in a fluctuating species under selective harvesting the aggregation parameter can alter the survival curve in the model depending on density and therefore that it interacts with harvest pressure.

## 7.3   Age, fecundity and harvesting

The results in chapter 3 showed that there was no simple relationship between age and fecundity. An earlier study did not find any effect of age-related fecundity in red grouse (Moss et al 1996). Similarly, in ptarmigan a relationship between age and fecundity was only found in some years of a long-term (14 year) study due to stochastic effects (Sandercock *et al.* 2005). Compared to that long-term study, it might be possible that the three-year study presented has not covered enough years to detect any age-related differences in fecundity in a fluctuating species like the red grouse. Additionally, individual-based data coupling important variables such as the condition and parasite intensity of the individual female or the aggressiveness of the male might be able to identify patterns in fecundity.

A theoretical study on the consequences of harvesting for the reproductive strategy of red deer showed that harvesting pressure might alter the reproductive strategy of females. Given the increased mortality probability, it is favourable to shift from reproducing at older age and high weight (prime condition) to reproducing earlier (Proaktor *et al.* 2007). Red grouse shooting has a long history and intensive harvesting has been practised since the late 19th century (Tapper 1992). Investing resources to ensure reproduction early in life might be a favourable strategy for red grouse and senescent effects on reproduction might not easily be detected, since grouse above the age of 4 years are rarely observed (chapter 2 and 3). This thesis showed that there might be a shift to early production in female red grouse since younger females had more fledglings than old females. The interaction with males is not yet fully explored and individual-based data might give further insights into this interaction of fecundity and age in red grouse (section 7.8).

## 7.4 Aggressiveness, parasites and harvesting

The consequences of harvesting on populations have been demonstrated widely and are manifold, including short-term effects such as demographic changes and a decrease in population size but also long-term evolutionary consequences such as a change in phenotype (Coltman *et al.* 2003).

Chapter 6 shows that in a species that is driven by the density-dependent factors of aggressiveness and parasites, further complexity is added by harvesting. Harvesting can alter the age- and sex-composition of the population and in many species the behaviour, reproductive ability and mortality risks depend on the age and sex of the individual (Coulson *et al.* 2001, Ezard *et al.* 2006). Therefore, the age- and sex-structure of the population can change the population dynamics. This thesis has made a first attempt to clarify the interaction between harvesting, parasites and behavioural mechanisms and the short-term consequences of these interactions.

Moss *et al.* (1996) and Mougeot *et al.* (2003a,b) showed in a field study that aggressiveness increased with grouse density and Matthiopoulos *et al.* (2005) demonstrated in a simulation model that an abrupt change in aggressiveness and exclusion of males is needed to create cycles in red grouse. However, harvesting has not been taken into account in these studies. Harvesting can create a rapid change in grouse density and this might have consequences for the degree of density-dependent aggressiveness. The timing of harvesting might also play an important role whereby harvesting early in the season might influence aggressiveness in a different way than harvesting later in the season. Harvesting early in the season might decrease competition for territories and therefore aggressiveness. The effect of harvesting later in the season might depend on the timing of territory establishment and selective removal of a specific age- and sex-class by harvesting (chapter 4). The effect of removing old territorial males might differ from removing young non-territorial males. Early in the season, young males might easily fill the vacant territories but later in the season non-territorial males might have left the area and these gaps will not be filled. This might decrease the breeding success in a

monogamous species in a similar way as demonstrated in chapter 6, where old males were selectively removed by harvesting.

## 7.5  Modelling and transients

Modelling of population dynamics often focuses on long-term dynamics and stable states of the model. However, most populations are frequently disturbed by extreme climatic events, disease outbreaks and harvesting, which can lead to short-term changes in the structure and growth rate of the population. These transient population dynamics are more likely to occur than a stable state in natural populations (Clutton-Brock and Coulson 2002). In particular when one aims to predict the outcome of management actions for conservation, transient dynamics are more likely to be informative than stable state population dynamics (Koons *et al.* 2005, Metcalf *et al.* 2007). Further research into the transient dynamics of red grouse populations would enhance our knowledge of populations after severe disturbance. This could occur, for example, when monitoring has imprecisely predicted population abundance and harvesting leads to local extirpation. Another example could be warm and wet summers coinciding with years of high population density; then grouse populations are likely to crash in the next year more severely than anticipated. Results from studies of transients in red grouse population dynamics would be helpful when aiming to restore species of major conservation concern. These are often at very low density facing high human pressure.

