Aspects of red grouse Lagopus lagopus scoticus population dynamics at a landscape scale in northern England and the implications for grouse moor management

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Aspects of red grouse *Lagopus lagopus scoticus* population dynamics at a landscape scale in northern England and the implications for grouse moor management

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The thesis is submitted for examination for the degree of
Doctor of Philosophy

Declaration

The material contained in this thesis has not previously been submitted for a degree at the University of Durham or at any other university. The research reported in this thesis has been conducted by the author, unless otherwise indicated.

Aspects of red grouse *Lagopus lagopus scoticus* population dynamics at a landscape scale in northern England and the implications for grouse moor management

ABSTRACT

Red grouse *Lagopus lagopus scoticus* are an important game species in the United Kingdom, with many areas of heather moorland managed specifically to produce them for driven shooting. In order to effectively manage red grouse populations it is important to have an understanding of their population dynamics and to determine which of the vital rates most effect population growth and recovery and whether these parameters can be influenced by management activities.

The focus of my research was to provide a greater understanding of the respective roles of juvenile dispersal, heather management and mortality causes in red grouse population dynamics at a landscape scale in northern England. The study was undertaken between 1999 and 2005 and encompassed four privately owned grouse moors, covering some 113 km^2 of heather dominated moorland. Central to my research was the ability to accurately and efficiently survey the distribution and abundance of red grouse across the study area. To facilitate this I evaluated a distance sampling method to survey red grouse across the study area pre-breeding in spring and post-breeding in summer. The distance sampling technique proved a reliable, repeatable and practical method for extensive surveys of red grouse. Grouse distribution data were used to construct spatial patterns of grouse abundance at a moor scale using a geostatistical interpolation technique.

Rotational heather burning is practised by grouse moor managers to create a mosaic of heather ages which provide food, shelter and nesting habitats for red grouse. To assess the spatial and temporal effects of heather burning on grouse, I used an earth observation technique, using satellite remote sensing to map the habitat mosaic across all four study moors in 2000. Temporal effects of heather burning, from 2000 to 2005 were studied on one moor, with annual heather burning mapped annually.

Dispersal is an important element of population dynamics which influences population growth and spread, gene flow and disease transmission. I used radio telemetry to investigate the timing, frequency and distances of dispersal in juvenile red grouse. Dispersal distance differed between sexes, with juvenile females dispersing on average 861 m (±120 SE) compared to 343 m (±31 SE) recorded in males. Population growth did not appear to be limited by dispersal and abundance increased until the density dependent effect of the parasitic nematode worm *Trichostrongyle tenuis* caused a population crash.

On the study moors, grouse moor management resulted in rapid population growth with population oscillations caused by density dependent strongylosis induced crashes. The main cause of mortality was found to be shooting and to dampen population oscillations, modified shooting programmes to limit population growth in conjunction with parasite control measures should be adopted to better manage grouse populations.

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CHAPTER 1

General Introduction

1.1 Population dynamics

An understanding of the population dynamics of individual species is important to inform conservation and management strategies. A 'population' is defined as a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and migration behaviour, and in which population changes are largely determined by the input processes of birth rates and immigration and the output processes of death and emigration (Berryman & Turchin 2001). The goal of many ecological studies is to gain an understanding of the factors which affect the distribution and abundance of species and the associated mechanisms that drive changes in population structure. The factors which influence these changes in populations, such as recruitment, competition, dispersal, food resources and disease are termed as limiting factors (Newton 1994).

The population dynamics of species are influenced by dispersal, that is, the rates and range of movement by the species involved. Natal dispersal, defined as the permanent movement of individuals from natal areas to locations where they breed is observed in most vertebrate species (Greenwood 1980). Dispersal strategies vary between individuals and between species (Paradis *et al.* 1998; Sutherland *et al.* 2000; Swingland 1983). Knowledge of the dispersal strategies of species is a fundamental element of population dynamics (Arcese 1989), which influences the growth and spread of populations (Hengeveld 1994; Paradis *et al.* 1998; Sutherland *et al.* 2000) and with it both gene flow (Neigel & Avise 1993) and disease transmission (Smith *et al.* 1996).

The population dynamics of red grouse *Lagopus lagopus scoticus* have been the subject of intense study since 1911 (Lovat 1911). These studies have identified several factors which determine red grouse distribution and abundance. They include the presence and management of heather *Calluna vulgaris* (Jenkins *et al.* 1963), predation (Jenkins *et al.* 1964), harvesting (Potts *et al.* 1984; Williams 1985) spacing behaviour (MacColl *et al.* 2000; Moss & Watson 2001) and parasites, in particular the caecal threadworm *Trichostrongylus tenuis* (Hudson 1992; Potts *et al.* 1984), but also the virus, louping ill (Laurenson *et al.* 2004). In order to effectively manage red grouse populations it is important to determine which of the vital rates most affect population growth and whether these parameters can be influenced by management activities. For instance the dispersal strategies of red grouse may be an important factor in their population dynamics and therefore may have repercussions for grouse moor management. The focus of my research was to provide a greater understanding of the respective roles of juvenile dispersal and mortality causes, and the role of heather management on the population dynamics of red grouse on managed grouse moor in northern England.

1.2 Study species: red grouse

Red grouse *Lagopus lagopus scoticus* (a subspecies of the willow grouse *Lagopus lagopus*) is a bird of heather moorland often regarded as an avian indicator species of 'upland' habitats in Britain (Fuller 1982). Red grouse are a favoured sporting quarry, with many areas of heather moorland managed specifically to produce grouse for shooting (Hudson 1992). Heather provides the birds with shelter, cover and forms at least 90% of their diet throughout the year (Jenkins *et al.* 1963; Savory 1978; Wilson 1911). They also feed on other moorland plants such as the flower buds of cotton grass *Eriophorum vaginatum*, which are a rich protein source in the early spring (Trinder 1975); the leaves and fruits of bilberry *Vaccinium myrtillus,* cowberry *Vaccinium vitis-idaea*, crowberry *Empetrum nigrum* and the seeds of heath rush *Juncus squarrosus*, sedges *Carex spp.* and grasses.

Red grouse are typically monogamous and territorial, with males establishing territories in the autumn. They defend their territories until the following breeding season, only abandoning them in harsh weather, such as prolonged snow cover when food resources may be limiting (Jenkins *et al.* 1963; Mougeot *et al.* 2003). Territorial males are less aggressive towards close kin rather than non-kin and favour the recruitment of close kin, resulting in clusters of related males (Matthiopoulos *et al.* 2002; Mountford *et al.* 1990; Watson *et al.* 1994). When densities reach peak levels, territory sizes reach a minimum size, as small as one hectare at high density and population decline occurs due to increased aggressiveness and reduced recruitment (Mougeot *et al.* 2003). Without recruitment sufficient to compensate for mortality, kin clusters decay and the reduced recruitment leads to decline (Mougeot *et al.* 2005). Experimentally increased male aggressiveness through testosterone injections resulted in males establishing larger territories, reducing both recruitment and breeding densities (Mougeot *et al.* 2005).

Females begin laying eggs in mid-April, with an average clutch size of eight eggs (Hudson 1986), varying from six to 11 eggs. The nests are a shallow scrape on the ground usually in areas of taller, denser heather (Campbell *et al.* 2002). The twenty two day incubation period is undertaken by the female. Chicks hatch in late May and early June, obtaining nourishment from their invaginated yolk sac for the first three days (Bergerud 1970). The parents lead their precocial young to foraging habitats where they peck at appropriate foods while giving a specific 'food call'. For the first 10-14 days they forage on protein rich insects (Butterfield & Coulson 1975; Park *et al.* 2001; Savory 1977), but also feed on heather shoots from day one. In late September, the family coveys begin to break up and juveniles become independent, with males establishing territories in October (Matthiopoulos *et al.* 2002).

Red grouse are affected by two parasites, the nematode worm *Trichostrongylus tenuis* which can cause the disease strongylosis (Hudson *et al.* 2002) and the virus, louping ill (Hudson *et al.* 1995). The Trichostrongyle worms live in the caecae of the grouse and most birds have them present in low numbers. High infestations lead to poor breeding productivity (Newborn & Foster 2002) and ultimately can cause death through starvation (Hudson 1986). Louping ill is transmitted by sheep ticks and is fatal to 80% of grouse chicks (Reid *et al.* 1978) and can suppress grouse abundance at low densities (Duncan *et al.* 1978; Hudson *et al.* 1995; Laurenson *et al.* 2004).

1.3 Population cycles

Red grouse populations demonstrate cycles with periods varying from four to ten years (Moss & Watson 2001). The actual mechanisms causing population cycles in red grouse are, like other species which demonstrate cyclic population fluctuations, such as snowshoe hare *Lepus americanus* and lemmings *Dicrostonyx groenlandicus*, still widely debated (Gilg *et al.* 2003; Hudson & Bjornstad 2003; Turchin 2003). Cycles observed in different species are affected by different extrinsic mechanisms (Newton 1994) and there are many inter-related causes and effects. One of the best examples, is the ten year cycle observed in snowshoe hare, where the role of predation by lynx *Lynx canadensis* is an important limiting factor (Krebs *et al.* 1992). A similar predator-prey relationship has been observed in the four year cyclic dynamics of lemmings in Greenland, which are driven by a one year delay in the numerical response of a specialist mammalian predator, the stoat (Gilg *et al.* 2003). The three to five year cycles observed in rodents in northern Europe and the arctic tundra, are widely accepted to be driven by specialist mustelid predators (Hanski *et al.* 2001; Turchin 2003), with the interaction with food resources found to be driving the dynamics of some lemming populations (Turchin *et al.* 2000).

In red grouse there are two main hypotheses for population cycles, kin selection (Matthiopoulos *et al.* 2002; Moss & Watson 1984) and parasites (Hudson *et al.* 1985, 2002). The parasite hypothesis associates the observed cycles with parasitism by the caecal nematode *T. tenuis* which at high grouse densities reduces both host fecundity (Newborn & Foster 2002) and survival (Wilson & Wilson 1978). The kin selection hypothesis suggests that an intrinsic mechanism where individuals show greater resistance to further settlement at higher densities, leading to reduced recruitment being the cause of cycles (Moss & Watson 1984; Mountford *et al.* 1990), rejecting the role of extrinsic factors such as food, predators and parasites. This is a viable hypothesis for red grouse population cycles, but there is no other published evidence where an intrinsic factor explained complex population dynamics in nature (Turchin 2003).

The two hypotheses to explain cycles in red grouse populations have been developed by researchers in two different and geographically distinct areas of the red grouse range in the United Kingdom. The kin selection hypothesis originated from moors in North East Scotland, which are relatively dry and on free draining soils (Moss & Watson 2001), whereas the parasite induced hypothesis was derived from research conducted on wetter moors on deep peat in northern England (Hudson *et al.* 2002). The cycles in the two regions differ, in North East Scotland the cycles are more symmetrical, with equal time in the increase and decrease phases (Moss *et al.* 1993). This contrasts to cycles in northern England, where distinct abrupt population crashes occur (Hudson *et al.* 1998). The shorter cycles observed in England are associated with higher growth rates in the population and more distinct crashes, in comparison to the lower growth rates and longer cycles observed in Scotland (Shaw *et al.* 2004).

Since 1911, the focus of red grouse research in the United Kingdom (Lovat 1911) has been to dampen the oscillations in red grouse populations caused by the nematode worm *Trichostrongylus tenuis*. The oscillations in red grouse have been successfully dampened experimentally in two different studies, by reducing parasite burdens in adults (Hudson *et al.* 1998) and by manipulating grouse density (Moss *et al.* 1996). The first study was undertaken in northern England where the experimental reduction of *T. tenuis*, through the direct oral dosing of individuals with an anthelminthic drug Levasimole hydrochloride dampened cycles and prevented extreme crashes (Hudson *et al.* 1998). The density manipulation study undertaken in North East Scotland (Moss *et al.* 1996) investigated the effects of removing territorial males each spring to maintain them at a (pre-peak) level. This experiment was successful at reducing spring density, with equal numbers of hens lost from the population.

To reduce the effects of strongylosis on red grouse populations, grouse moor managers practise parasite control. Two main methods are practised, direct oral dosing of individuals with an anthelminthic drug Levasimole hydrochloride and through an indirect method, providing medicated grit, which is a normal quartz grit coated with a layer of fat containing the anthelminthic Fenbendazole hydrochloride, grouse regularly ingest grit to aid the digestion of heather and therefore receive a dose of anthelminthic (Hudson & Newborn 1995). Both these methods can be effective at reducing worm burdens and subsequently increasing breeding success (Newborn & Foster 2002).

1.4 Grouse moor management

Heather moorland is largely restricted to the uplands of Britain and Ireland, a few other areas on the European mainland and the western coast of Norway (Thompson *et al.* 1995). In Britain the characteristic open heather moorland landscape was mostly created from woodland, by the influence of man. From 1945 to 1995 there was a 20-40% loss of heather due to over-grazing by sheep and deer and loss through commercial afforestation (Bardgett *et al.* 1995). Heather moorland in the United Kingdom is recognised as a habitat of international importance (Gimingham 1981) with the United Kingdom upland heath resource estimated at two to three million hectares. Large areas of upland heath now have legal protection and are designated either nationally as Sites of Special Scientific Interest (SSSI) or internationally as Special Areas for Conservation (SAC) and Special Protection Areas (SPA).

Since the mid 19th century many areas of heather moorland in the United Kingdom have been managed for grouse shooting (Tapper 1992). Today, grouse moor management is still one of the major land uses in the uplands and is economically important for many land-owners (White & Wadsworth 1992). The numbers of red grouse shot in the United Kingdom has declined, with shooting bag records showing an 82% decline between 1911 and 1980 (Tapper 1999). The rates of decline have varied between regions with the most significant declines being in Scotland and Wales, in contrast to northern England where on many moors, numbers have remained stable. The causes of decline are linked to the loss of heather moorland due to overgrazing by sheep and deer and to commercial afforestation (Hudson 1992; Robertson *et al.* 2001), but are also linked to increases in predator numbers, both of mammals and birds of prey (Redpath & Thirgood 1997) and the reductions in the numbers of gamekeepers employed (Tapper 1992).

To create harvestable surpluses of red grouse for sport shooting, gamekeepers are employed to manage the heather moorland through rotational burning of heather and to control the predators of grouse, mainly red fox *Vulpes vulpes*, crows *Corvidae*, stoat *Mustela erminea*, weasel *Mustela nivalis*, and brown rat *Rattus norvegicus* (Hudson & Newborn 1995). Heather burning is accepted as an important part of grouse moor management to maintain high grouse densities (Miller *et al.* 1970; Picozzi 1968). The objective of heather burning is to produce a mosaic of different heather habitats within each grouse territory (Miller *et al.* 1966). Typically strips are burnt which are 20-30 m wide and several hundred metres long, in an eight to 30 year rotation.

The preferred method of harvesting red grouse in the United Kingdom is by driven shooting, which begins on the 12th August and ends on the 10th December (Hudson 1984). Driven shooting typically occurs when summer grouse densities exceed 60 birds per km^2 (Hudson 1992), with most shooting occurring within the first six weeks of the season (Hudson 1984). A typical shoot day includes four or five drives, each encompassing some 0.5 km^2 to 2.5 km^2 of moorland (Hudson 1984). Red grouse are driven by a team of ten to 20 beaters towards a line of eight to ten standing guns, hidden within stone, earth or wooden hides known as 'butts'. The shooting 'bag' or harvest on any one driven day is typically between 100 and 600 birds (Hudson & Newborn 1995).

1.5 Sampling techniques

To provide a greater understanding of the vital rates and dispersal strategies of managed red grouse populations at a landscape scale in northern England, suitable survey techniques are required. Counting techniques are widely used to study and monitor birds (Bibby *et al.* 1992; Gilbert *et al.* 1998) and this information is used to quantify the presence or absence of species and to assess their distribution and population dynamics. There are a wide variety of survey techniques which can be broadly categorized into two groups, empirical modelling techniques and index counts. Empirical modelling techniques directly estimate density, such as distance sampling (Buckland *et al.* 1993).

Distance sampling is an integrated approach to sampling which includes study design, data collection and statistical analysis which offers a cost-effective and statistically robust method for evaluating population distribution and abundance at landscape scales. Index counts are methods which use maps or counts of birds as an index of abundance. A review by (Rosenstock *et al.* 2002) found that the current preferred survey methods for birds are index counts, 95% of studies conducted from 1989 to 1998 used index count methods. Limitations of index counting methods have been recognized for some time (Burnham 1981; Nichols *et al.* 2000; Verner 1985), with three recognized main causes of bias, being observer bias (Cyr 1981; Faanes & Bystrack 1981; Kepler & Scott 1981; Sauer *et al.* 1994), environmental bias (Karr 1981) and the bias caused by behavioural and physical attributes of the study species (Sayre *et al.* 1978; Wilson & Bart 1985). In this thesis, I evaluated the distance sampling method to survey red grouse at the spatial scale of the moor.

1.6 Objectives

Fundamental to my study, was being able to accurately and efficiently survey the distribution and abundance of grouse at a grouse moor scale, which in this study encompasses four privately owned grouse moors, comprising some 113 km^2 of heather moorland in northern England. Accordingly in Chapter 3, I assessed the suitability of a distance sampling technique to survey grouse distribution and abundance at this spatial scale. In Chapter 4, I used an earth observation technique to map the habitat mosaic created by heather burning and investigated the impacts of this management on grouse density and breeding success. I investigated the dispersal strategies of juvenile grouse on the study area using radio telemetry in Chapter 5, and in Chapter 6, I evaluated breeding success, harvest rates and over-winter losses on the population dynamics of grouse on the study moors and compared and contrasted the causes of mortality found here with data collected from other telemetry studies on red grouse from two other regions in the United Kingdom, the Scottish Highlands and the Scottish Borders.

1.7 Hypotheses tested

The following hypotheses were tested in this thesis:

(1) Is distance sampling suitable for surveying red grouse at the moor spatial scale and do the density estimates generated compare with those from other methods (Chapter 3).

(2) Is Remote Sensing suitable for mapping the heather moorland mosaic created by heather burning (Chapter 4).

(3) If heather burning improves red grouse habitat, then smaller and more frequent fires may increase settling densities and breeding success (Chapter 4).

(4) If dispersal of juvenile red grouse is density dependent, then at high grouse density may the frequencies and distances of dispersal increase (Chapter 5).

(5) If shooting is a major cause of mortality in red grouse, may it be used to limit population growth and therefore control population cycles (Chapter 6).

CHAPTER 2

Study area, general methods and timetable

2.1 The study area

The study was conducted between 1999 and 2005 on an extensive area of 113 km^2 of dwarf shrub heath, dominated by heather in the North Pennines, England (Figure 1). The study area comprised four privately owned grouse moors, all of which employed full-time gamekeepers. The moors were separated into two distinct geographic sections by the River Wear valley. The southern section comprised three adjacent moors, the Bollihope, Raby and Eggleston moors, covering 81 km^2 of continuous moorland. The Edmondbyers moor in the northern section covered 32 km^2. The altitude at the sites ranged from 240 m to 650 m above sea level.

The open landscape and habitats which are characteristic of the study area are strongly influenced by the two main land uses; grouse shooting and hill sheep farming. The heather moorland was burned in rotation by the moorland gamekeepers to create a mosaic of different heather ages for red grouse. The heather moorland was also subject to collective grazing from hefted sheep flocks from adjoining hill farms, with some parts of the moorland not grazed during the winter to prevent heather damage and with other areas subject to all year grazing.

The vegetation on the study area was chiefly dwarf shrub heath, characterised by the predominance of dwarf shrubs such as heather, bilberry, bell heather *Erica cinerea* and cross leaved heath *Erica tetralix* and various grasses, sedges and rushes. The structure and composition of the shrubby heath was dependent on local geology, drainage, sheep grazing pressure and the frequency of heather burning (Gimingham 1975). On the high plateau, where grazing pressure was lowest and the drainage was impeded, a blanket bog community dominated by cotton grass and heather was present on the deep peaty soils. At low altitude on the well-drained soils, dry *Calluna* heath was dominant, with bracken *Pteridium aquilinum* present on the shallow soils of steep slopes. On the edges of the heather moor, where the sheep grazing intensity has historically been the highest, the shrubby heath had been replaced by grassy heath vegetation locally known as 'white grass moorland' characterised by coarse grasses *Deschampsia flexuosa*, *Festuca ovina* and *Nardus stricta* and heath rush.

Figure 1 The location of the study moors in County Durham, England.

2.2 Fieldwork

The collection of field data began in the summer of 1999. The study commenced too late in summer 1999 to undertake a full survey of red grouse distribution and densities post-breeding across the study area using the distance sampling method (Chapter 3). I began fieldwork (Table 1) with the investigation of juvenile dispersal in red grouse using radio telemetry (Chapter 5). Juvenile grouse were caught and fitted with radio transmitters in the core of the proposed study area and their movements followed through the following year.