## 7.6  Modelling and complexity

There is a tendency in ecological modelling to increase the degree of complexity. However, simple models offer conceptual clarity, which helps the researcher in framing the research questions and facilitates the comprehension of the results by the target audience once the research is published. Starting out with simple caricature models provides a good opportunity to build a solid grounding in ecological theory and can provide a justification for a more complex approach if the simple models fail to explain the qualitative behaviour of the observed system. Nevertheless, it is

crucial that more complex models are rooted in, and their results interpreted based on, general ecological theory (see also Grimm *et al.* 2005, 2006). In fact, the lack of orientation towards more general (theoretical) issues is one of the main critiques of complex models. Indeed, even for complex models the aim is not "realism" but using a tool to answer a research question (Mangel *et al.* 2001, Kokko 2005). The results obtained from simple models can highlight key conceptual faults before a series of time-expensive simulations is carried out, just as pilot studies are undertaken before a large-scale experiment is started. For example, Ludwig & Walters (1985) used a relatively complex age-structured model to generate a dataset, and then used this dataset to compare the predictive power of the generating model against a simple lumped population model. The simple model performed better, even though it had not been used to generate the data, because of correlations among parameters, especially when they were estimated from a limited amount of data. This thesis used a simplified model, parameterised with the available data, which captured the dynamics of the system and facilitated the exploration of the effect of harvesting on red grouse population dynamics. A more complex model might give better insight into grouse population fluctuation but unless these data are available a general model is more informative (see section 7.8).

## 7.7   Scale of ecological studies

The scale at which animal populations should be studied is an ongoing question. Johnson (1980) proposed a hierarchical approach to scaling where the largest scale is the geographic range, the next one is the home range, then patch use and the smallest scale is the selection of food items within a patch. Scientific studies on scale dependence have been mostly concerned with species characterised by large body mass and large movements such as ungulates (Hobbs 2003, Månsson *et al.* 2007) and grizzly bears (*Ursus arctos*, Ciarniello *et al.* 2007). However, the scale at which population fluctuations are studied has also been proven to be important for species with shorter movement distances such as field voles (*Microtus agrestis*, Sherratt *et al.* 2002).

So far studies on red grouse harvesting have been conducted at the scale of the entire moor (Hudson *et al.* 1998). However, moors compromise large areas (20-50 km$^2$) subdivided into smaller areas called drives, both between gamekeepers and for shooting (Hudson 1992). Areas within the moor can also differ in topography and therefore weather and habitat variables as well as having differences in treatment by gamekeepers and harvesting pressure. All harvesting data for this thesis were collected at the drive level and were compared with count data from the same area and the same scale. Statistical mixed effects models have shown that studying shooting selectivity at this scale left little variation to be explained by differences between moors or between drives within moors and thus indicates that the scale chosen was appropriate to study shooting selectivity (chapter 4). The unexplained variation in the full model could be due to small-scale movement of birds from one drive to the next during the shooting season but these are logistically difficult to capture because moor owners are keen to reduce disturbance of grouse as much as possible between shooting events. The simulation model was parameterised for a small spatial scale but interconnectivity between different parts of the moor was not included into the modelling process (chapter 5). Dispersal distances in red grouse vary considerably between the sexes and females generally disperse further than males (861 meters vs. 343 meters; Warren *et al.* 2007). Dispersal was not found to be density dependent in the same study but all data was collected at relatively high densities. Because of such small distances, it seems rather unlikely that dispersal in red grouse influences the sex ratio of a local population significantly and that it plays a role in population dynamics. However, a study on field voles showed that short-distance dispersal can synchronise larger scale population dynamics, especially when some individuals move farther than the nearest neighbour (Sherratt *et al.* 2002). Therefore, movements between different parts of the moor might affect population fluctuations of red grouse; particularly given that the same study on red grouse dispersal has observed a few individuals travelling distances of more than 4.5 kilometres (Warren *et al.* 2007). Synchronisation of population fluctuations in red grouse has so far been assumed to be due to weather effects (Cattadori *et al.* 2005)

but distance to neighbouring populations and dispersal are also discussed as possible drivers (Kerlin *et al.* 2007).

## 7.8 Further research

Harvesting, parasites and aggressiveness might interact and affect population dynamics of red grouse in a way that has not been studied so far. This study demonstrates that harvesting can change the demographic structure and the density of the population and therefore alter the extent to which grouse are affected by aggressiveness and parasites. Studying the interaction between aggressiveness and harvesting could lead to new insights since an experimental removal of old males prevented a population crash (Watson *et al.* 1988, Moss *et al.* 1996) and old males are in most cases selectively harvested (Hudson 1985, 1986, chapter 4). Furthermore, old red grouse carry more parasites than young grouse and removal of old males during shooting might decrease the overall parasite load of the population beyond the effect of reducing population density. A similar effect has been proposed by Dobson and Hudson (1995) studying the effect of selective removal of highly parasitized individuals by predation. They showed that even a small number of predators could decrease the parasite burden in the red grouse population and therefore increase population size.