To assess whether grouse dispersal rates or distances were influenced by post-breeding summer densities or densities the following spring, grouse density and distribution were assessed using a line-transect distance sampling technique (see Chapter 3) across all four study moors in spring and summer 2000. A second sample of juvenile grouse were caught and fitted with radio transmitters in summer 2000, in areas of calculated high and low density (see Chapter 5). In spring 2001, I intended to resurvey grouse densities and distributions across all four moors to assess settling patterns of radio tagged grouse and to facilitate the investigation of over-winter mortality across the survey area in relation to calculated autumn densities, breeding success, parasite burdens and harvest rates. Unfortunately in spring 2001, fieldwork was restricted due to an outbreak of Foot and Mouth Disease, which prohibited access to the study area. Data collection commenced again in the summer of 2001 but with access limited to only two of the moors, Raby and Eggleston. A third sample of juvenile grouse were caught and tagged in summer 2001, again in areas of calculated high and low densities.

Table 1 A summary of the fieldwork undertaken during the study, 1999-2005.

	Fieldwork completed						
	1999	2000	2001	2002	2003	2004	2005
Distance sampling surveys (Chapters 3,4,5&6)		All four moors in spring and summer	Eggleston and Raby in summer	Eggleston and Raby in spring. Eggleston only in summer	Eggleston in spring and summer	Eggleston in spring and summer	Eggleston in spring and summer
Habitat mapping using earth observation (Chapter 4)		Image acquired and ground control measures					
Mapping of heather burning (Chapter 4)		Eggleston study moor only	Eggleston study moor only	Eggleston study moor only	Eggleston study moor only	Eggleston study moor only	Eggleston study moor only
Radio telemetry (Chapter 5&6)	61 radio tagged individuals	26 radio tagged individuals	59 radio tagged individuals				

To assess the effects of heather moorland management, particularly heather burning, on the density, distribution and breeding success of grouse across the study area, a Landsat ETM+ satellite image for May 2000 was acquired and processed (see Chapter 4). Field measures to identify distinct heather habitat types and ground control information were collected in that year.

To quantify the temporal effects of heather burning on grouse population dynamics, the study concentrated on one moor, Eggleston from 2000 to 2005, where heather burning management was mapped annually and grouse surveyed in spring and summer, up to and including 2005.

CHAPTER 3

Evaluation of a distance sampling technique to survey red grouse at a landscape spatial scale

Abstract

This Chapter evaluates a line-transect distance sampling technique as a suitable method for surveying red grouse at a landscape spatial scale. Red grouse were surveyed across the study area pre-breeding in spring and post-breeding in summer. Density estimates generated using distance sampling were compared with those from three other independent survey methods; counts of calling males in spring, drive counts in spring and gamekeepers' own counts in summer.

Measures of grouse abundance from counts of calling males and drive counts were made in random sample blocks in areas of high, medium and low grouse density. These blocks were selected from a grouse distribution map created from the flushed grouse coordinates from the line transects using a spatial interpolation measure, known as Kriging. Estimates of grouse density in summer in each management unit (beat) across the study area were compared with the results of counts undertaken by gamekeepers.

The estimates of grouse abundance in spring from the distance sampling were strongly correlated with the spring drive counts and also with indices of abundance from calling males at low and medium density, but not at high density. Post-breeding densities were positively correlated with those from gamekeepers' own counts.

Distance sampling appears to be a reliable and practical method for extensive surveys of red grouse and geostatistical interpolation can be used to construct spatial patterns of grouse distribution at a moor scale.

3.1 Introduction

Fundamental to the conservation and management of many bird species are accurate and cost effective survey techniques to estimate abundance and distribution (Bibby *et al.* 1992; Gilbert *et al.* 1998). Distance sampling is a method for estimating the abundance of biological populations (Buckland *et al.* 1993; Burnham *et al.* 1980) and is an integrated approach to sampling which includes study design, data collection and statistical analysis. Distance sampling provides estimates of density which are not confounded by the detectability of the study species, even though a large proportion of individuals may go undetected, as the theory allows accurate estimates to be made under mild assumptions. Distance sampling is a widely used survey technique and has been used successfully to survey a wide range of fauna, from birds (Cassey & Ussher 1999; Oliveira *et al.* 1999) and butterflies (Brown & Boyce 1998) to large African herbivores (Jachmann 2002) and cetaceans (Hammond *et al.* 2002).

In this Chapter I evaluated whether a line-transect distance sampling technique using trained pointing dogs, is an appropriate and effective method to survey red grouse at a landscape spatial scale. Many red grouse monitoring programmes use sample units of one km^2, surveyed with pointing dogs to assess pre-breeding densities in spring and post-breeding densities and breeding success in summer. This approach provides data on annual variations in densities and breeding success, making it possible to predict cyclic changes (Moss & Watson 2001), but yields little direct information on population processes other than birth rates. The one km^2 count area is small relative to prospective scales of red grouse movements, with mean natal distances of 11.4 km recorded in female willow grouse (Smith 1997) and 9.3 km in female black grouse *Tetrao tetrix* (Warren & Baines 2002). Therefore the effects of immigration, emigration and mortality on subsequent population dynamics cannot be readily taken into account. Many management decisions by grouse moor managers regarding the levels of shooting or the need for parasite control are, however, taken at the 'beat' (management unit) or moor scale, hence spatially reliable data on red grouse at extensive 'moor' scales are required.

3.2 Methods

The study was conducted over an area of 113 km^2 of heather moorland, managed as four separate grouse moors in the North Pennines, England and comprised the following aspects:

1) **Distance sampling:** Red grouse were surveyed pre-breeding in spring and post-breeding in summer using a line-transect distance sampling method. Grouse moor population estimates in spring and summer were derived using the DISTANCE computer program (Laake *et al.* 1994).
2) **Evaluating the method:** Three different measures of grouse abundance were collected to compare against those derived from the distance sampling method; calling males in spring, drive counts in spring and gamekeepers' surveys in summer. To select samples of calling males and drive counts in areas of low, medium and high grouse density I used a spatial interpolation measure, Kriging (Burrough & McDonnell 1998; Lam 1983), to create a continuous surface of grouse distribution for that corresponding period using the flushed grouse coordinates from the line transects.

3.2.1 Distance sampling

Distance sampling is based on the measurement of distance of objects from a point or a line and is based on the concept of the detection function, which is the probability of detecting an object with distance from the line or point (Buckland *et al.* 1993). The detection function compensates for the decreasing detection of objects with increasing distance from the observer. Statistical inference in distance sampling rests on the validity of the following assumptions (Buckland *et al.* 1993):

Assumptions

1) The survey design must be competently designed and conducted, as no analysis can repair fundamental flaws in survey procedure.
2) Study objects are spatially distributed in the area to be sampled according to some stochastic process with rate parameter D (=number per unit area).
3) Randomly placed lines are surveyed and a sample of n objects is detected, measured and recorded.
4) Objects on the line are always detected.
5) Objects are detected at their initial location, prior to any movement in response to the observer.

6) Distances are measured accurately.

These assumptions are essential for reliable estimations of density from line transect sampling.

Survey design

The survey was restricted to moorland where heather, the key food plant of red grouse (Jenkins *et al.* 1963; Wilson 1911) was a component in the sward (>5%), therefore the survey omitted pasture, in-bye allotments, and a large area of white grass dominated moorland. Within this habitat, a stratified random sampling technique was adopted. A systematic design using parallel transects, recommended by Buckland (1993) as the most appropriate were aligned at 500 m intervals across the survey area (Figure 2, Figure 3). The random start was selected as a function of wind direction (It is preferable to work pointing dogs in a direction with the wind directly towards or from behind, as the dogs work on scent). The distance of 500 m between transects were decided upon due to a number of factors, the first being that a distance of 500 m allowed full coverage in the survey time available and secondly this distance was deemed adequate that flushed birds were not recounted on the adjacent transect. From personal observations grouse flights were generally in the region of 200 m to 300 m, both in spring and summer when the surveys were conducted. In spring grouse were reluctant to leave their territories (they can be observed returning to their territories shortly after being flushed), and in summer their flights are short as juvenile birds are still developing their flight muscles.

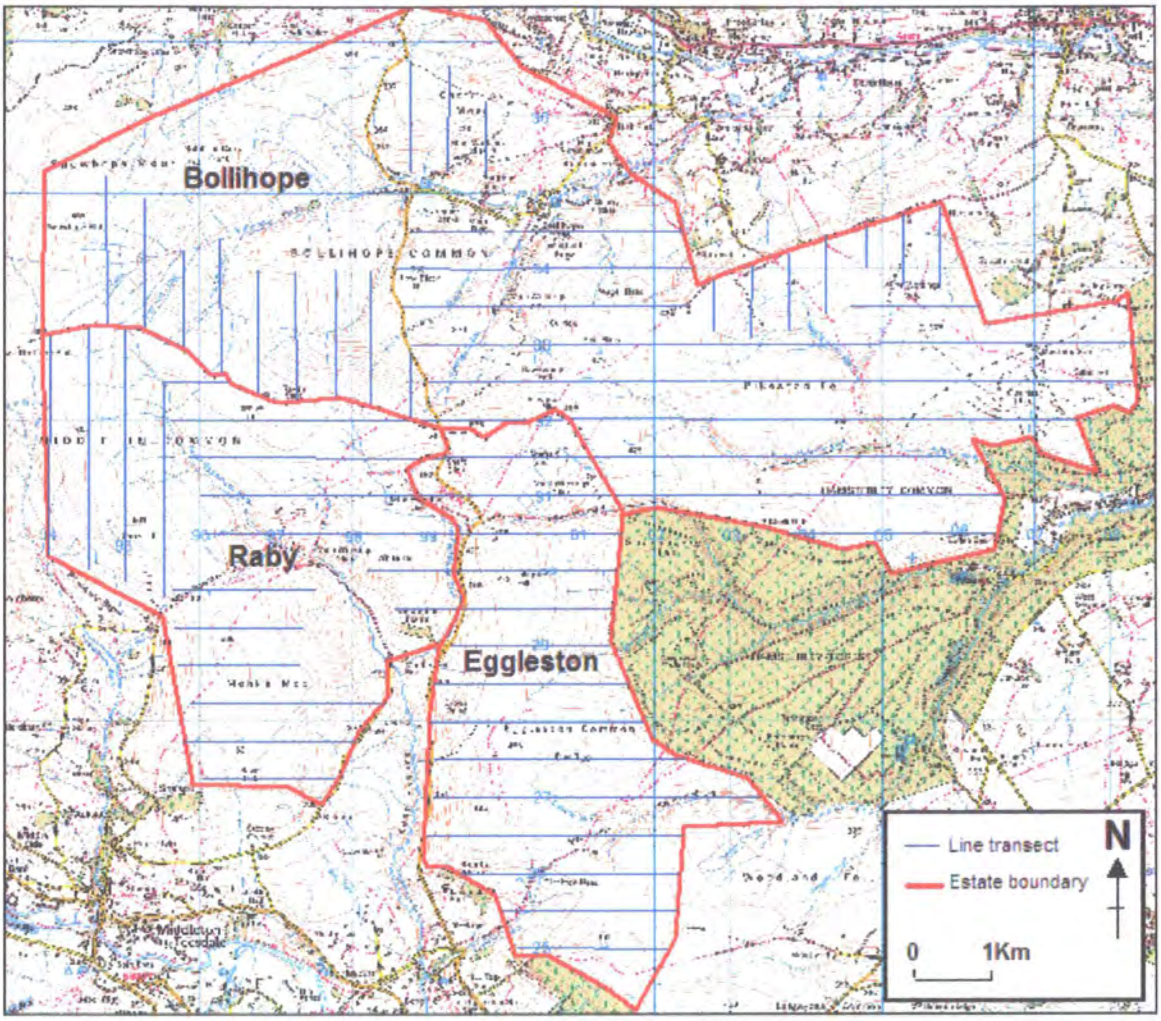


Figure 2 The survey design for distance sampling transects across the southern moorland block in spring 2000.

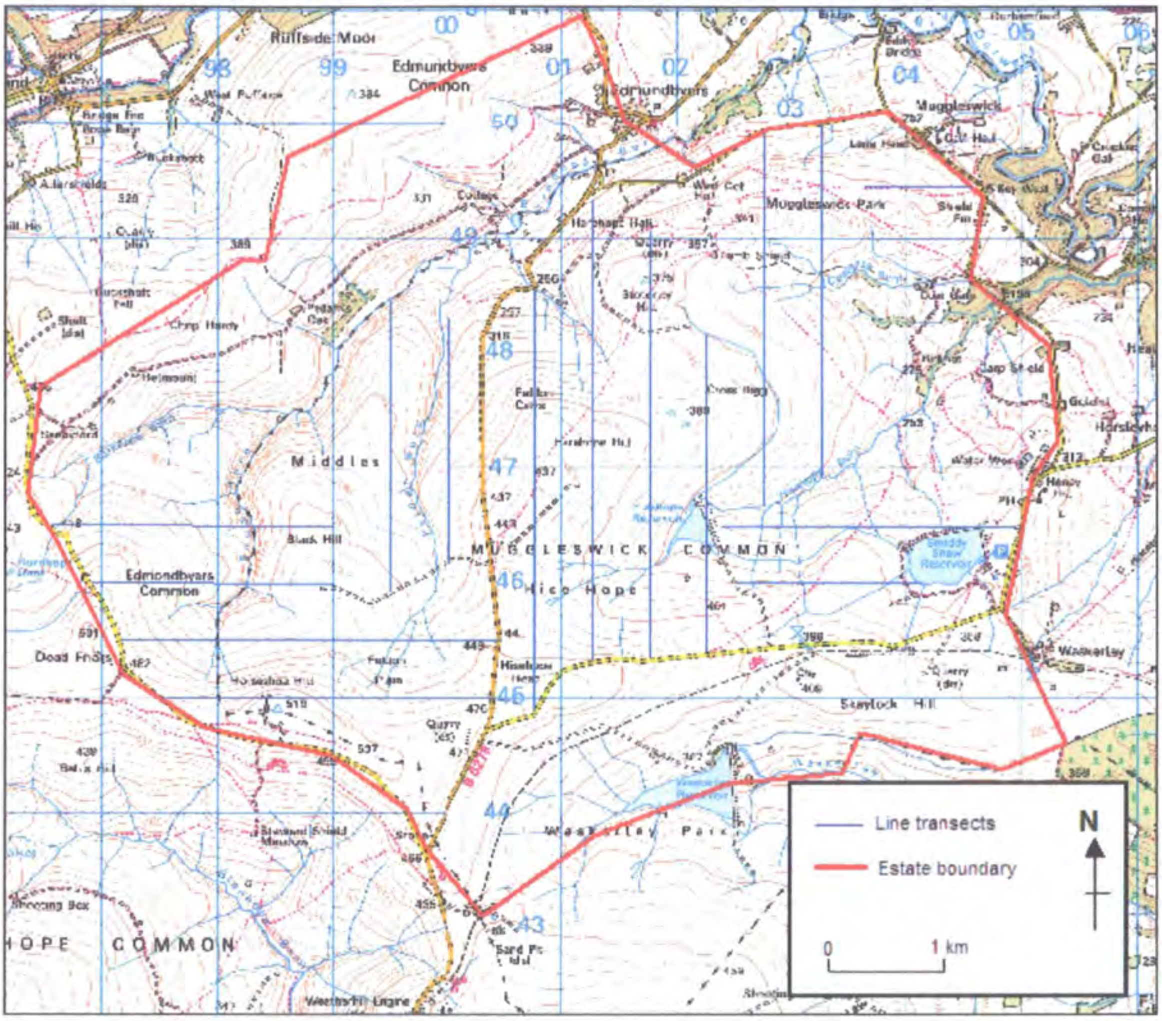


Figure 3 The survey design for the distance sampling transects across the northern moorland block in spring 2000.

Procedure

Sampling began on all moors, Eggleston, Raby, Bollihope and Edmondbyers in spring and summer 2000 (Table 2). In 2001, following a Foot and Mouth Disease (FMD) outbreak, no data was collected in the spring. In the summer, data were collected on two moors, Eggleston and Raby, which were both surveyed again in spring 2002. The study was continued on only one of the moors, Eggleston (19 km^2) with surveys in both spring and summer from 2002 to 2005.

Red grouse abundance was determined by distance sampling during the pre-breeding period in spring, between 6th March and 2nd April when males are highly territorial and again post-breeding in summer, between 11th July and 3rd August when grouse are in family groups or coveys.

Table 2 Summary of the distance sampling line-transect field data collected during the study, pre-breeding in spring and post-breeding in summer (FMD= outbreak of Foot and Mouth Disease).

Estate	Red Grouse Surveys											
	2000		2001		2002		2003		2004		2005	
	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer
Eggleston	*	*	FMD	*	*	*	*	*	*	*	*	*
Raby	*	*	FMD	*	*							
Bollihope	*	*	FMD									
Edmondbyers	*	*	FMD									

The surveyor walked along the route of each transect line whilst systematically working a pointing dog to search for grouse on either side of the transect line. When the dog located a grouse, the surveyor measured the perpendicular distance from the transect line to the dog using a Coincidence 400 range finder, replaced in 2001 with a Leica LRF800 Rangemaster, and recorded his position along the transect using a hand-held Magellan GPS 300 (Global Position System) satellite navigator (Figure 4). Prior to 2000, accuracy of the GPS was only ±100 m (Hulbert & French 2001), so the observer verified his position using 1:25000 Ordnance Survey (OS) maps. The surveyor and dog then flushed the grouse, recording the sex and age of individuals before both returned to the transect line to recommence the survey. Only one measure of distance to each group of birds was recorded. Care was taken to ensure that flushed birds were not recounted along the survey line by watching to see where the birds resettled. Survey work was conducted only in good weather, beginning shortly after dawn in summer to maximise scenting conditions for the hunting dogs, with surveys on average conducted for two to three hours to maintain the searching effectiveness of the dogs. The survey was undertaken by myself, using two dogs and another surveyor, using a further four dogs. Only one dog was used at any one time by each surveyor.

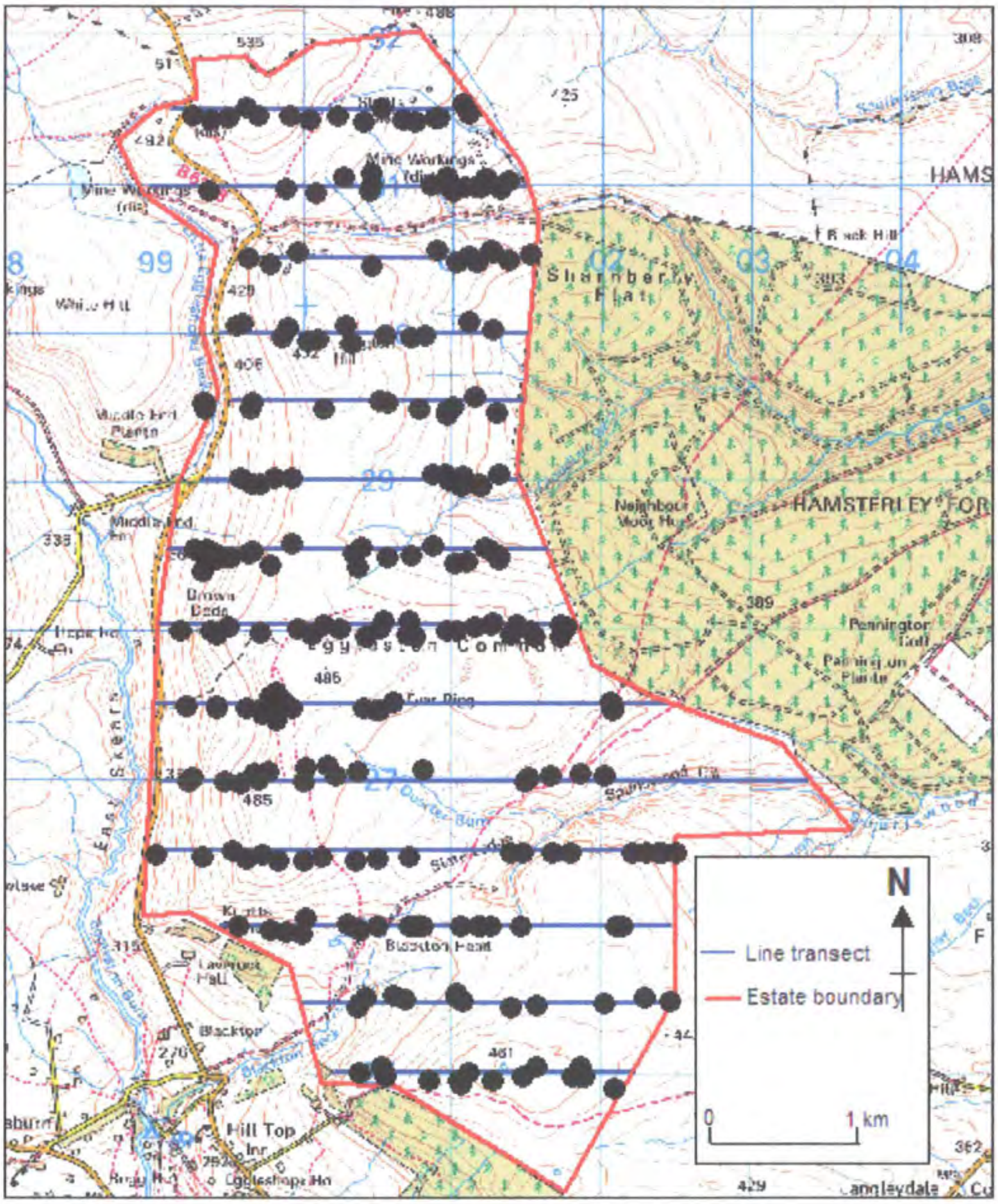


Figure 4 The distribution of grouse flush points along the transect lines on the Eggleston study moor in spring 2003.