Detailed observations of individually marked grouse coupled with data on their aggressiveness and parasite burden might deliver new insights for the study of population dynamics. The success of this approach would depend largely on the degree of detail and precision of monitoring the demographic structure of the population and the bag; only detailed information on a small scale would be able to tease apart the relative roles of harvesting, age-sex structure, aggressiveness and parasites. An individual-based study would further clarify the mechanism that connects vital rates with aggressiveness and parasite burdens under varying harvest pressure. Individual-based data collection using radio-collars has already shown the interaction between parasites and aggressiveness (Mougeot *et al.* 2006). So far it is assumed that shooting is unselective but field data presented in chapter 4 showed

susceptibility to shooting depends on the age and the sex of the bird and this is hypothesised to be driven by differences in behaviour. If and how behaviour and shooting selectivity interact with elevated aggressiveness and parasites at the individual level remains to be studied.

Availability of individual-based field data would make individual-based modelling feasible and realistic because sufficient high quality data are required to form the basis of complex models (section 7.6). Individual-based models were first mentioned by Lomnicki (1978, 1980) and have been especially useful to predict population dynamics under novel circumstances, incorporating spatial and behavioural mechanisms (Pettifor *et al.* 2000). This approach would be helpful in capturing processes in red grouse such as the interaction of aggressiveness and parasite burdens and their effects on fecundity, mortality and population dynamics. An individual bird with high aggressiveness would have high reproductive output but high parasite burdens next year (Mougeot *et al.* 2006). The effect of a short-term increase in fecundity and a decrease in survival due to high parasite burdens of individuals on the dynamics of the whole population could be investigated.

## 7.9   Wildlife management

### 7.9.1   *Management of herbivores*

The goal of wildlife management is sustainable harvesting to ensure long-term off-take and a decreased risk of overexploitation and extinction of the species (Mace and Reynolds 2001). Management of harvested species is becoming more important and faces new challenges because of the need to adjust harvest rates to increased populations. In several parts of the world herbivore populations have increased substantially, in part due to change in agricultural practices and release from predation and harvesting (Côté *et al.* 2004, Milner *et al.* 2006). In addition, the number of hunters is declining and it is now a major concern that hunters might not be able to control ungulate populations in North America (Brown *et al.* 2000, Côté *et al.* 2004) and in some countries in Europe (Milner *et al.* 2006). Overabundance of

herbivores can have drastic effects on ecological processes; reduced plant biomass and changes in plant community composition can lead to loss of vertebrate and insect biodiversity (Côté *et al.* 2004, Tremblay 2006). Harvesting may be able to play an important role in controlling population size and mitigate the impact on the ecosystem. However, applying a selective harvesting regime to an age- and sex-structured population can influence the effectiveness and feasibility of population control because it can have dramatic and unforeseen effects on the population dynamics of the species.

Information on harvesting selectivity is increasing (Martinez *et al.* 2005, Hörnell-Willebrand *et al.* 2006, Mysterud *et al.* 2006) but population composition and the contribution of different age- and sex-classes to the population growth rate have only been studied for a few species (Gaillard *et al.* 1998, Ezard *et al.* 2006). However, this information is essential for the sustainability of harvesting strategies and the feasibility of population control and management (Milner *et al.* 2006, Milner-Gulland *et al.* 2004). In some cases management totally fails to meet the target of reducing population size when the most fecund age-class is excluded from harvesting, as a study on wild boar (*Sus scrofa*) in Switzerland showed (Hebeisen *et al.* submitted). Harvesting is also driven by ethical considerations and this might introduce a clear bias towards a certain age class by avoiding others that are considered as unethical to harvest (e.g. females accompanied by offspring). Simple models have been proven to be able to show the consequences of this strategy and can identify successful management strategies (Hauser *et al.* 2006b). This study on red grouse harvesting highlights the consequences of selective harvesting and further studies on interactions between population dynamics and harvesting are encouraged.