Analysis

Separate analyses were performed separately for each survey year and period (spring and summer) using the DISTANCE program (Laake *et al.* 1994). Density ***D*** was estimated, using the standard equation:

$$D = \frac{n}{(2\,u\,L)}$$

Where ***n*** was the number of sightings, ***L*** was the total transect length and ***u*** was the effective strip (half) width.

As red grouse occur in clusters, in spring generally in pairs and in summer in family groups or coveys varying in size from one to twenty, density D was estimated for a clustered population using the standard equation:

$$D = \frac{n\,f(0)\,E(s)}{2L}$$

Where n was the number of sightings, $f(0)$ was the detection function, $E(s)$ was the mean cluster size and L was the total transect length.

A frequency histogram of the perpendicular distance of grouse from the transect line was plotted for each survey season (Figure 5). The histogram was inspected for any evidence of the distance sampling assumptions being invalidated. After removal of outliers using a truncation point of 5%, grouse flush distances were grouped into 20 m intervals and fitted with a curve. Depending on the shape of the curve, the detection function can be modelled using four different estimators, hazard rate, negative exponential, half normal and uniform and three different adjustment terms, cosine, polynomial and hermite. The curve which gave the best fit according to Akaike's Information Criterion (AIC) was selected (Akaike 1973) which for all seasons was a half-normal estimator.

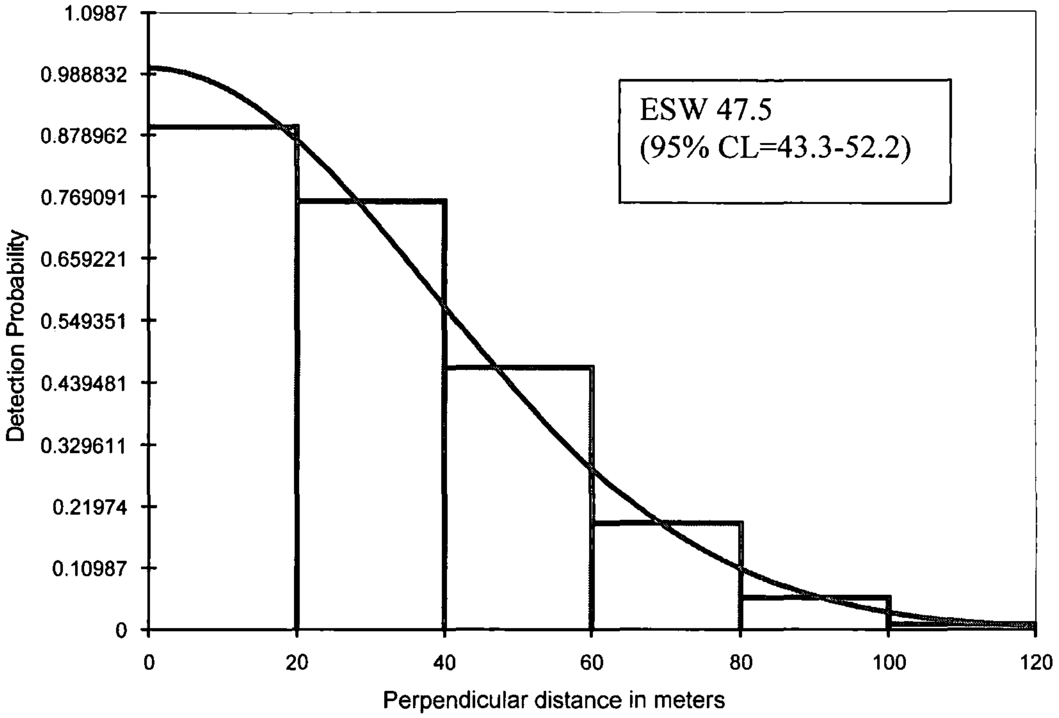


Figure 5 A histogram of the perpendicular distances from the transect line to grouse flushes recorded for Eggleston moor in spring 2003, with the data grouped into 20 m categories. A half-normal detection function was fitted to the data and this model was used in the analysis (ESW= Estimated Strip Width, CL=95% Confidence Limits).

Surveys of clustered populations may require additional care in the analysis as there may be a size bias in the survey technique with the pointing dogs finding larger coveys at greater distances from the transect line. To consider this I correlated covey size against distance from the transect line for both the spring and summer datasets, with the data log transformed to normalise the distributions.

To consider the effects of bias between observers (Graham & Bell 1989; Jachmann 2001), in this case individual pointing dogs, a mean detection function was calculated for each pointing dog for each season of the study. To test for differences in Effective Strip Width (ESW) between year, season and the pointing dogs, a General Linear Model was used, with ESW as the dependent variable and year, season, observer and pointing dogs as the categorical independent variables.

To test for differences in ESW and grouse density in relation to moor, year and season a General Linear Model was used with ESW and grouse density (grouse/km^2) as the dependent variables and moor, year and season as the categorical independent variables.

3.2.2 Evaluation of the distance sampling method

In addition to the distance sampling survey data, three independent measures of grouse abundance were collected:

1) Counts of calling males pre-breeding in spring 2000
2) Drive counts pre-breeding in spring 2000 and spring 2003
3) Gamekeepers' counts conducted post-breeding in summer 2000

To facilitate selection of the sampling locations for the calling males and the drive counts in areas of low, medium and high grouse density on the study area, maps of the spatial abundance of grouse were generated by a spatial interpolation technique, Kriging (Burrough & McDonnell 1998; Krige 1981; Lam 1983) for spring 2000 and spring 2003.

Kriging

Spatial interpolation has been used in ecological studies to determine the spatial distribution of organisms such as carabid beetles (Thomas *et al.* 2001), barnacles (Liebhold *et al.* 1993) and songbirds (Villard & Maurer 1996). I used a spatial interpolation measure, Kriging within the Idrisi computer program (Isaacs & Srivastava 1989; Stein 1999) to create a continuous surface of grouse distribution for the study area, using the grouse location data collected on the line transects.

Kriging was selected as an appropriate interpolation technique in preference to SPLINE or Inverse Distance Weighting (IDW) techniques as it is widely recognised as the most appropriate method (Isaacs & Srivastava 1989). This method uses a variogram to express the spatial variation and it minimizes the error of predicted values which are estimated by spatial distribution of the predicted values. Kriging is based on the assumption that the parameter being interpolated can be treated as a regionalized variable. A regionalised variable is one which takes on values according to its spatial location and is intermediate between a truly random variable and a completely deterministic variable in that it varies in a continuous manner from one location to the next and therefore points that are near each other have a certain degree of spatial correlation, but points which are widely separated are statistically independent (Davis 1986).

Geostatistics are used to identify and model the spatial pattern of the point data and the analysis is a two step process (1) defining the degree of autocorrelation among the measured data points, and (2) interpolating values between measured points based on the degree of autocorrelation encountered (Robertson 1987). Autocorrelation is the propensity for data values to be similar to surrounding data values and describes the error structure within it (Cliff & Ord 1981). Two spatial statistical methods were used to assess spatial autocorrelation, Moran's I (Moran 1950; Sokal & Oden 1978) and semivariance (Rossi *et al.* 1992), which like autocorrelation describes the correspondence between measurements taken on samples located some distance apart. Once spatial dependency is established, the semi-variogram parameters which characterise the spatial structure of the data in terms of the spatial variance are used to interpolate values at un-sampled locations via Kriging.

Procedure

To generate the maps of spatial abundance for the three study moors, Eggleston, Raby and Bollihope in spring 2000 and Eggleston in spring 2003. The line transects used to survey grouse were split into 500 m sections, with the total grouse seen along the section allocated a coordinate for the centre of the section. I then assessed the spatial autocorrelation of the numbers of grouse at the sample points using the Moran's I statistic (Rook's Case), an add-in program for Excel (Sawada 1999).

I investigated the semivariance of the sample point data in Idrisi by constructing a semivariogram, a plot of semivariance against distance (or distance class) (Figure 6). The semivariogram has three characteristic values, the sill, range, and nugget. The sill is the value where the semivariogram levels off and is equal to the total variance of the dataset, the range is the distance at which this occurs and the nugget is the semivariance at distance 0 (the intercept). Strictly the semivariance at lag zero should be zero, a non zero nugget indicates short scale variability in the data and causes discontinuity in the variogram which restricts the range of weightings used in the estimation (Isaacs & Srivastava 1989).

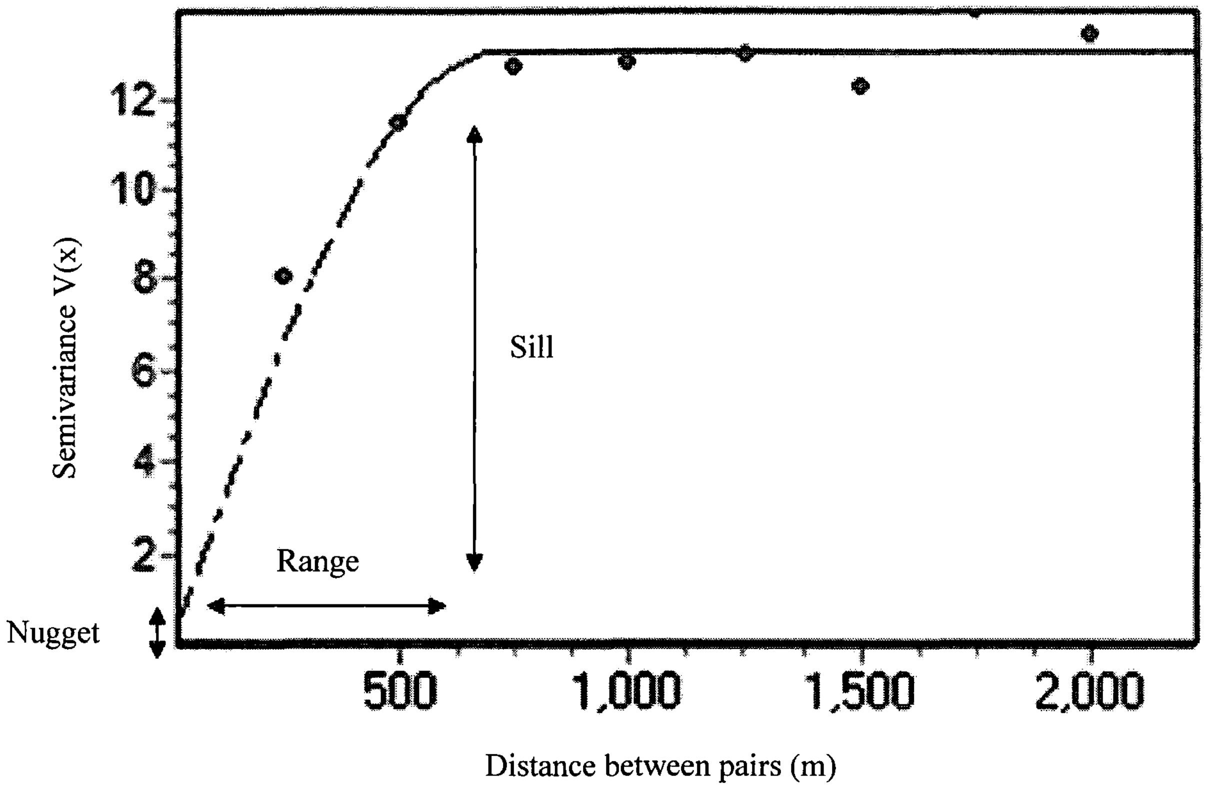


Figure 6 A sample variogram, with the semivariance V(x) on the y axis and the distance between pairs on the x axis. Characteristic features include the range, sill and nugget are included with a theoretical spherical variogram model fit to the data.

The next stage is to fit a mathematical model to the variogram that describes the pattern of spatial variability of the measured surface. This model variogram is a simple mathematical function that models the trend in the experimental variogram and different theoretical variogram models such as linear, exponential, spherical and gaussian can be used to predict values at unmeasured locations. The empirical semivariogram is converted to a theoretic one by fitting one of these statistical models.

As most of the spatial variance is within the first part of the variogram, high quality parameter fitting for short distance lags is important. To fit these algorithms the Restricted Maximum Likelihood Method (REML) (Christensen 1993; Kitanidis 1985) was used as the data did not have a well defined Gaussian distribution in the sample data across lags (Cressie 1993).

The model variogram is utilised to compute the weights used in Kriging. To create an accurate surface of grouse distribution on the study area a 'mask file' which defined the boundaries of the study area was created and incorporated into the Kriging analysis.

3.2.3 Independent measures

Spring calling males

Procedure

Territorial 'calling' red grouse males were surveyed at dawn in April and early May 2000 within 17, each of 25 ha blocks (Figure 7). The sample points were stratified in relation to the Kriged map of spatial abundance in spring 2000, with five blocks randomly positioned in areas with low (<10 grouse per km^{-1}), six blocks in medium (10-20 grouse per km^{-1}) and six blocks in high (>20 grouse per km^{-1}) grouse abundance. The sample blocks were positioned where a distance sampling survey line transect had run through the centre of the block, equidistant to the opposing block edges (Figure 7).

The call counts were conducted at dawn by four independent observers, one positioned in each area, with the observers concealed on site before it was light in a position so they could see and hear from all parts of the survey block. All calling male grouse seen and/or heard were recorded. Call counts began at dawn and continued until 06.45, thus coinciding with the peak of male display activity (Hudson 1992).

Analysis

Density estimates for males only and all adults were calculated for each 25 ha block using the DISTANCE computer program. Due to the low encounter rates on the 500 m line transect which dissected the sample block, on average only eight encounters per km of transect in spring 2000, it was not feasible to calculate a detection function for each sample block, so therefore the detection function calculated from all the surveyed moors in the equivalent spring 2000 period, was used to estimate density within each of the sample blocks.

The mean numbers of males recorded calling at dawn within the 25 ha block in the low, medium and high density categories were compared with the distance sampling estimates for males only and adults by means of a paired t-test.

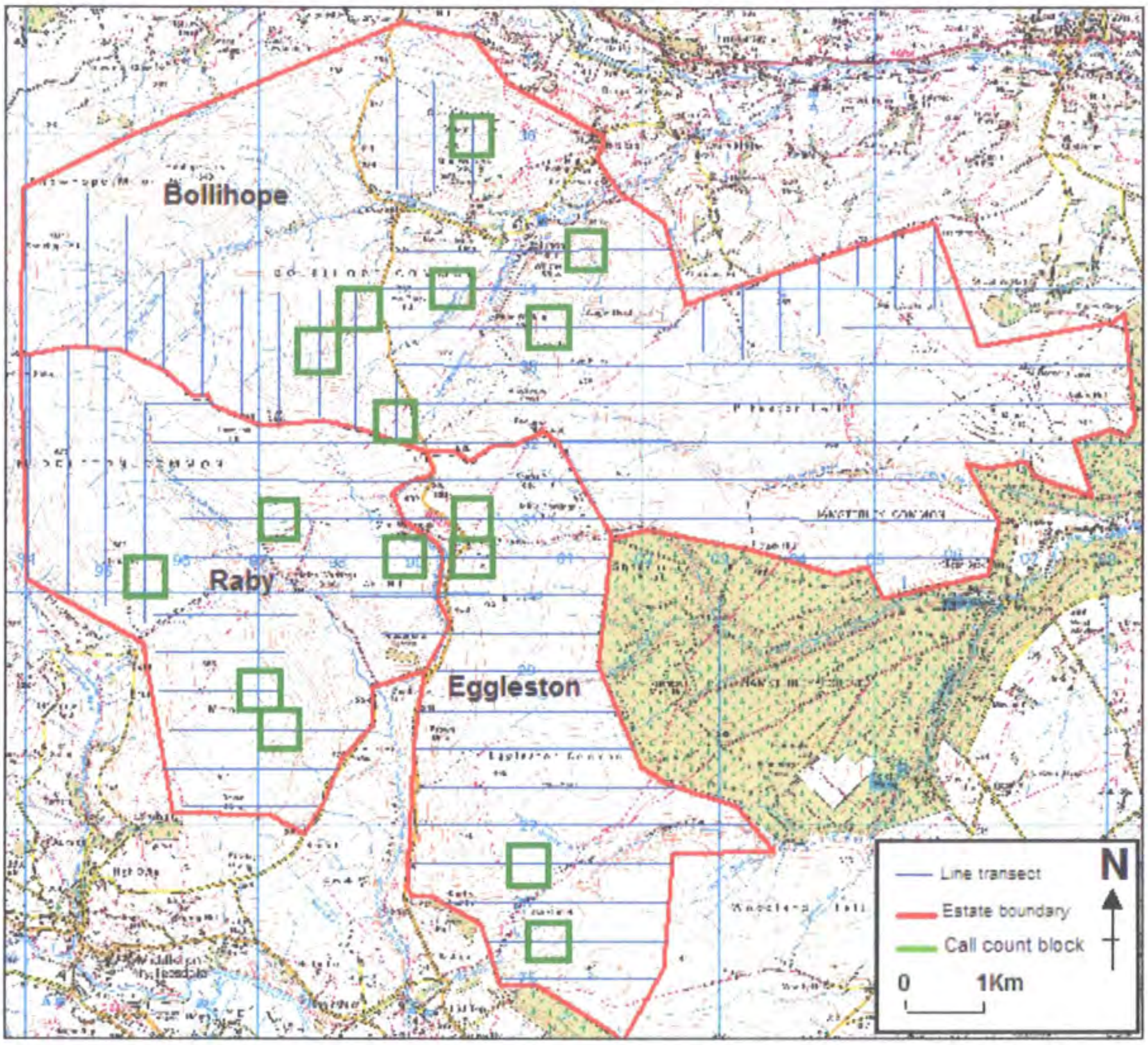


Figure 7 The locations of the 25 ha survey blocks where the numbers of males calling at dawn in spring 2000 were observed, in relation to the distance sampling transects used to estimate grouse density.

Spring drive counts

Procedure

Grouse were flushed by drive counts in April and early May from four 25 ha blocks in 2000 and a further eight in 2003. The sample blocks were randomly stratified in relation to abundance from the map of spatial abundance for that spring. In spring 2000, two blocks were positioned in areas with low (<10 grouse per km^{-1}) and two in medium (10-20 grouse per km^{-1}) grouse abundance. In spring 2003, two blocks were positioned in areas with low (<10 grouse per km^{-1}), three in medium (10-20 grouse per km^{-1}) and three in high (>20 grouse per km^{-1}) abundance from the spring 2003 abundance map.

In an attempt to flush all grouse from the block, a line of surveyors were evenly spaced at 30 m intervals and walked waving flags through each block. The surveys were undertaken between the hours of 09.00 and 17.00, and not in inclement weather.

Analysis

Density estimates for adults were calculated for each 25 ha block using the DISTANCE computer program. Due to the low encounter rates on the 500 m line transect which dissected the sample block, it was not feasible to calculate a detection function for each sample block, so the detection function calculated from all the surveyed moors in the equivalent spring period, four moors in spring 2000 and one moor in spring 2003 was used to estimate density within each of the sample blocks.

The mean numbers of grouse recorded by the drive counts within the 25 ha blocks in the low, medium and high density categories were compared with the distance sampling estimates for adults by means of a paired t-test.

Gamekeepers' summer surveys

Procedure

Gamekeepers routinely assess grouse numbers and breeding success in summer (July and early August) each year to estimate numbers of birds available for shooting in August. They use all their available dogs to flush grouse (usually an assortment of spaniels and labradors) and walk a series of pre-defined routes each of which corresponds to a shooting drive. All grouse flushed on the route were counted, but their positions were not recorded. The length and direction of the route remained constant across years to enable predictions of birds available for shooting to be made by considering past summer counts in relation to the corresponding shooting bag records for that year. An index of grouse abundance (grouse per km^{-1}) was calculated from the total number of grouse seen divided by the length of transect walked.

Gamekeepers' counts of adults and young in summer from a 1 km transect counted annually using this method between 1992 and 2003 were compared with total counts undertaken by an independent surveyor and his pointing dogs within a 100 ha block that encompassed the gamekeepers route over the same time period.