## 7.9.2   Wildlife diseases

The diseases of wild animal populations and their adaptive management are a major concern in the modern world where transport and travel increase the spread of diseases and epidemics. Therefore, a case study such as the red grouse, where interactions between behaviour (aggressiveness and territoriality) and parasites play a role in population fluctuations (Redpath *et al.* 2006a), is highly topical. The control of diseases by management intervention has gained attention in epidemics (Merl and Mangel in press) and conservation (Cleaveland *et al.* 2002), where susceptible individuals are removed, vaccinated or a combination of both. There are many examples where prevention of disease spread is aimed for in order to minimise economic costs for the community, e.g. badger (*Meles meles*) culling in the UK to prevent cattle infection with bovine tuberculosis (Woodroffe *et al.* 2006), and bison (*Bison bison*) culling, vaccination and winter feeding to prevent movement into cattle areas and infection of cattle (Cross *et al.* 2007).

In red grouse, anthelmintic drugs are applied by gamekeepers to prevent disease outbreaks and population crashes (Newborn and Foster 2002). Harvesting has not been incorporated into these experiments but might serve as an important component because of its ability to reduce population size and alter population structure. The interaction of increased harvesting rates, harvesting early in the season and application of drugs might allow higher yields from a more stable population. The information gained from such experiments might be useful for other species threatened by disease outbreaks. In particular the indirect application of anthelmintic drugs without handling the animal, combined with controlled removal of the most infected age and sex classes, might benefit a population under threat.

*7.9.3   Monitoring*

In a variable environment, detailed knowledge of the population size and structure are important, as uncertainty increases the chance of overexploitation and local extinction. Hauser *et al.* (2006a) showed that in exceptional years the monitoring effort has to increase, so that the management strategy can be adjusted appropriately. However, it is not just the effort put into monitoring that is important. The data that are collected determines whether the difference in population size and structure is detected by the monitoring regime. Katzner *et al.* (2007) demonstrate that the predictive power of monitoring for population size and growth depends on the life stage that is monitored. This stresses the importance of monitoring important age- and sex-classes. For red grouse, the sex of old birds might be crucial to monitor because the overall assumption of equal numbers of males and females in the population might not be valid due to selective shooting and sex differences in dispersal. A skewed sex ratio can decrease population size and harvest yield in a monogamous species where equal numbers of females and males are needed to ensure reproduction (chapter 6). Therefore, monitoring adult sex ratio in spring before the start of the breeding season might be able to give a first estimate of the expected number of young of the year and the harvestable population.

Including the demographic structure of a population into monitoring and management can provide valuable information as outlined above. Just increasing the monitoring effort might pose unnecessary costs, however, since recent work has shown that the accuracy and optimal frequency of monitoring depends on environmental variables (Hauser *et al.* 2006a). At low population density, red grouse show a tendency to aggregate in relatively large groups in July. This is especially pronounced during periods of drought and high temperature, when grouse can be found in wetter areas. These factors might be important to take into account if one aims to reduce the costs of monitoring and keep reliability high. It remains to be tested what drives monitoring uncertainty in red grouse, but monitoring effort might be more important at extreme low density when grouse are more aggregated.

## 7.10 Conclusion

This thesis aimed to increase knowledge of age-related processes in red grouse. In the second chapter age-related parasite burdens were estimated, with the old age class (> 1-year-old) being split for the first time into 2-year-old and 3+-year-old grouse. The study showed that parasites were not evenly distributed and that the degree of aggregation was different between all three age classes on this moor during the time of the study. This finding had important implications in the population model in chapter 6, where the aggregation of the parasites created a nonlinear mortality curve and this interacted with the harvesting pressure.

The relationship between fecundity and age investigated in chapter 3 showed that variation between years and nesting habitat influences reproductive success in a fluctuating species. Chapter 3 indicated that a long-term study collecting individual-based data might be able to disentangle important processes determining fecundity in red grouse.

The factors affecting shooting selectivity were investigated empirically in the fourth chapter, showing that red grouse shooting was unintentionally selective for specific age- and sex-classes. The effect on the population dynamics were explored in the modelling chapters (5 & 6), which showed that shooting can alter the sex ratio and affect the fecundity of a monogamous bird.

A stochastic age and sex-structured population model enabled exploration of the findings from the field data (chapters 2-4) and the provision of recommendation for management. The combination of observations in the field and modelling is a useful approach to investigate complex mechanisms. This thesis showed that the demographic structure of the population is important to understand if one aims to manage harvested species in a sustainable way. The current management with harvesting rates rarely exceeding 50% seems to be a good precautionary approach for sustainable management of red grouse. The timing of the harvesting season and the uncertainty in the harvest rate are important determinants of the sustainability

and yield of red grouse shooting and it might be useful to take these issues more fully into account in future management planning.

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