Analysis

To enable comparison between the data from the gamekeepers' counts (grouse per km walked) and estimates from the distance sampling estimates, the survey area was divided into 22 shooting drives/beats (management units), 15 on the Bollihope estate and seven on the Raby estate, where grouse counts were conducted in summer 2000 (Figure 8). A regression analysis was performed with the gamekeeper count for the management unit as the dependent variable and the distance sampling estimates as the independent variable, weighted by 1/distance sampling estimate.

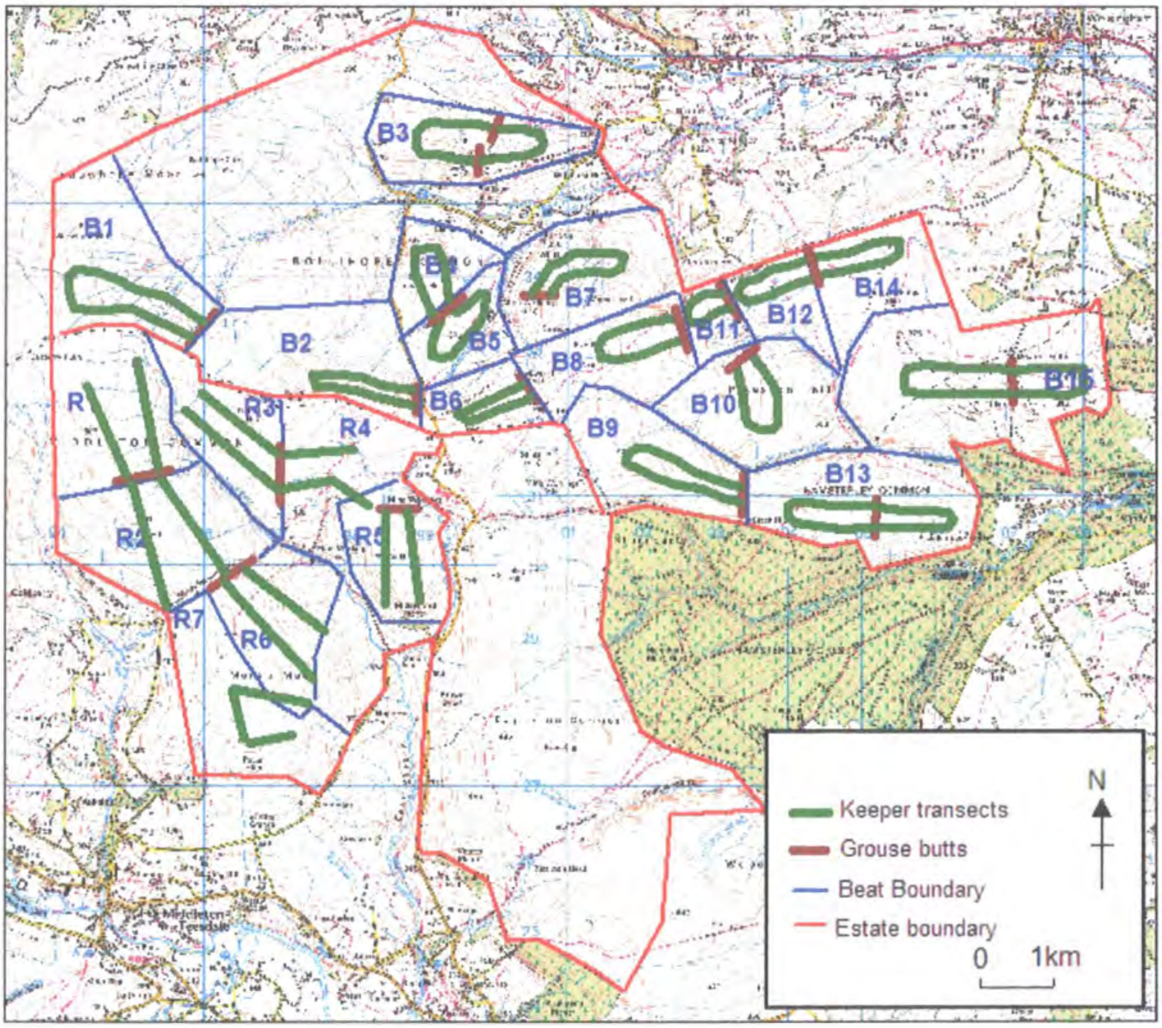


Figure 8 Gamekeepers' summer grouse transects and management units (beats) for which estimates of summer density were calculated using distance sampling.

3.3 Results

3.3.1 Grouse density from distance sampling

There was no evidence of the pointing dogs demonstrating size bias, i.e. finding larger grouse coveys at further distance from the transect in either spring ($y=0.01x+0.96$, $r^2=0.01$, $p=0.001$, $n=2929$) or summer ($y=0.06x+1.51$, $r^2=0.01$, $p=0.000$, $n=2641$). The linear regressions demonstrate statistical significance, i.e. there is a small effect of size bias which is quite precise, but this relationship is too small to be biologically significant. Following Buckland (1993) the data were truncated by 5% during the distance sampling analysis to reduce bias caused by outliers.

There was no significant variation in ESW between the six pointing dogs used ($F_{5,20}=1.59$, $p=0.209$), between years ($F_{5,20}=2.24$, $p=0.090$), seasons ($F_{1,20}=0.16$, $p=0.695$), or the two observers ($F_{1,20}=0.15$, $p=0.699$). Accordingly the data were pooled for all dogs to create one detection function for each season to estimate density.

The mean ESW in spring was 52.0 m ($\pm$2.4 SE) and in summer was 56.7 m ($\pm$1.7 SE). The ESW differed between season ($F_{1,9}=5.59$, $p=0.042$), but not between years ($F_{5,9}=2.83$, $p=0.083$) or between moors ($F_{3,9}=1.94$, $p=0.194$). The ESW was not correlated with grouse density ($y=-0.16x+240.13$, $r^2=0.008$, $p=0.975$).

Grouse densities differed significantly between season ($F_{1,9}=25.58$, $p=0.001$). With on average two to three times more grouse per km^2 in summer than in spring (Table 3, Table 4), due to the presence of both adults and young in the post-breeding period (mean 322 $\pm$39 grouse per km^2) compared to just adults in the pre-breeding period (mean 131 $\pm$15 grouse per km^2). Grouse density differed significantly between years ($F_{5,9}=4.78$, $p=0.021$) but not between moors ($F_{3,9}=0.23$, $p=0.874$).

Table 3 A summary of the distance sampling results for all the surveyed moors pre-breeding in the spring (ESW= Estimated Strip Width, %CV= Percentage Coefficient of Variation, 95% CL= 95% Confidence Limits).

Moor (area km^2)	Year	Total transect length (km)	No. flush events (n)	ESW (%CV)	Encounter rate (flush events/km)	Density (grouse/ km^2)	Population size (95% CL)
Eggleston (19.2)	2000	37.2	242	53.9 (5.1)	6.5	97.5	1873 (1495-2346)
Raby (20.7)	2000	40.1	254	67.2 (10.7)	6.3	81.0	1678 (1265-2224)
Edmondbyers (32.5)	2000	46.5	354	48.6 (4.1)	7.6	130.2	4230 (3662-4885)
Bollihope (41.3)	2000	78.8	666	55.2 (3.1)	8.4	138.6	5722 (4862-6735)
Eggleston	2002	35.3	319	40.7 (5.7)	9.0	192.8	3702 (3110-4407)
Raby	2002	34.7	419	49.8 (3.7)	12.1	215.3	4457 (3776-5260)
Eggleston	2003	34.9	250	47.5 (4.7)	7.1	119.2	2289 (1963-2669)
Eggleston	2004	34.4	237	50.8 (4.9)	6.9	120.9	2320 (1974-2727)
Eggleston	2005	34.4	188	54.5 (5.4)	5.5	84.5	1623 (1301-2025)

Table 4 A summary of the distance sampling results for all the surveyed moors post-breeding in the summer (ESW= Estimated Strip Width, %CV= Percentage Coefficient of Variation, 95% CL= 95% Confidence Limits).

Moor	Year	Total transect length (km)	Number of flush events (n)	ESW (%CV)	Encounter rate (flush events/km)	Density (grouse/ km^2)	Population size (95% CL)
Eggleston	2000	33.6	231	62.1 (5.4)	6.9	277.1	5319 (4248-6661)
Raby	2000	36.3	253	63.1 (5.2)	7.0	345.3	7147 (5726-8921)
Edmondbyers	2000	51.5	301	56.9 (4.5)	5.8	230.1	7477 (6136-9111)
Bollihope	2000	74.9	564	58.3 (3.3)	7.5	328.0	13546 (10869-16882)
Eggleston	2001	35	242	51.7 (4.9)	6.9	491.8	9443 (7507-11879)
Raby	2001	38	302	52.3 (4.4)	7.9	433.0	8963 (7049-11396)
Eggleston	2002	35.1	278	61.7 (9.7)	7.9	355.8	6830 (5274-8847)
Eggleston	2003	34.4	167	49.6 (5.8)	4.9	276.0	5299 (4210-6671)
Eggleston	2004	34.1	255	50.6 (4.8)	7.5	425.2	8164 (6407-10403)
Eggleston	2005	34.1	48	60.5 (11.5)	1.5	53.5	1026 (673-1566)

3.3.2 Kriging

Moran's I values indicate statistically significant positive spatial autocorrelation in spring 2000 (Moran's I=0.28, z random=6.17, p=0.002) and near significant positive autocorrelation in spring 2003 (Moran's I=0.13, z random=1.62, p=0.053).

The semivariogram for spring 2000 data was fitted with a spherical model, with a nugget value of 0, a sill of 21 and a range of 1400. The semivariogram for the spring 2003 data was fitted with a spherical model, with a nugget value of 0, a sill of 14 and a range of 1500. The interpolated grouse distribution and the error variance surfaces for the spring 2000 dataset are illustrated in Figure 9 and Figure 10; with the spring 2003 interpolated surfaces illustrated in Figure 11 and Figure 12.

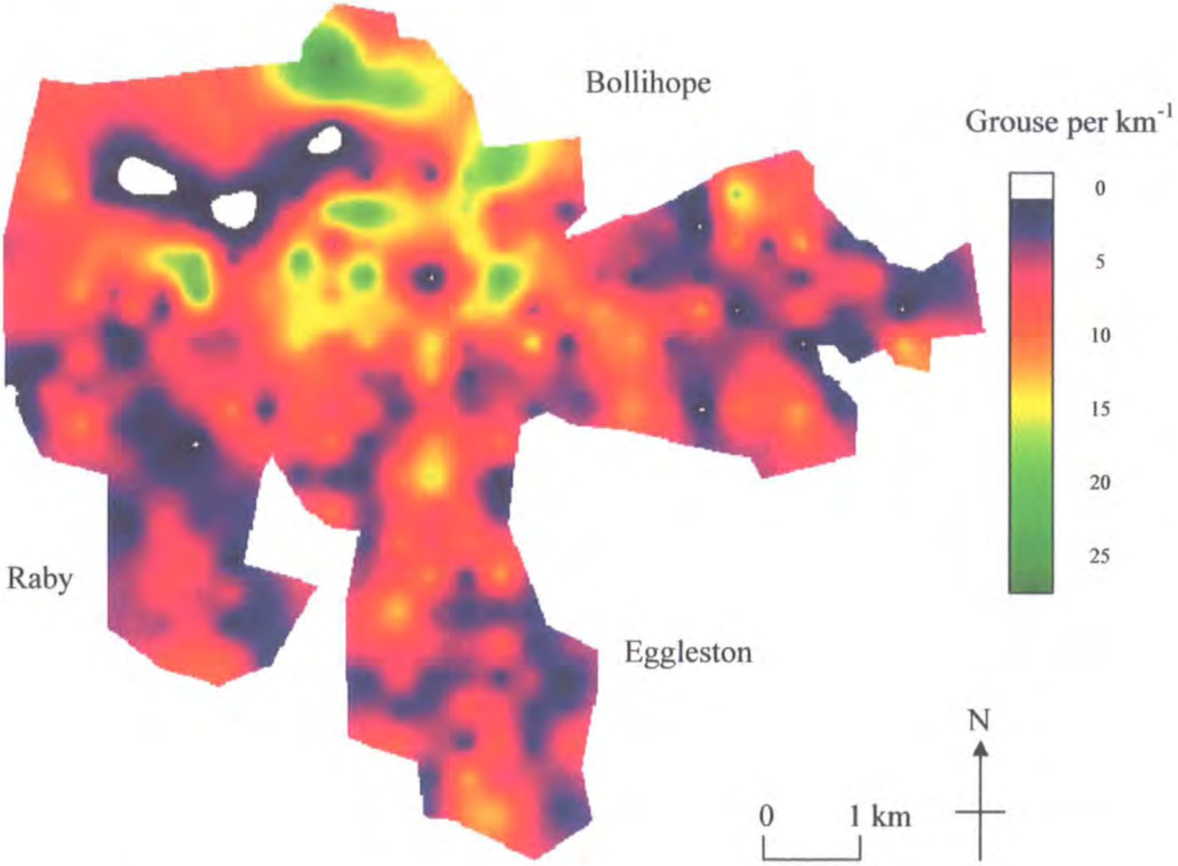


Figure 9 **The spatial distribution of red grouse across the Bollihope, Raby and Eggleston moors study area in spring 2000.**

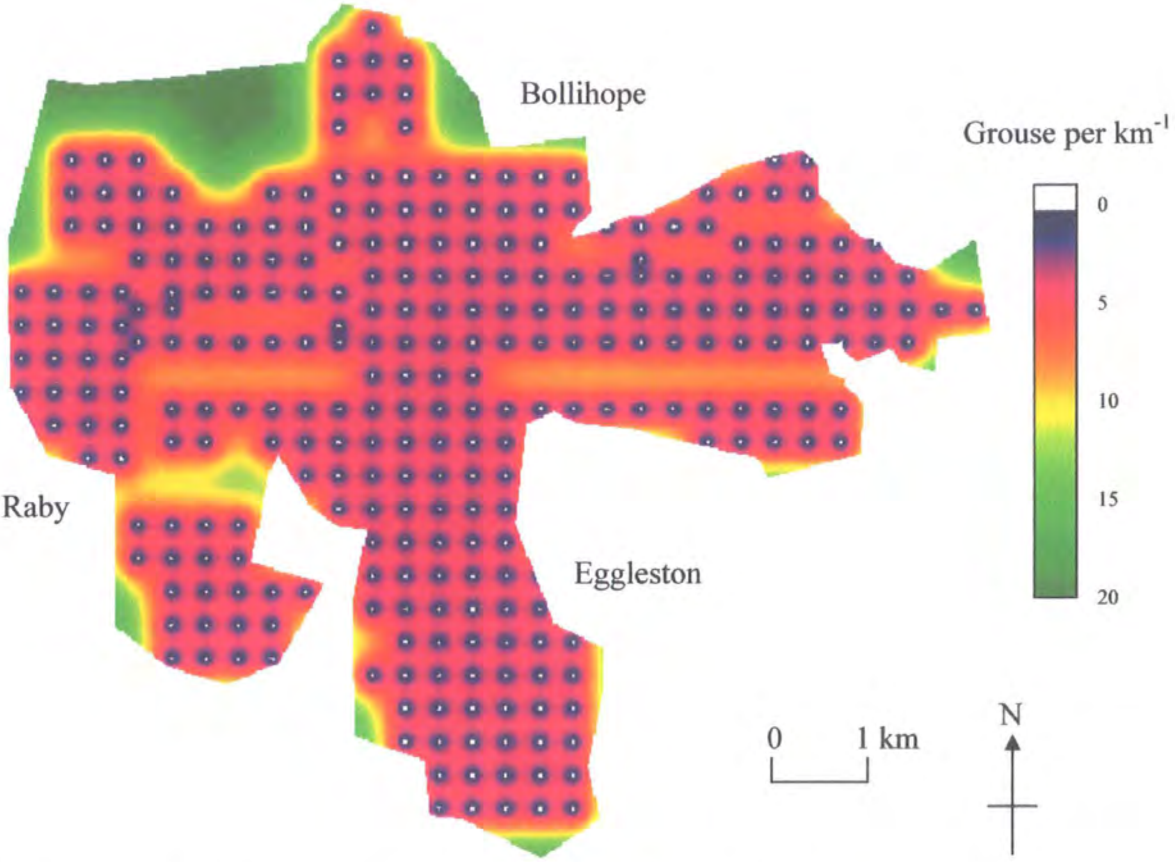


Figure 10 The variance map for spatial distribution of red grouse across the Bollihope, Raby and Eggleston moors study area in spring 2000.

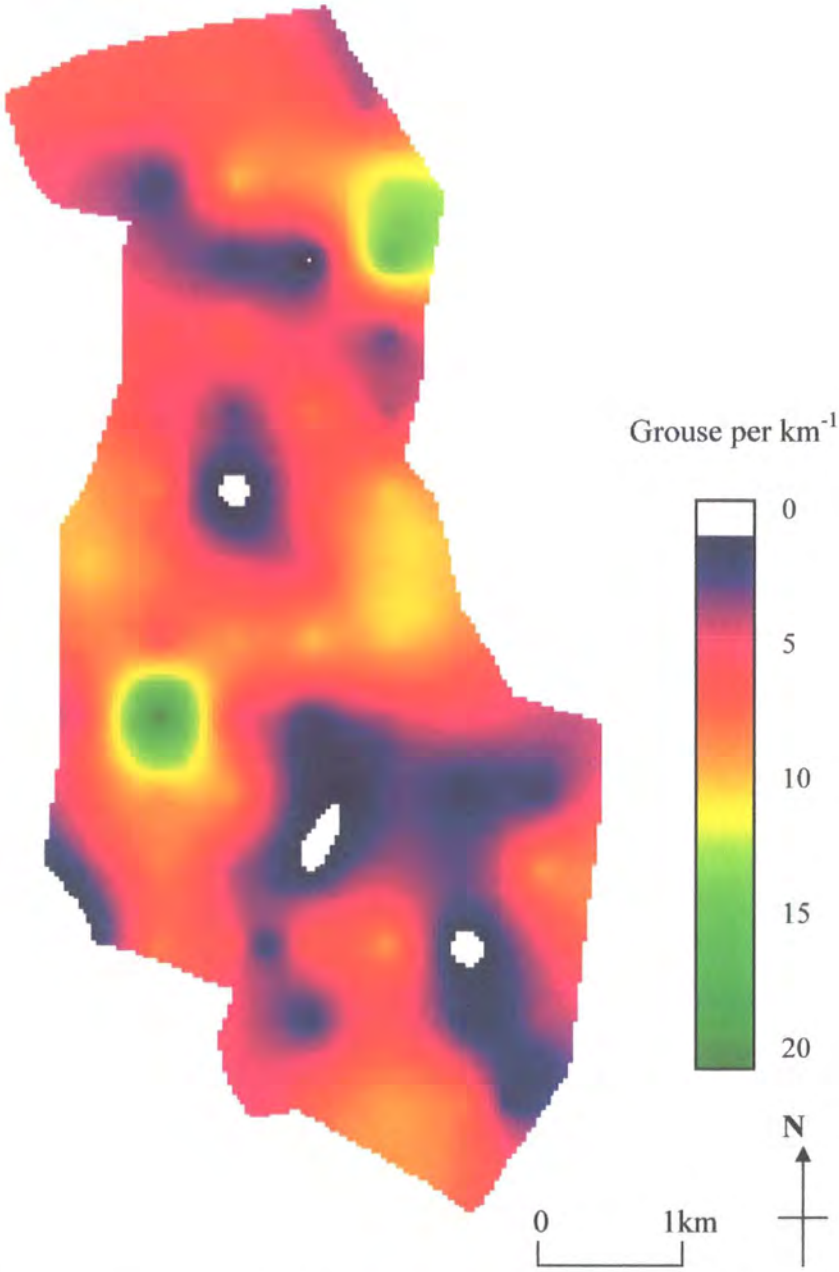


Figure 11 **The spatial distribution map of red grouse in spring 2003 on the Eggleston study moor.**

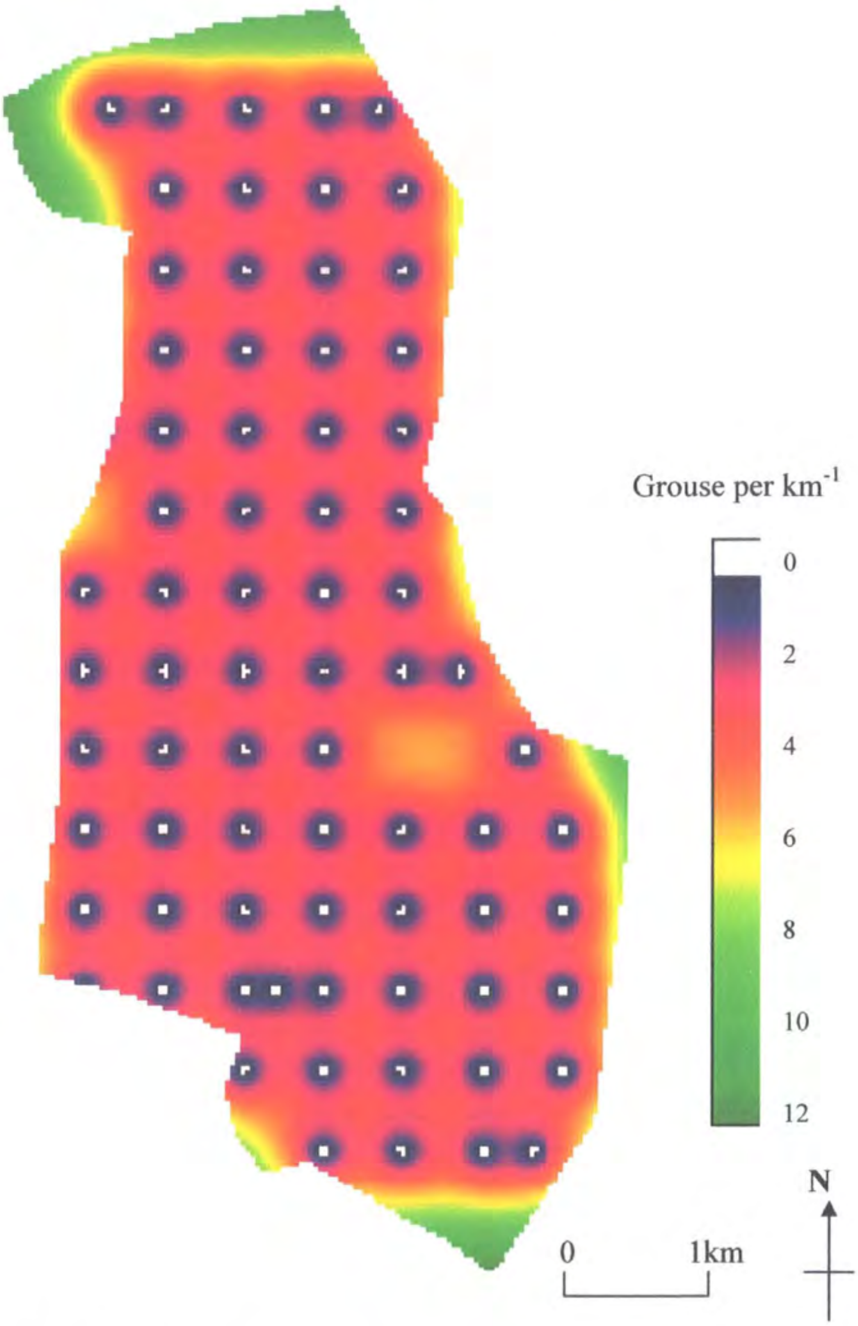


Figure 12 The variance map of red grouse distribution in spring 2003 on the Eggleston study moor.

3.3.3 Distance estimates in spring and calling males

The mean numbers of calling males observed within the 25 ha blocks was significantly lower than the distance estimates for adults for the same block at low (t_4=-4.67, p=0.010), medium (t_5=-6.60, p=0.001) and high densities (t_5=-10.60, p=0.000) (Figure 13).

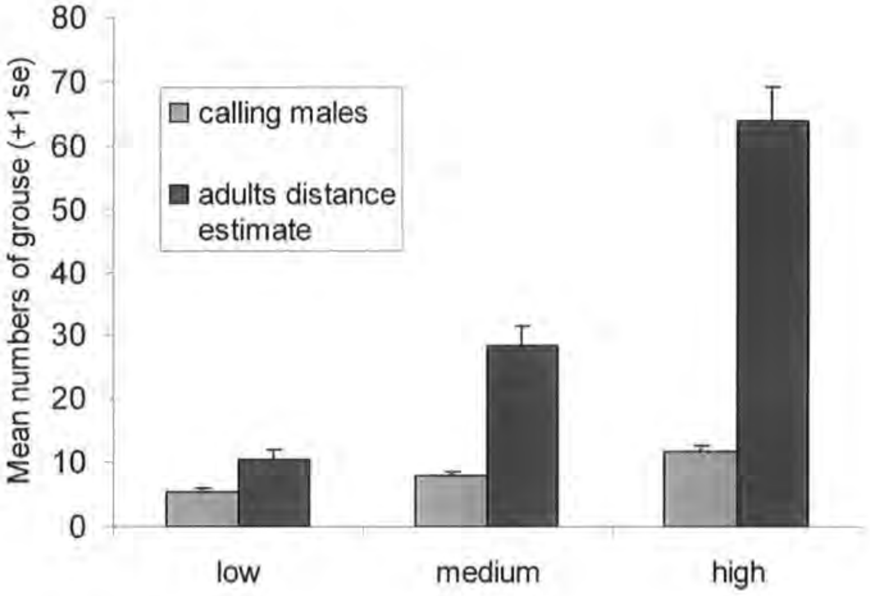


Figure 13 The mean numbers of males calling in spring (males per 25 ha) and the distance sampling estimates for the mean numbers of adults within the 25 ha sample block at low (n=5), medium (n=6) and high grouse densities (n=6).

The abundance of calling males did not differ to the estimates of male abundance from distance sampling at low (t_4=0.46, p=0.670) or medium density (t_5=-2.31, p=0.069), but was significantly lower at high densities (t_5=-3.21, p=0.024) (Figure 14).

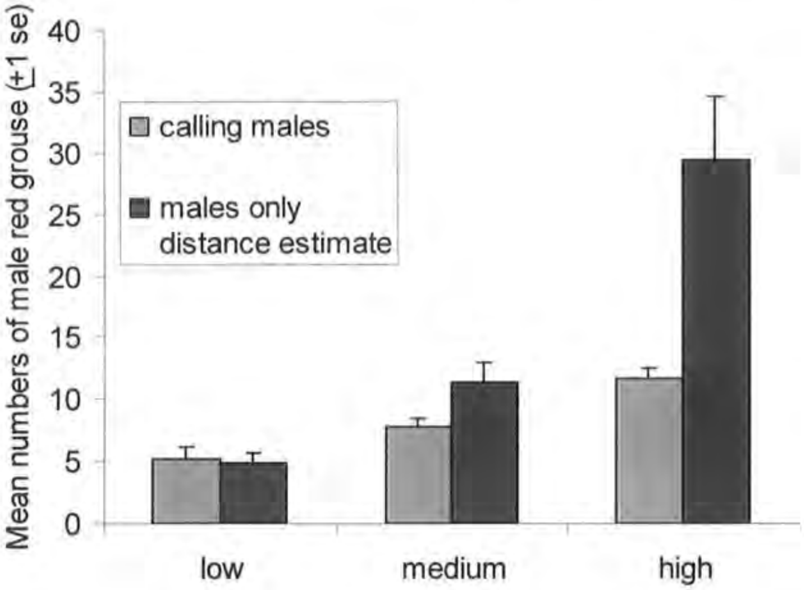


Figure 14 The mean numbers of males calling in spring (males per 25 ha) and the distance sampling estimates for the mean numbers of males within the sample 25 ha block at low (n=5), medium (n=6) and high grouse densities (n=6).

3.3.4 Distance estimates in spring and drive counts

The abundance of grouse on the drive counts did not differ from those derived from distance sampling at either low (t_3=-1.64, p=0.200), medium (t_4=-1.95, p=0.123) or high densities (t_2=-1.75, p=0.222) (Figure 15).

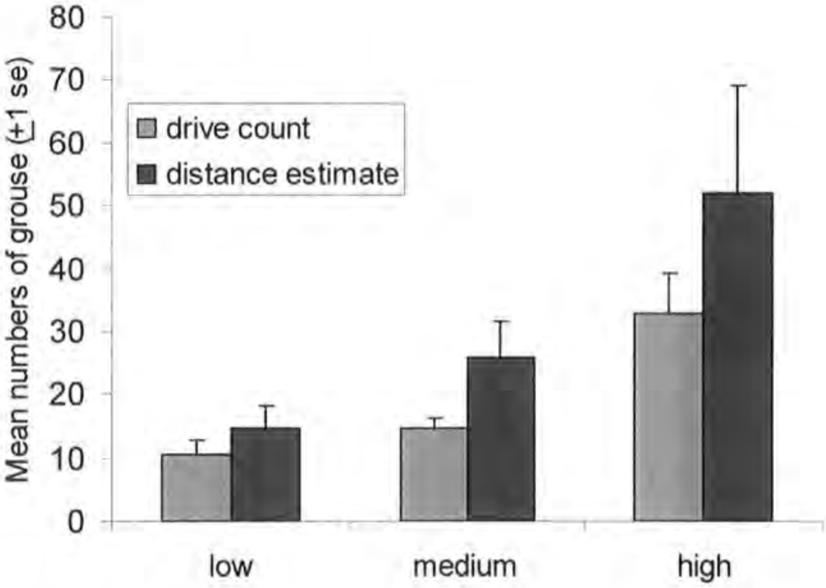


Figure 15 The numbers of adults in spring (adults per 25 ha) observed during the drive counts with the distance sampling estimates for the mean numbers of adults within the sample 25 ha block at low (n=4), medium (n=5) and high grouse densities (n=3).

3.3.5 Distance estimates in summer and gamekeepers' counts

Counts of adults and juveniles in summer by gamekeepers between 1992 and 2003 were positively correlated with a count of grouse undertaken by an independent surveyor within a 100 ha block that encompassed the gamekeepers route over the same time period ($y=0.68x+102.24$, $r^2=0.49$, $p=0.017$, $n=11$) (Figure 16).

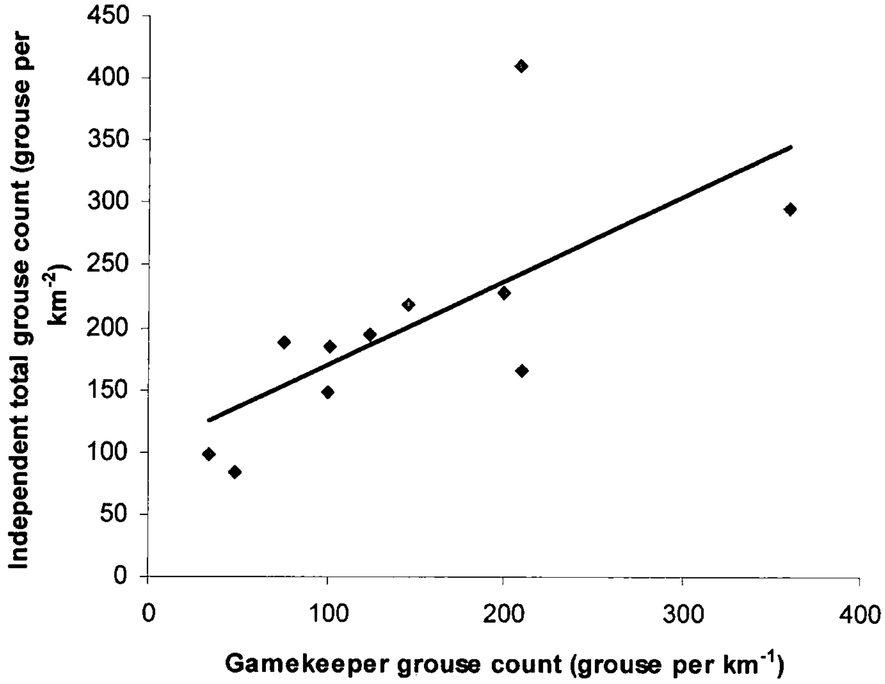


Figure 16 Relationship between red grouse counted on a shooting drive by gamekeepers in summer and those counted independently in the same season over a 100 ha count area on the same piece of moorland 1992 to 2003 ($y=0.68x+102.24$, $r^2=0.49$, $p=0.017$).

The gamekeeper counts (grouse per km^{-1}) were significantly positively correlated with the distance sampling estimates (grouse per km^2) for the same beat (management unit) ($y=3.83x+0.11$, $r^2=0.54$, $p=0.000$, $n=22$) (Figure 17).

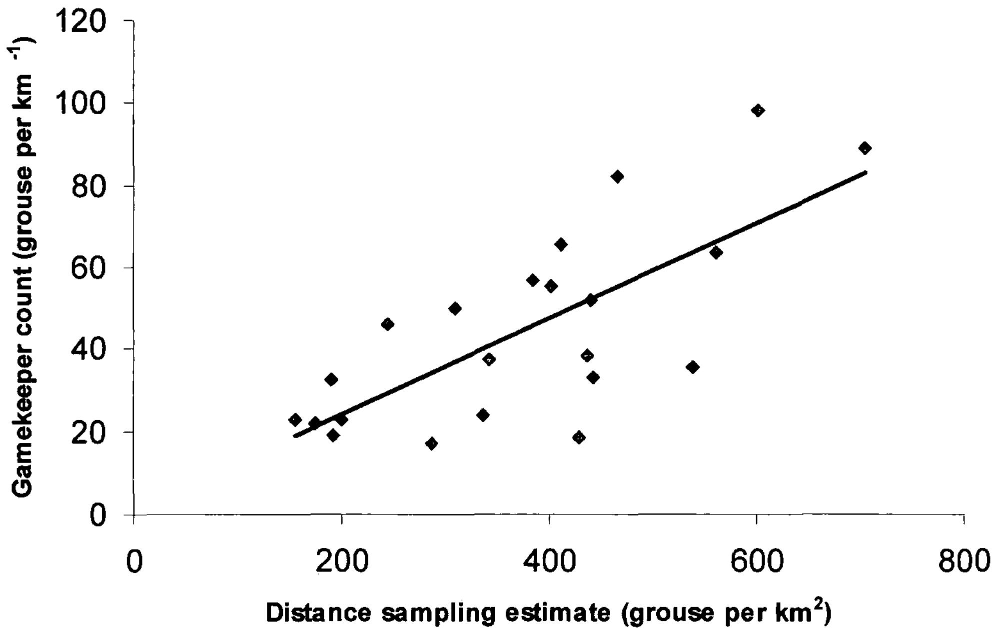


Figure 17 The abundance of red grouse in summer (grouse per km $^{-1}$) recorded by gamekeepers and the distance sampling density estimates for the same beat (grouse per km ^{2}) weighted by 1/distance estimate ($y=3.83x +0.11$, $r^2=0.54$, $p=0.000$, $n=22$).

3.4 Discussion

3.4.1 Suitability of methods

The study assessed the consistency of a line-transect distance sampling technique in surveying red grouse relative to other survey methods. I observed significant positive relationships between estimates of density from the distance sampling method with the spring drive counts and with the gamekeepers' summer counts. Counts of calling males in spring compared well with the distance estimates at low and medium densities, but not at high density. This may be explained by an under-estimation of the numbers of calling males at high density, due to individual males not being easy to identify from one another and that the observer may be distracted by displaying males close to the observer, under estimating the presence of males further away.

A fundamental prerequisite for the success of the distance sampling survey technique is knowledge of the behaviour, characteristics and habitats of the study species. Different bird species can react differently to moving and stationary individuals (Conant *et al.* 1981) and the habitats which study species frequent may also impact on the detection of the study species (Bibby & Buckland 1987). Therefore the first consideration of the study was to evaluate whether the distance sampling technique using pointing dogs was suitable for surveying red grouse and whether it met the assumptions of distance sampling theory. Red grouse have not previously been surveyed by this method in the United Kingdom, but willow grouse have been successfully surveyed in Norway (Pederson *et al.* 1999) using pointing dogs and a distance sampling technique. In addition, willow ptarmigan, rock ptarmigan *Lagopus mutus* and white tailed ptarmigan *Lagopus leucurus* have been surveyed using an aerial distance sampling technique (Pelletier & Krebs 1997).

A basic assumption of the distance sampling method is that measures of distance from the transect line to the pointing dog are accurate. The open homogenous nature of moorland habitats on the study area allows good visibility to record these measures. The behaviour of red grouse to the trained pointing dogs also allowed accurate measures of distance to be obtained. Red grouse in spring are highly territorial (MacColl *et al.* 2000) and therefore reluctant to leave their defended territories. Similarly post-breeding in summer, grouse are in family groups of young and adults and again are reluctant to flush, allowing the dog to accurately 'point' their position. Outside of these key periods, grouse are less territorial and in autumn and winter occur in loose packs (Hudson 1992) and readily flush when up to 200 m from the observer. In these conditions, accurate measures of distance were impossible and the method proved impractical.

Other surveys of mammals have shown evidence of either evasive movement away from the observer, or failure to detect animals close to or on the transect line (Ruette *et al.* 2003; Turnock 1991). This has been due to a number of factors, including behaviour of the study animals, the sampling design and technique. Movement by grouse towards the transect line would result in over estimation of density, while movement away from the transect line would result in an under estimation of density. We expect some movement by grouse prior to detection by the pointing dogs, the effect of this was minimised by dogs pointing scent where birds were prior to any movement. Subsequent inspection of the distance data showed no evidence of any evasive movement prior to detection or any evidence of failure to detect close to the transect line. Any movements which may have occurred appeared to be relatively small and of a random nature, which did not cause bias to the density estimates.

Adequate sample sizes were also important, with Buckland (1993), recommending surveys to have sample sizes of at least 60-80 sightings per study period to give adequate estimates of density. Red grouse were present at densities from an average 81 to 215 grouse per km^2 in the spring on the study area, so the sample sizes recommended too calculate accurate estimates of density were readily achieved. These high densities are as a result of direct management to maximise harvestable surpluses for driven grouse shooting (Hudson & Newborn 1995). These densities of red grouse are high compared to a similar study in Norway (Pederson *et al.* 1999) where spring densities of willow ptarmigan estimated by distance sampling were between 5.3 and 8.2 grouse per km^2.

The systematic study design using parallel transects at 500 m intervals was also important to accurately estimate grouse density at the moor scale. The spatially interpolated maps of grouse distribution show that the distribution of grouse is spatially aggregated, therefore fewer transects or randomly placed lines would be more likely to bias the density estimates generated.

3.4.2 Use of methods

The distance sampling technique using pointing dogs was developed to enable red grouse to be surveyed over extensive areas in a cost-effective and rigorous manner. On average, complete counts of 1 km^2 sample blocks of heather moorland takes a surveyor and his pointing dog, approximately three hours to search for grouse along six parallel transects. This being the maximum amount of time a pointing dog can work effectively for the day due to factors such as scenting conditions and dog fatigue. Therefore to survey 113 km^2 of heather moor using this method, 113 man/dog days would be required. In comparison, using a distance sampling method, with line transects systematically distributed at 500 m intervals and assuming one surveyor and his dog can survey on average 6 km of line transect per day, the same 113 km^2 of heather moor can be surveyed in 38 days, approximately one third of the time.

The creation of accurate maps of red grouse abundance at a grouse moor spatial scale and estimates of density across the moor is fundamental to facilitate further spatial scale grouse studies. In subsequent Chapters I investigated the effects of habitat quality and management in this case heather burning on grouse density (Chapter 4) and the effects of density on juvenile dispersal (Chapter 5). The adoption of this method to map the spatial distribution of grouse allows dispersal/movement studies and patterns of over winter losses in relation to variations in habitat quality/extent to be considered.

The success of this method has wider repercussions for the conservation of other species as it allows large areas of ground to be surveyed economically and within practical periods of time. The method is repeatable and delivers reliable estimates of density. The suitability of the method though is dependent on the species of interest, with the success of this method in this case due to the response of red grouse to the pointing dogs.

CHAPTER 4

Earth observation and spatial modelling techniques to map heather moorland and an assessment of the effects of heather burning on the abundance and breeding success of red grouse

Abstract

To evaluate the habitat mosaic created by rotational heather burning across the study area, a Landsat 7 Enhanced Thematic Mapper (ETM+) scene was acquired for the study area in May 2000 and processed. The overall accuracy of the output image was 79.8%, with a Kappa coefficient value of 0.78. Individual class accuracy ranged from 56% for a heather and grass mix to 100% for conifer woodland.

The composition of the heather sward in 2000 across all four study moors was compared with grouse density data collected using the distance sampling method (Chapter 3) for the same period. The temporal effects of rotational heather burning on grouse density and breeding success was investigated from 2000 to 2005 on the Eggleston study moor only. Grouse were surveyed in spring and summer using the distance sampling method and new heather burns since the preceding year, were mapped annually in the field.

Heather burning programmes were significantly different between the study moors in 2000, with the proportion of the heather sward burned on Eggleston twice that on Raby and Edmondbyers and fourfold that on Bollihope. In 2000, high spring grouse densities were associated with areas of moor with a high proportion of heather in the building phase.

The size of heather burns on Eggleston reduced five-fold through the course of the study from few large fires to many small fires. The temporal study on Eggleston identified that density dependence was more important than the burning variables in determining grouse breeding productivity.

4.1 Introduction

Earth observation data has been used since the early 1970's to map land cover (Tucker *et al.* 1975) and since the 1980's has been recognised as a feasible way of mapping vegetation at landscape scales (Puhr & Donoghue 2000). Previous studies have shown that heather dominated areas can be differentiated from other habitat types using satellite imagery (Wright *et al.* 1977) and that differences in heather biomass can be identified (Egan *et al.* 2000; Robertson *et al.* 2002). Earth observation data, in conjunction with Geographic Information Systems (GIS) has allowed the assessment and understanding of many species-habitat relationships (Gottschalk *et al.* 2005). Birds have been the focus of many of these studies (Austin *et al.* 1996; Avery & Haines-Young 1990; Osbourne *et al.* 2001; Tucker *et al.* 1997), as they are relatively easy to identify, survey and are recognised as indicator or umbrella species for ecosystems which are sensitive to environmental change (Evans 1992; Furness & Greenwood 1993; Usher 1986).

Rotational heather burning is an integral component of grouse moor management in the United Kingdom (Hudson & Newborn 1995). The quality of heather available to red grouse is improved by burning old heather in small patches which leads to reduced territory size (Miller & Watson 1978) and higher densities (Miller *et al.* 1966; Picozzi 1968). Although red grouse only remove around 2% of heather shoots available to them per annum (Savory 1978), they are selective foragers and can respond to differences in the nutrient content of heather plants (Moss 1972; Savory 1978), preferring to forage on heather which is 10-30 cm high (Moss *et al.* 1972).

To produce harvestable surpluses of grouse for sport shooting, gamekeepers are employed to burn heather in rotation to create a mosaic of different heather habitats within each grouse territory. Heather is burned annually during the heather burning season, 1st October to 15th April, in accordance with the Heather and Grass Burning Regulations 1986 (MAFF 1996). Heather is typically burned in strips which are 20-30 m wide and several hundred metres long, with a burn cycle of every eight to 30 years depending on heather growth.

There is currently considerable debate and controversy regarding the use of heather burning as a management tool to maintain dwarf shrub habitats in the English Uplands (Yallop *et al.* 2006). The main controversy is between heather burning for red grouse shooting and that for conservation interests, with English Nature reporting that 32% of moorland Sites of Special Scientific Interest (SSSI) were in unfavourable condition as a result of inappropriate burning (English Nature 2006). It is recognised that heather burning is an important component of grouse moor management (Hudson & Newborn 1995; Picozzi 1968; Tharme *et al.* 2001), but no study to date has assessed the spatial and temporal effects of heather burning on grouse settling densities and breeding success. In this Chapter I investigated both spatially and temporally the effects of heather burning on grouse settling densities and breeding success at a grouse moor scale in northern England.

In this Chapter I assessed whether heather moorland and the patterns of heather burning could be accurately mapped using earth observation and spatial modelling techniques. This information was then used to assess the spatial relationship between the components of the heather sward created by heather burning with grouse settling patterns and productivity both spatially across all four study moors in 2000 and temporally on the Eggleston study moor from 2000 to 2005.

4.2 Methods

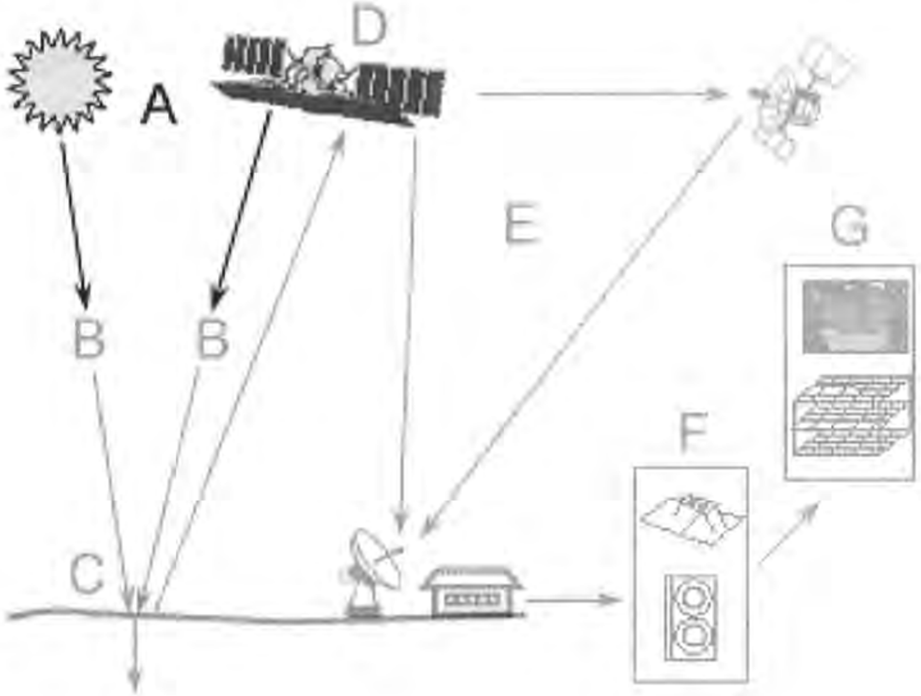
To collect habitat data over the study area, encompassing four grouse moors and some 113 km^2 of heather moorland in 2000, an earth observation technique using satellite remote sensing was used. Satellite remote sensing was selected for a number of reasons, the first being that the spatial resolution of 30 m x 30 m was deemed suitable for identifying patterns of heather burning across the study area, secondly the data was available for the study area in 2000 and thirdly this data was more cost effective than similar aerial photography data.

To assess the temporal effects of heather burning, heather burns were mapped annually in the field on one of the moors, Eggleston (19 km^2) from 2000 to 2005. Grouse were surveyed pre-breeding in spring and post-breeding in summer across the study moors for the equivalent period using a distance sampling technique, as described in Chapter 3. I assessed the habitat and grouse variables spatially across all four grouse moors in 2000, and temporally on the Eggleston study moor from 2000 to 2005. The processes in the study are as follows:

1) **Satellite imagery:** A Landsat 7 Enhanced Thematic Mapper (ETM+) scene was acquired for the study area in May 2000 and processed by supervised classification using the Idrisi computer program.
2) **Mapping of annual heather fires:** Annual heather burning was mapped in the field on the Eggleston study moor only from 2000 to 2005.
3) **Red grouse density and breeding success:** The density and breeding success of grouse was surveyed using the distance sampling technique pre-breeding in the spring and post-breeding in the summer across all four moors in 2000. Surveys continued on Eggleston moor up to and including 2005.
4) **Analysis:** Three separate analyses were undertaken, (a) an assessment of the habitat composition and heather burning regimes of the four study moors; (b) an assessment of the spatial relationship between habitat variables and grouse density and breeding success in 2000; (c) an assessment of the temporal relationship between heather burning and grouse productivity on the Eggleston study moor 2000 to 2005.

4.2.1 Satellite imagery

Earth observations from satellites orbiting the earth have facilitated the mapping of vegetation cover at landscape scales. This remote sensing can be defined as “the science and the art of obtaining information about an object, area or phenomenon through the analysis of data acquired without actually being in contact with it” (Lillesand & Kiefer 2000). This is done by sensing and recording reflected or emitted energy and processing, analysing, and applying that information (Figure 18).



Legend

A	Energy Source or Illumination, which provides electromagnetic energy.
B	Radiation is the energy, which travels through the atmosphere from its source to the target.
C	Interaction with the surface depending on the properties of both the surface and the radiation.
D	Energy recording by the Sensor, which collects and records the electromagnetic radiation.
E	Transmission, Reception, and Processing of the energy recorded by the sensor.
F	Visually and/or digitally interpretation and analysis of the data recorded.
G	Extraction of useful information from the imagery.

Source (Lillesand & Kiefer 2000)

Figure 18 Illustration of the remote sensing process.

The first satellite designed for monitoring the earth's surface, Landsat-1, was launched by NASA in 1972. All Landsat satellites are placed in near-polar, sun-synchronous orbits and the Landsat 5 and 7 are at altitudes around 700 km and orbit the earth in a period of 16 days.

A number of sensors have been on board the Landsat series of satellites, including the Return Beam Vidicon (RBV) camera systems, the MultiSpectral Scanner (MSS) systems, the Thematic Mapper (TM) and the Enhanced TM (ETM+) with an additional panchromatic band. Each of these sensors collected data over a swath width of 185 km, with a full scene being defined as 185 km x 185 km. The Enhanced Thematic Mapper (ETM+) sensor collects information on eight spectral bands and this data has been used for a wide variety of applications, including resource management, mapping, environmental monitoring, and change detection (Table 5).

Table 5 The spatial and spectral resolution of Landsat Enhanced Thematic Mapper (ETM+) bands and some useful applications.

Channel	**Band**	**Ground resolution (m)**	**Wavelength range (μm)**	**Application**
1	Blue	30	0.45-0.52	soil/vegetation discrimination; bathymetry/ coastal mapping; cultural/urban feature identification
2	Green	30	0.52-0.60	green vegetation mapping; cultural/urban feature identification
3	Red	30	0.63-0.69	vegetated vs. non-vegetated and plant species discrimination; cultural/urban feature identification
4	Reflective-infrared	30	0.76-0.90	identification of plant/ vegetation types, health, and biomass content; water body delineation; soil moisture
5	Mid-infrared	30	1.55-1.75	sensitive to moisture in soil and vegetation; discriminating snow and cloud-covered areas
6	Thermal-infrared	60	10.40-12.50	vegetation stress and soil moisture discrimination; thermal mapping (urban, water)
7	Mid-infrared	30	2.08–2.35	discrimination of mineral and rock types; sensitive to vegetation moisture content
8	Panchromatic	15	0.52–0.90	monitoring urban growth, updating maps, integrating cartographic features with GIS

((Lillesand & Kiefer 2000))

The interpretation and analysis of remote sensing imagery involves the identification and/or measurement of various objects in an image in order to extract useful information about them. The image is represented in a computer as arrays of pixels, with each of these pixels corresponding to a digital number, representing the brightness level of that pixel in the image. Image processing operations modify the numeric values contained in an image according to specific algorithmic rules, to highlight or extract certain trends in the data, which indicate features of interest. Such algorithms are generally based on assumptions relating to either the image data or the required features.

Image processing is performed in two stages (a) Pre-processing, Image rectification and restoration, and (b) Image classification, the process of developing interpreted maps from earth observation data.

Image acquisition and pre-processing

A Landsat 7 Enhanced Thematic Mapper + (ETM+), Path:204, Row:022 scene for 7th May 2000 was acquired for the study area (Supplied by US Geological Survey http://edcsns17.cr.usgs.gov/EarthExplorer/) and processed using Idrisi, a raster-based GIS image processor program (Eastman 2001). Image enhancement through atmospheric and radiometric corrections were omitted, as these are really only essential for direct comparisons between different images (De Wulf *et al.* 1990). Image pre-processing included the geometric correction to British National Grid, using nearest neighbour assignment resulting in a residual mean square (RMS) error of 0.05.

Classification

There are two primary methods for classifying the locations of an image, unsupervised and supervised classification. Unsupervised classification is a technique for the computer-assisted interpretation of remotely sensed imagery and uses clustering statistics to uncover commonly occurring spectral classes within the image, with the analyst providing an interpretation of this information. In supervised classification the analyst trains the computer to look for surface features with similar reflectance characteristics to a set of examples of known interpretation within the image. The analyst identifies known areas of habitat (information classes) and uses these as training sites to identify spectral characteristics. These are then used to assign individual pixels into information classes. A supervised classification technique was used to interpret the image, the processes in the supervised classification were:

Identification of training sites

The first step was to identify and define samples of each cover type in the image to be used as training sites. To facilitate this, field data were collected in May 2000 to identify land cover classes of interest. The heather mosaic was mapped within a 1 km^2 block using a non-differential, hand-held Global Positioning System (GPS) receiver, with each homogenous patch of habitat categorised into one of the 16 classes described in Table 6.

Table 6 The sixteen identified representative land cover classes for which training site polygons were digitized.

Land cover classes	**Categorisation/description**
Mature heather and cotton grass	Mature *Calluna vulgaris* (taller than 40 cm) dominant (>75%), with *Eriophorum vaginatum* co-dominant in the sward.
Blanket bog	*Eriophorum vaginatum* dominant (>75%) with *Calluna vulgaris* co-dominant in the sward.
Burns	Areas of *Calluna vulgaris* burned in the 1999-2000 burning season. Characterised by evidence of recent fire.
Grey Fires	Areas of *Calluna vulgaris* burned prior to the 1999-2000 burning season. Heather sticks may still be present and regenerating heather is infrequent and in the pioneer stage (0-5 cm).
Regenerating heather	*Calluna vulgaris* dominant, height 5-15 cm.
Building heather	*Calluna vulgaris* dominant, height 15-40 cm.
Heather (75%)/grass (25%)	*Calluna vulgaris* dominant (>75%), interspersed with grasses and rush (*Deschampsia flexuosa*, *Nardus stricta*, *Juncus effusus* and *Juncus squarrosus*).
Heather (50%)/ grass (50%)	*Calluna vulgaris* co-dominant with grasses and rush (*Deschampsia flexuosa*, *Nardus stricta*, *Juncus effusus* and *Juncus squarrosus*).
Heather (25%)/ grass (75%)	Grasses and rush dominant (>75%), (*Deschampsia flexuosa*, *Nardus stricta*, *Juncus effusus* and *Juncus squarrosus*) interspersed with *Calluna vulgaris* (<25%).
White grass moor (1)	Grass and rush, with *Nardus stricta*, *Juncus effusus* and *Juncus squarrosus* dominant.
White grass moor (2)	Grassland, with *Festuca ovina* and *Juncus squarrosus* dominant.
Bracken/rush dominant	Dominant species being *Pteridium aquilinum* and/or *Juncus effuses.*
Improved grassland	Hay meadows, pastures and other agricultural land.
Water	Areas of standing water, reservoirs and mill ponds.
Conifer woodlands	Non-native forestry dominated by sitka spruce *Picea sitchensis.*
Bare rock/urban	Towns and quarries.

In addition, during the course of other field work (grouse surveys and telemetry studies) the position of large areas of continuous habitat, such as mature heather and new fires, were recorded and mapped by GPS. Secondary data to support this work were taken from English Nature's National Vegetation Classification (NVC) maps for the study area to identify broad areas of vegetation communities (Averis *et al.* 2004) and from

Ordnance Survey 1:25000 maps to locate conifer woodland and urban features such as towns and quarries in the landscape.

To aid the selection of good training sites which are representative of the feature of interest, a true colour composite image of the raw data was displayed using the blue (band 1), green (band 2) and red (band 3) bands only, which displays the image in approximately natural colours (Figure 19).

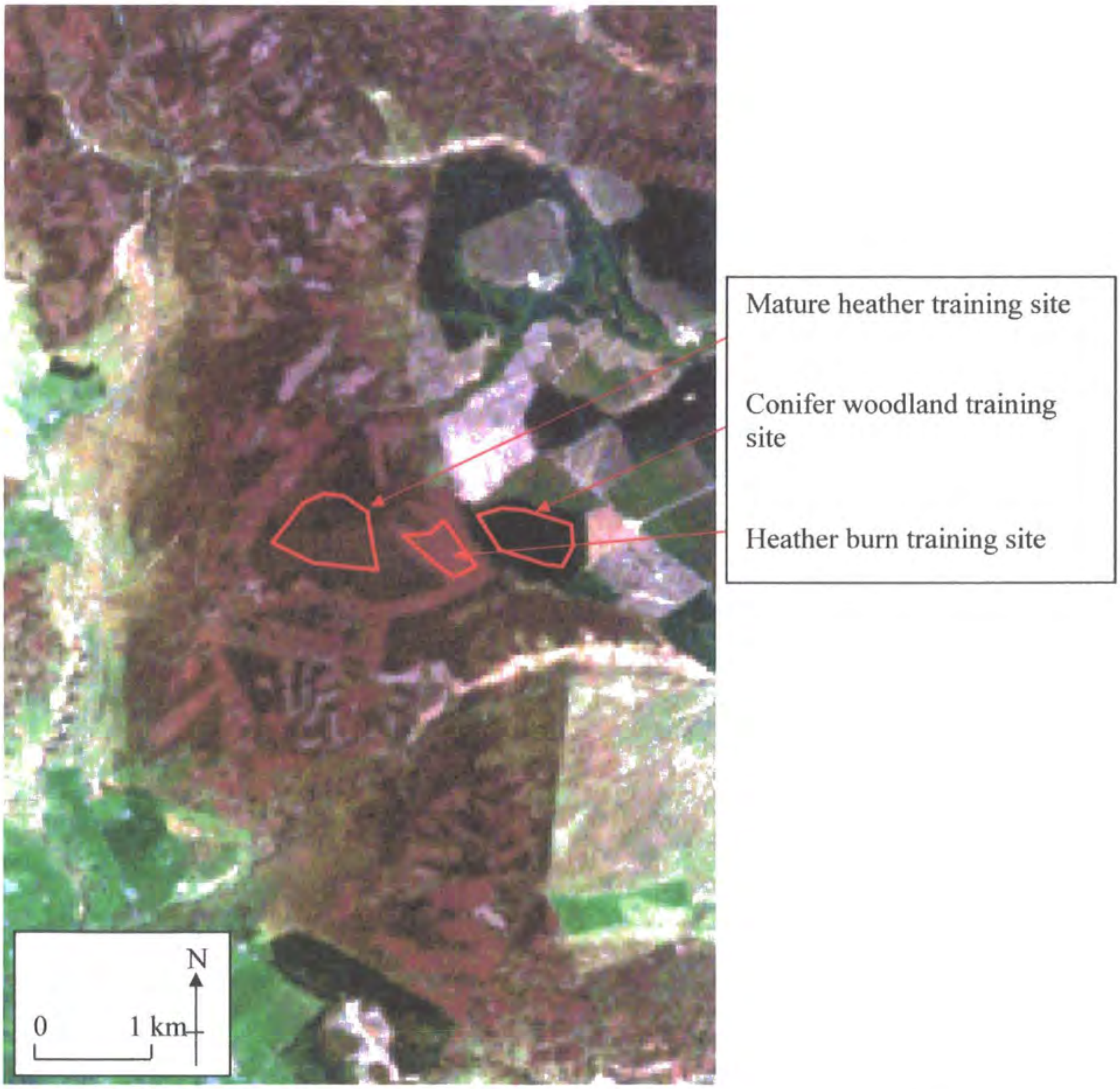


Figure 19 Natural colour composite image of Eggleston moor from a Landsat ETM+ image, May 2000, using blue, green and red bands. This figure is used to illustrate the selection of some of the training site polygons used in supervised classification of the image.

To aid the identification of newly burned areas, a Normalised Difference Vegetation Image (NDVI) was displayed. This is an index derived from the reflectance measured in the red band (channel 3) and the near infrared band (channel 4) of the image to describe the relative amount of green biomass in the raw image (Figure 20). The image measurement scale ranges from -1 to 1, with 0 representing the approximate value of no vegetation, which is useful for detecting vegetated from non-vegetated areas.

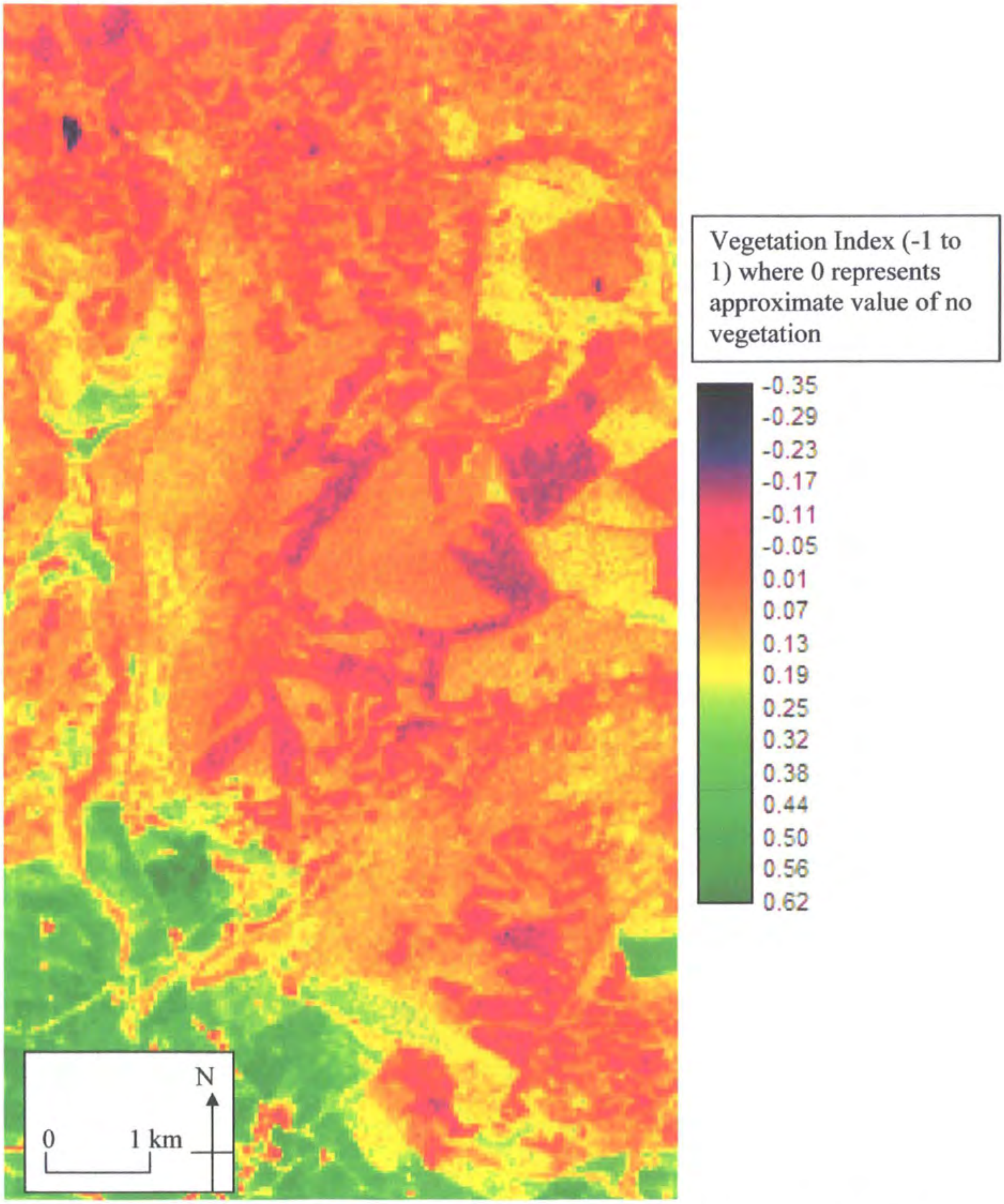


Figure 20 Normalised Difference Vegetation Image (NDVI) image of Eggleston moor, May 2000.

A total of sixteen landcover features were selected as representative land cover classes (Table 6). Training site polygons were digitised for each land cover class and assigned a unique identifier (Figure 19), with a minimum of 70 pixels (30 m x 30 m) selected as training sites for each class. Good training sites are those with as pure a sample of the information class as possible, which are greater than one pixel (30 m x 30 m) in area. Due care was taken when digitising the polygons around the training sites to avoid including pixels which are on the edge adjoining other land cover types.

Signature extraction

Spectral signatures, which contain the statistical characterisations about the reflectance values of the pixels within the training site for each land cover class were extracted for band 1 to band 5 and band 7. The mean spectral signatures for the heather moorland classes (Figure 21) and for the other land cover classes (Figure 22) illustrate that the two mid-infra red (bands 5 & 7) and the reflective infra red (band 4) best differentiate the vegetation land cover types.

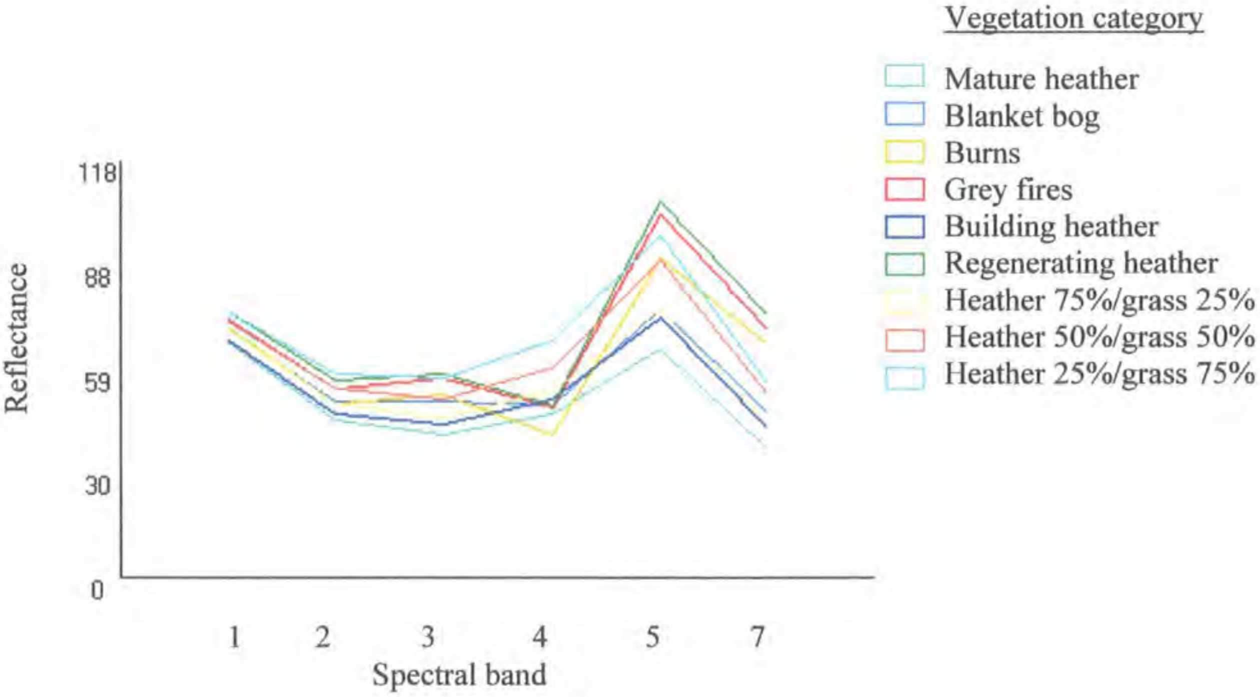


Figure 21 **The spectral signatures for the nine heather classes identified.**

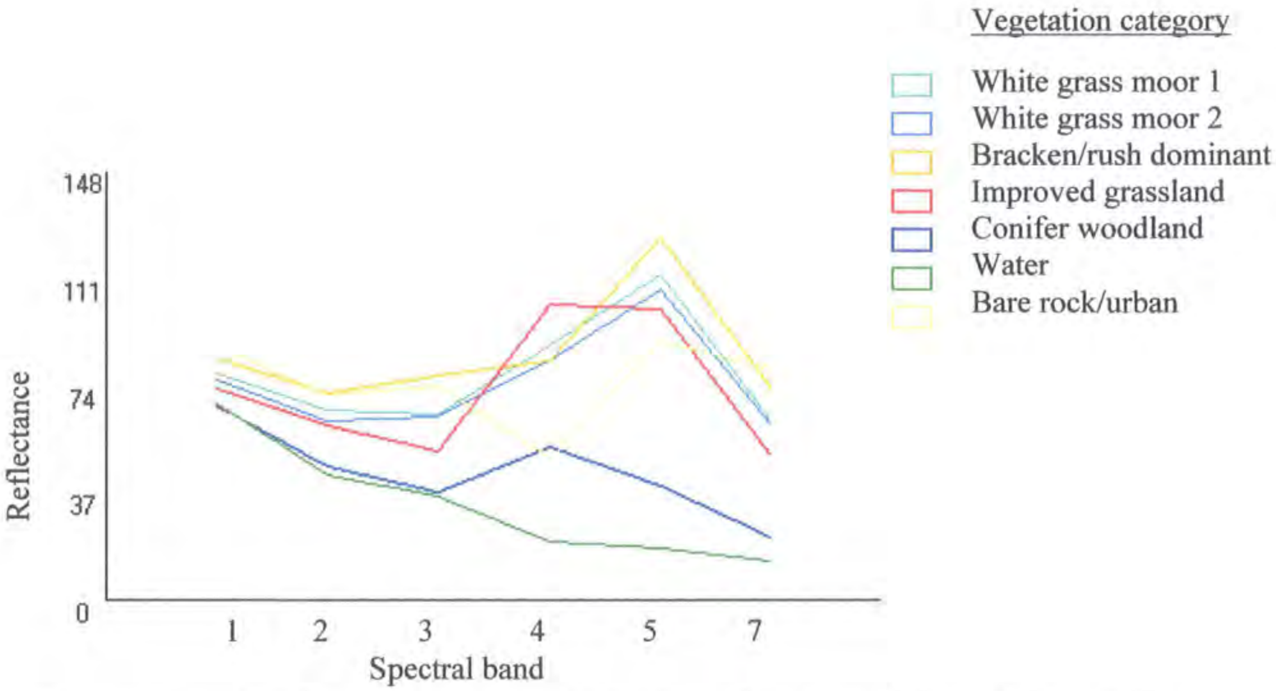


Figure 22 **The spectral signatures for the other land cover classes identified in the image.**

Image Classification

The spectral signatures were used to classify the image into the identified habitat types. The two main techniques used, are referred to as 'hard' or 'soft' classifications. A hard classification assigns each pixel to the cover type with the most similar signature, whereby a soft classification, evaluates the degree of membership of the pixel with all classes under consideration. As the spectral signature files (Figure 21, Figure 22) for the training sites were well defined, a hard classification technique was used to categorise the continuum of spectral data in the entire image by using a maximum likelihood classifier. This classifier evaluates the probability that a given pixel will belong to a given category and classifies the pixel to the category with the highest probability of membership. The maximum likelihood classifier was run on all the spectral signatures, involving band 1 to band 5 and band 7 in the image.

Accuracy Assessment

Accuracy assessment is an important step in the process of analysing remotely sensed data. To assess the accuracy of the classified scene a combination of a stratified and random sampling technique, following Congleton (1991) were used. For each distinct land cover class, actual data were collected at 50 points identified by Congleton (1991) as a sufficient sample size, using a combination of ground information taken from OS maps for man-made features such as urban areas, conifer forest and water; and aerial photographs from 2000 and NVC maps of the study area supported by field data for the heather moorland classes. The classification accuracy is expressed in an error matrix (Congleton 1991), which cross tabulates predicted (classified) land class with actual land cover. The overall accuracy is defined as the number of correctly classified pixels divided by the total number of pixels checked. There are two measures of accuracy: the 'user's accuracy' calculated as the number of correctly classified samples divided by the row total, which provides information on the accuracy of the land-cover data and is a measure of the reliability of the map; and the 'producer's accuracy' calculated by dividing the number of correctly classified samples by the column totals, which provides information on the percentage of samples of land-cover class which were correctly classified. The Kappa coefficient, a measure of the overall agreement of the matrix was calculated, which measures the proportion of agreement after chance agreements have been removed. This is a widely used measure for classification accuracy and is recommended as a standard (Rosenfield & Fitzpatrick-Lins 1986).

4.2.2 Mapping of annual heather burning on Eggleston moor

The locations of new burns on the Eggleston study moor were mapped annually from 2000 to 2005 in spring at the end of the burning season. The locations of the new burns were mapped from field observations taken at various vantage points across the moor and ground controlled using a hand-held GPS. The locations of all burns were digitised into a MapInfo GIS package (www.mapinfo.com) as individual layers for each burning season (Figure 23).

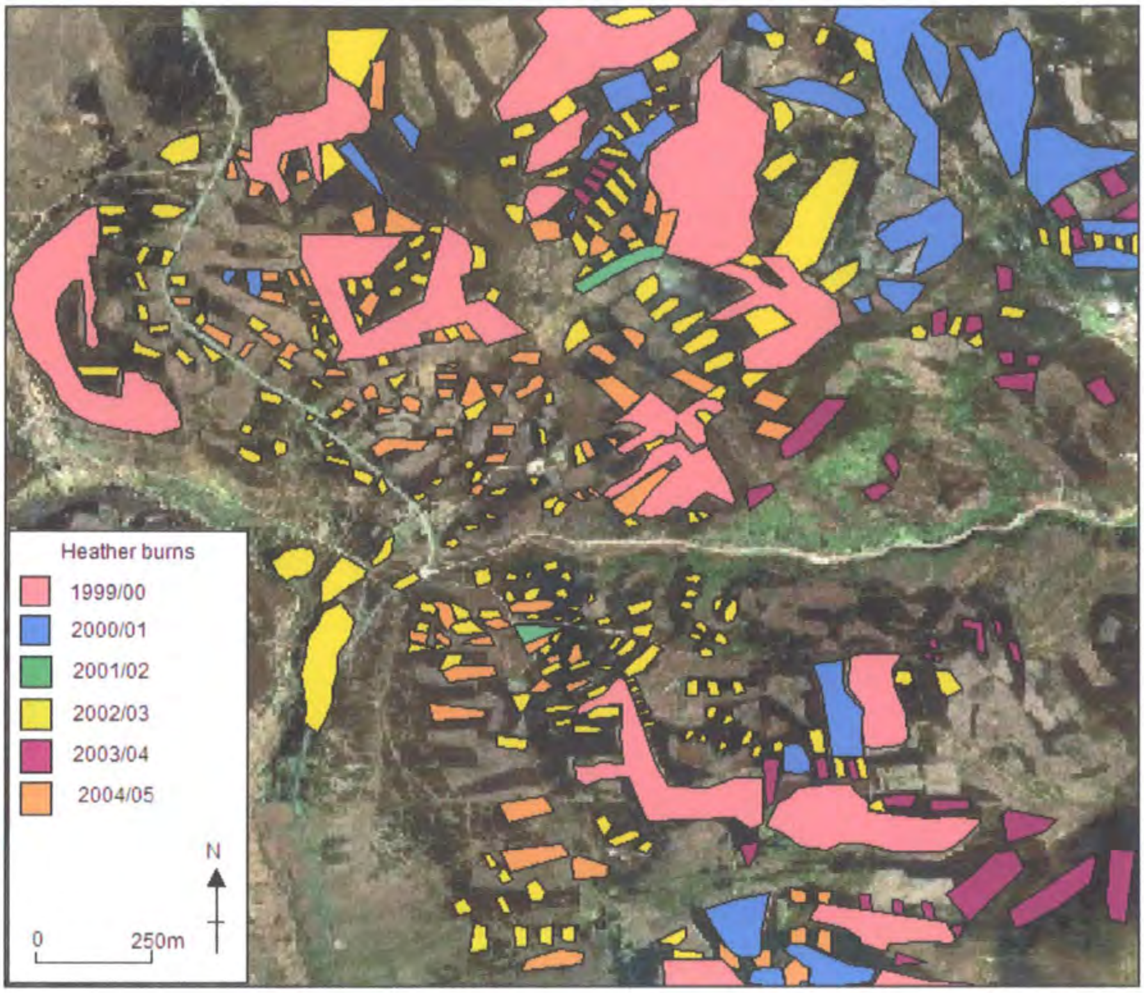


Figure 23 Annual heather burning 1999/2000 to 2004/05 on the northern section of the Eggleston study moor, overlaid onto an aerial photograph of the study area from July 2000.

4.2.3 Grouse surveys

The abundance of red grouse was surveyed using the distance sampling methods described in Chapter 3. Surveys were conducted pre-breeding in spring and post-breeding in summer across all four moors, Bollihope, Eggleston, Raby and Edmondbyers in 2000 and from 2001 to 2005 on one moor, Eggleston.

4.2.4 Statistical analysis

(a) Habitat composition and heather burning regimes

The habitat composition of 23 areas across the moors was extracted from the classified Landsat image (Figure 24). These areas were selected as they had distance sampling transects through them to enable grouse density to be estimated and the borders were based upon clear geographical boundaries particularly watercourses, roads and estate boundaries (Figure 24).

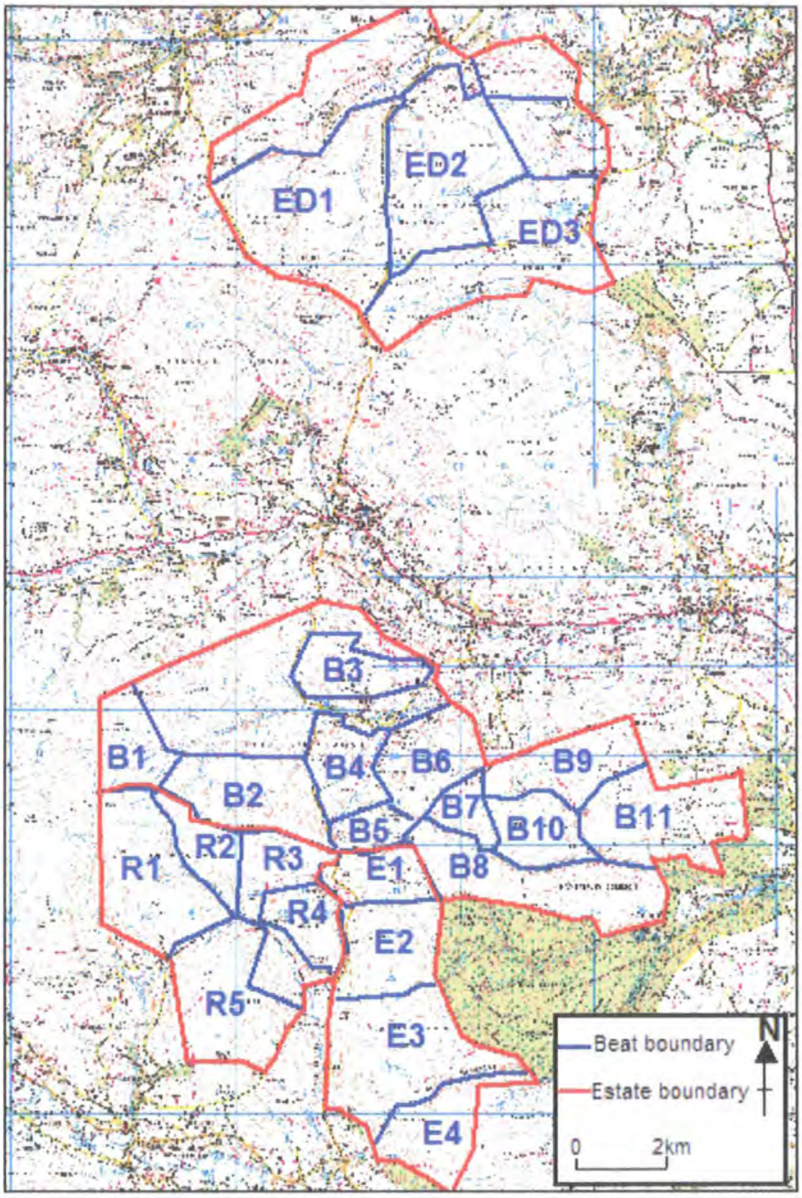


Figure 24 The 23 management units for which grouse density and breeding success were compared with habitat factors in 2000.

To assess whether the composition of the heather sward differed between moors, I compared the proportion of four categories of the heather sward, the proportion of new fires, pioneer heather (grey fires only), building heather (regenerating heather and building heather combined) and mature heather (mature heather and blanket bog combined) using compositional analysis (Aebischer *et al.* 1993). Compositional analysis was used as the proportion of each category which, when summed, totalled unity and therefore could not be considered independent of each other (Aitchison 1986). The data were made independent by calculating the ratio of proportions using one group as a denominator, in this case 'building heather'. The results of the analysis do not depend on which category was used as the denominator. The ratios were log transformed to normalise the data. Analyses of differences between moor were carried out using multivariate analysis of variance (MANOVA) applied to the log-ratios.

The differences in the size of fires between all the moors in 2000 and between years 2000 to 2005 on Eggleston moor only, were tested by ANOVA, with fire size log transformed to normalise the distribution.

(b) Composition of the heather sward and its effect on grouse density and breeding success in 2000

I utilised the log-ratios of the composition of the heather sward individually as potential explanatory variables for grouse density (grouse per km^2) in spring and summer and breeding success (young to old ratio) for each unit, calculated using the DISTANCE program in linear regression.

To assess whether the spatial distribution of grouse in spring 2000 was influenced by the proportion of heather burned and the frequency of burns, the study area was split into 1 km grid squares. From each square the area of heather, proportion of heather burned, number of burns and mean grouse density were extracted. Only squares which had a minimum of 30% heather cover were used in the analysis. The dependent variable mean grouse density was compared separately by linear regression with the proportion of heather burned (arc sine transformed to normalise) and number of burns (log transformed to normalise).

(c) The effects of rotational heather burning on red grouse density and breeding success 2000-2005

To assess the temporal effects of annual heather burning on Eggleston moor from 2000 to 2005 on grouse abundance and breeding success, the study moor was divided into 17, one km blocks (Figure 25). To test that each block was an independent sampling unit and not influenced by the surrounding blocks, an analysis of the spatial autocorrelation of the number of fires within each block (taken as the coordinate of the centre of the block) was undertaken using the Moran's I statistic. This was calculated using Rook's Case, an add-in program for Excel (Sawada 1999).

Each block was dissected by two parallel grouse survey transects, from which an index of grouse abundance in spring (grouse per km^{-1}), summer and breeding success (proportion of young to old) was extracted. Two variables of heather burning were extracted from each 1 km^2 block for each year, (a) the proportion of heather that was burned, and (b) the total perimeter of heather burns. The available data on the known age of heather following burning for each year is presented in Table 7.

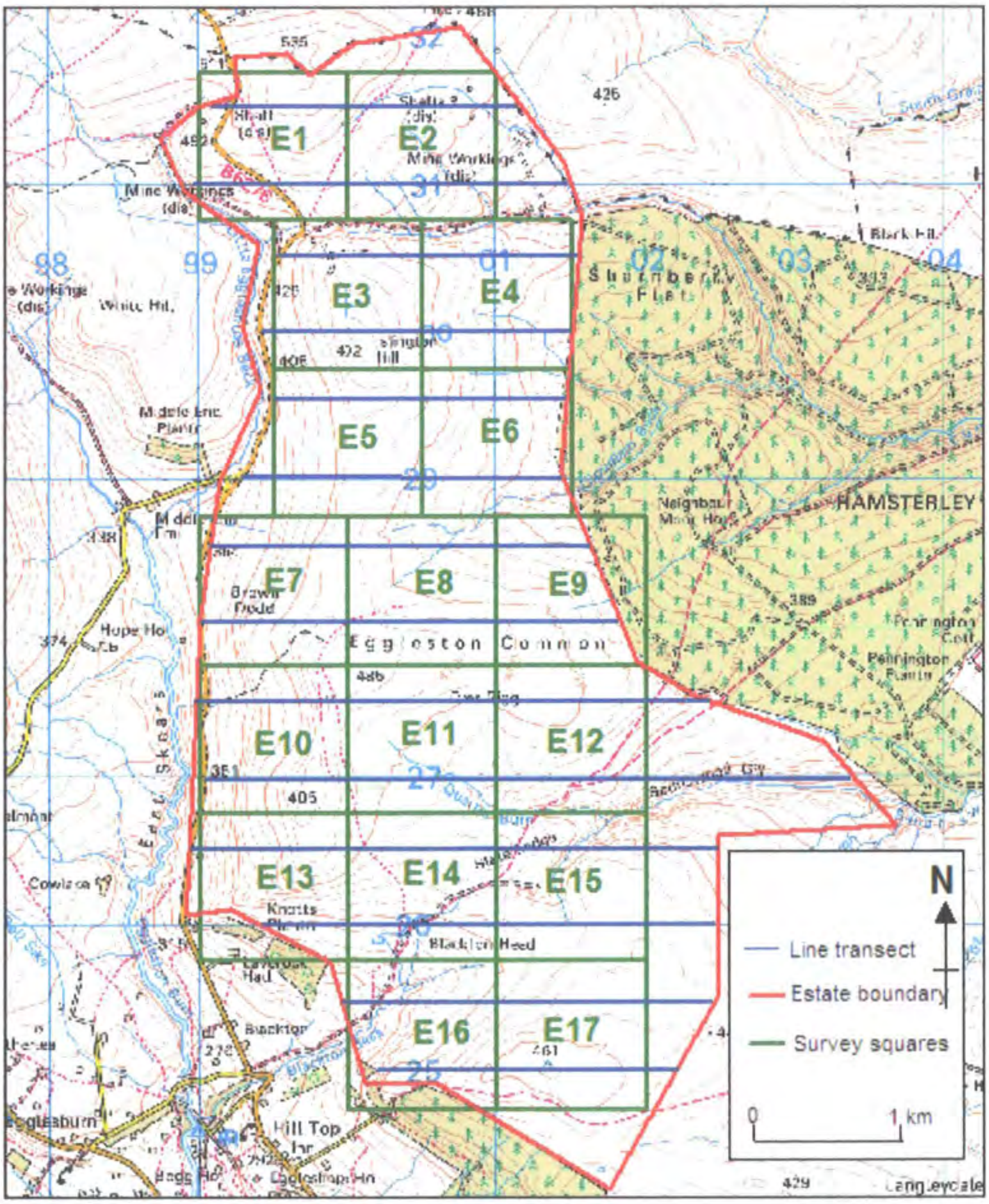


Figure 25 The Eggleston study area, illustrating the 17, one km^2 grid squares from which the relationship between grouse variables and heather burning was investigated.

Table 7 The available data on heather ages for each year, as a result of annual monitoring of heather burning on the Eggleston study area 2000-2005.

	Known heather ages				
Year	Burned that season	One year	Two year	Three year	Four year
2000	*				
2001	*	*			
2002	*	*	*		
2003	*	*	*	*	
2004	*	*	*	*	*
2005	*	*	*	*	*

To consider the effects of heather burning on grouse productivity, an information-theoretic methods approach (Anderson & Burnham 2002) was used. Candidate models to predict grouse productivity were developed by Dr Shane Richards. Factors which were assessed in the model were density dependence and the perimeter and area of heather burned in the year classes year t, year t-1 and year t-2.

The expected growth rate of the grouse population between spring and summer when spring count is *M*, was assumed to have the form,

Equation 1:

$$\bar{\lambda}(M,P_1,P_2,P_3) = \exp(\alpha_0 + \alpha_1 M + \alpha_2 P_1 + \alpha_3 P_2 + \alpha_4 P_3),$$

where P_j are covariates describing the length of perimeter burnt in the sampling area *j* seasons prior. Similarly, the growth rate is calculated when perimeter burnt *j* seasons ago is replaced by area burnt *j* seasons ago, denoted A_j. Yearly variation was modelled by allowing the parameter α_0 to differ across years. Models were constructed that differed in their assumptions regarding whether or not density, year, or the covariates affected grouse population growth.

The probability of counting *M* grouse in summer, given prior spring count *N*, was described by the negative-binomial distribution,

Equation 2:

$$\Pr(N \mid M) = \frac{\Gamma(N+a)}{\Gamma(N+1)\Gamma(a)} \left(\frac{b}{1+b}\right)^{a} \left(\frac{1}{1+b}\right)^{N},$$

where $a = \bar{\lambda} M/(v-1)$, $b = 1/(v-1)$, and $v \geq 1$ is the variance inflation factor that describes how much more variable the data is compared to the Poisson distribution. Using Equation (2), in its most general form, the log-likelihood of the model parameters $\boldsymbol{\theta} = (\alpha_0, \alpha_1, \alpha_2, \alpha_3, \alpha_4)$, given all the data, is,

Equation 3:

$$LL(\boldsymbol{\theta} \mid \text{data}) = \sum_{i=1}^{I} \left[\ln\Gamma(N_i + a) - \ln\Gamma(N_i + 1) - \ln\Gamma(a) + a[\ln b - \ln(1+b)] - N_i \ln(1+b)\right],$$

where data is the set of all I summer counts, individually denoted N_i, and their associated covariates denoted $P_{j,i}$ (or $A_{j,i}$).

The Akaike's Information Criterion (AIC) associated with the model having parameters $\boldsymbol{\theta}$, of which k were non-zero and estimated using maximum likelihood, is,

Equation 4:

$$\text{AIC}(\boldsymbol{\theta}) = -2LL(\boldsymbol{\theta} \mid \text{data}) + 2k$$

AIC was then computed for each model in Excel using the Solver Add-in. Data were ranked in order of their lowest AIC value.

4.3 Results

4.3.1 Accuracy assessment of the classified image

The classified image for the entire study area is illustrated in Figure 26, with the Eggleston study moor shown in more detail in Figure 27. The overall accuracy achieved was 79.8%, (Table 8) with a Kappa coefficient value of 0.78. The spectrally distinct classes such as expanses of water, conifer woodland, bare rock/urban, in-bye grasslands and mature heather were classified with a high degree of accuracy >90%. The greatest error was associated with the grass and heather mix categories (56%) which were not used in any further analysis.

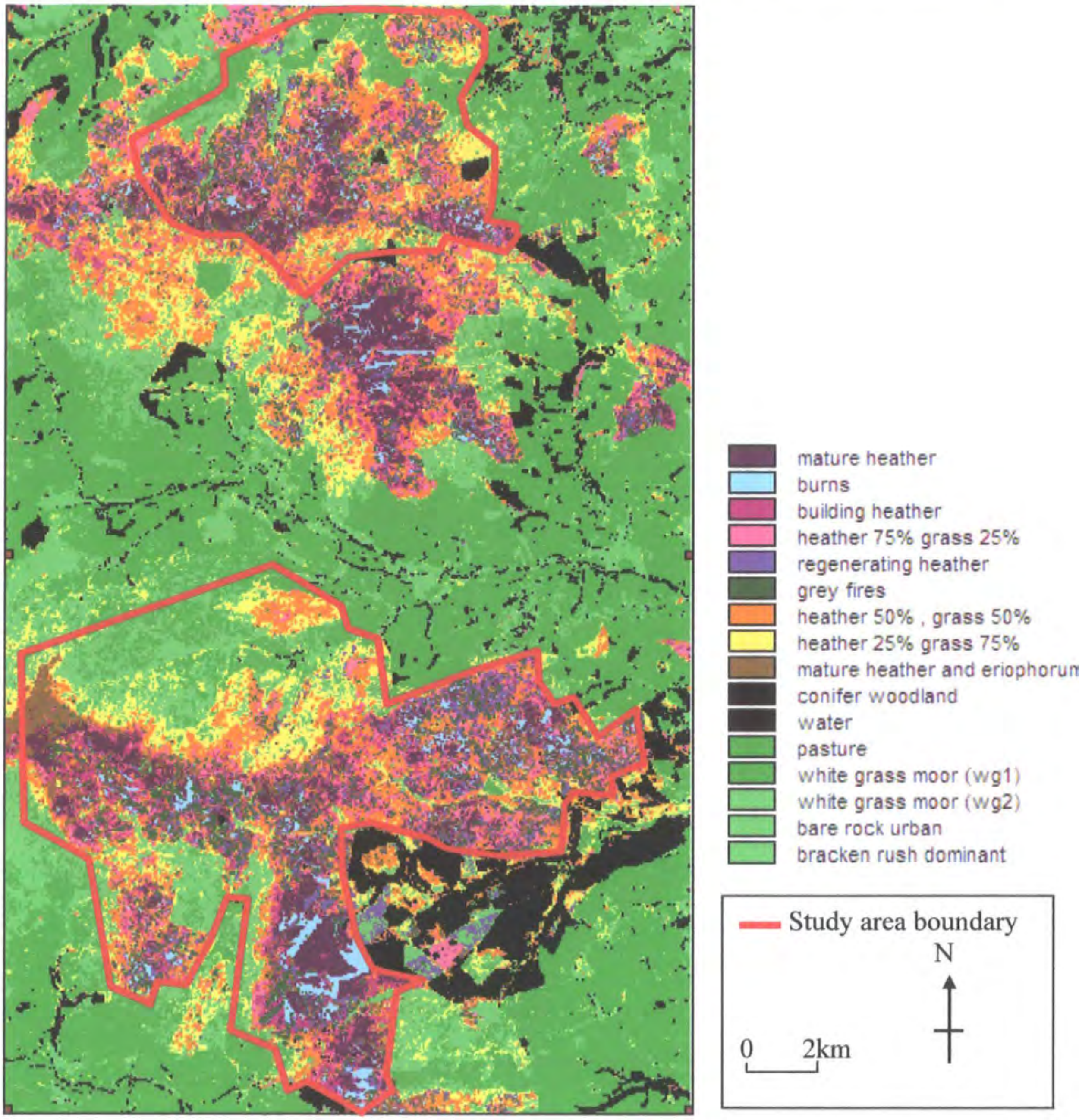


Figure 26 Supervised maximum likelihood classification of the northern and southern sections of the study area, May 2000

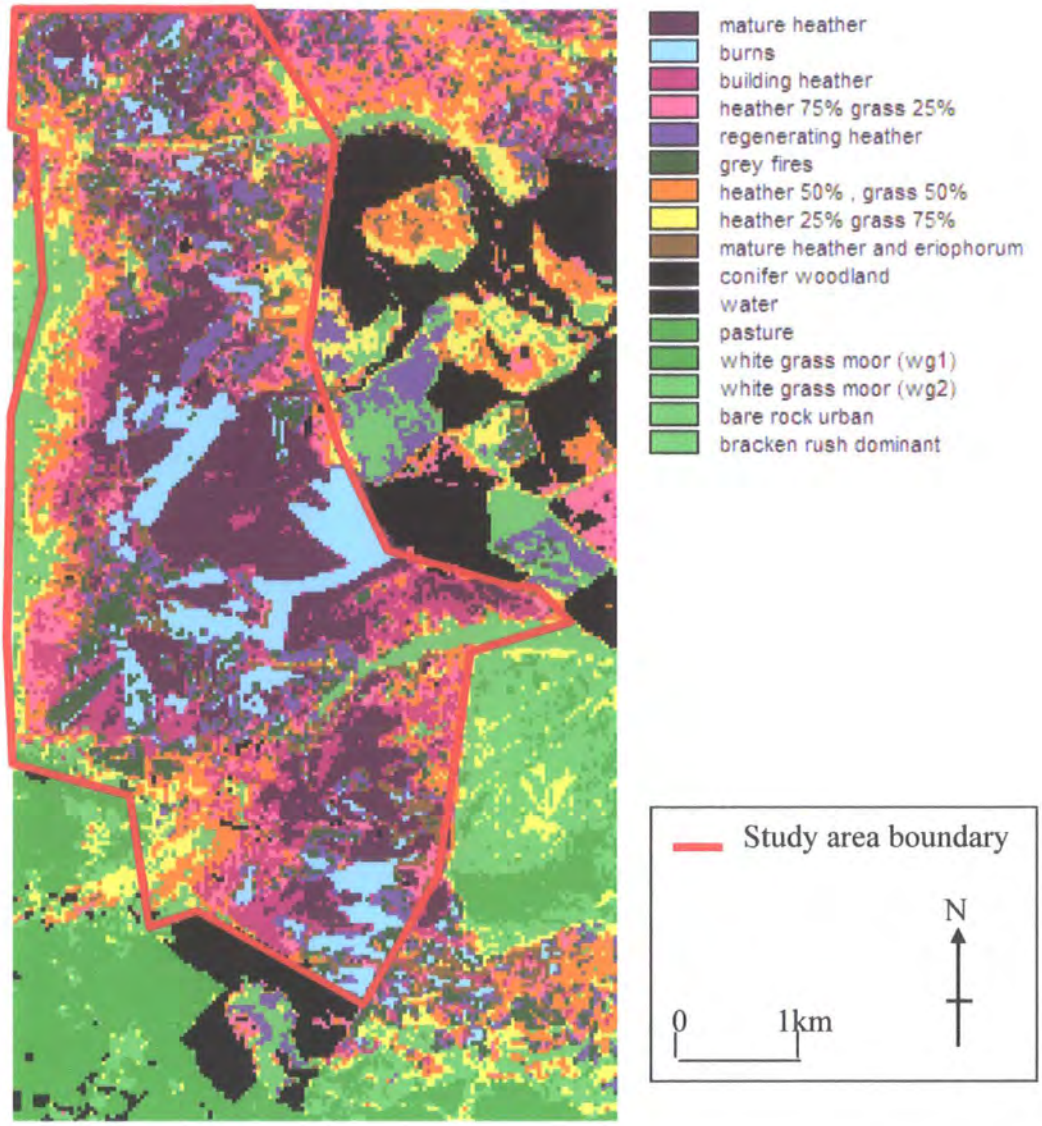


Figure 27 Supervised maximum likelihood classification of the Eggleston moor study area, May 2000.

		Pixels of Reference data																	
		Water	Conifer woodland	Bare rock/urban	Mature heather and cotton grass	Blanket Bog	Burns	Grey fires	Regenerating heather	Building heather	Heather 75%/gras	Heather 50%/ grass	Heather 25%/ grass	White grass moor (WG1)	White grass moor (WG2)	Bracken/rush dominant	In-bye grassland	Sum	Users accuracy
Pixels of Classified data	Water	47																47	100
	Conifer woodland		50															50	100
	Bare rock/urban			48														48	100
	Mature heather and cotton grass	2			66	9	3		2	3	2							87	75.9
	Blanket Bog	1			5	37			3									46	80
	Burns						42	2	3			1						48	88
	Grey fires						1	39	5	1								46	84.8
	Regenerating heather						3	9	34		2							48	70.8
	Building heather					2			3	43	3	1						52	82.7
	Heather 75%/ grass					1	1				28							30	93.3
	Heather 50%/ grass									1	7	28	9		2			47	59.6
	Heather 25%/ grass			2		1					8	15	37	1	7			71	52.1
	White grass moor (WG1)													36	6	9		51	70.5
	White grass moor (WG2)									3		4	4	8	34		4	57	59.6
	Bracken/rush dominant													4		41		45	91.1
	In-bye grassland											1		1	1		46	49	93.9
	Sum	50	50	50	71	50	50	50	50	51	50	50	50	50	50	50	50	822	
	Producers accuracy	94	100	96	93	74	84	78	68	84.3	56	56	74	72	68	82	92		

Table 8 Classified image accuracy assessment.

Overall accuracy=total correct pixels/total number checked 79.8%

4.3.2 Habitat composition and heather management

There were near significant differences in the overall structure of the heather sward between moors (Wilks' $\text{Lambda}_{12,42}=0.31$, $p=0.054$) in 2000 (Table 9). On Eggleston the proportion of new burns was twice that of Raby and Edmondbyers and four-fold that of Bollihope ($F_{3,19}=7.06$, $p=0.002$).

Table 9 The composition of the heather sward on the study moors in 2000, extracted from the classified image.

Moor	New burns % ($\pm$1 SE)	Pioneer heather % (grey fires) ($\pm$1 SE)	Building heather % (regenerating plus building heather) ($\pm$1 SE)	Mature heather % (blanket bog plus mature heather) ($\pm$1 SE)
Edmondbyers	6 ($\pm$1)	9 ($\pm$1)	54 ($\pm$3)	31 ($\pm$2)
Raby	7 ($\pm$1)	15 ($\pm$3)	50 ($\pm$3)	28 ($\pm$5)
Eggleston	12 ($\pm$3)	9 ($\pm$2)	43 ($\pm$4)	36 ($\pm$1)
Bollihope	3 ($\pm$1)	9 ($\pm$2)	61 ($\pm$7)	26 ($\pm$7)

The size of heather burns (Table 10) did not differ significantly between grouse moors in 1999/2000 ($F_{3,768}=1.06$, $p=0.366$). Fire size reduced on Eggleston moor during the 2000 to 2005 period, with five-fold larger burns in the first three years than the last three years ($F_{5,1010}=74.81$, $p=0.000$).

Table 10 Summary of heather burning management practiced on the study moors, illustrating the mean size, frequency and the percentage of the heather resource burned in that burning season.

Moor	Burning season	Total area (km^2) and heather cover (%)	Mean burn area (ha) (±1 SE)	Numbers of fires in that season	Percentage of total heather cover burned per annum
Bollihope	1999/00	41.1 (83)	0.45 (±0.06)	253	3%
Edmondbyers	1999/00	32.3 (87)	0.42 (±0.04)	260	4%
Raby	1999/00	20.6 (80)	0.69 (±0.16)	114	5%
Eggleston	1999/00	19.2 (90)	1.41 (±0.52)	145	10%
Eggleston	2000/01	19.2 (90)	1.70 (±0.31)	45	4%
Eggleston	2001/02	19.2 (90)	2.19 (±0.55)	46	6%
Eggleston	2002/03	19.2 (90)	0.19 (±0.02)	361	4%
Eggleston	2003/04	19.2 (90)	0.28 (±0.03)	209	3%
Eggleston	2004/05	19.2 (90)	0.25 (±0.02)	210	3%

4.3.3 Grouse density and breeding success in relation to habitat composition in 2000

The proportion of heather in the building phase (regenerating and building heather combined) explained 17% of the variation in pre-breeding spring grouse densities ($y=1.69x +4.16$, $r^2=0.17$, $p=0.050$) (Table 11).

The spatial distribution of grouse in spring 2000 was weakly negatively correlated both with the proportion of heather burned ($y= -4.36x +7.35$, $r^2=0.15$, $p=0.003$) and with the frequency of burned patches ($y= -0.60x +7.52$, $r^2=0.11$, $p=0.011$).

Table 11 Results of linear regression with grouse abundance in spring, summer and breeding success (proportion of young to old) as the dependent variables and the log-ratios of the components of the heather sward as the independent variables.

Dependent variable and predictors **Spring abundance (grouse per km^{-1})**	Regression	r^2	P
Pioneer heather	y=-1.39x +5.09	0.09	0.160
Building heather	y=1.69x +4.16	0.17	0.050
Mature heather	y=-0.12x +4.89	0.02	0.546
Summer abundance (grouse per km^{-1})			
Pioneer heather	y=-0.20x +5.83	0.00	0.801
Building heather	y=1.20x +5.32	0.14	0.084
Mature heather	y=-0.24x +5.92	0.12	0.103
Breeding success (young to old ratio)			
Pioneer heather	y=-0.07x +1.16	0.00	0.825
Building heather	y=0.04x +1.13	0.00	0.897
Mature heather	y=-0.04x +1.17	0.02	0.501

4.3.4 Grouse density and breeding success in relation to heather burning through time

There was no significant spatial autocorrelation in the burning data (Moran's I=0.04, z-random=0.53, p=0.290). Therefore the survey squares were assumed to be independent of one another within the analysis.

The best ranked model explaining grouse productivity was a simple model, including density dependence, no heather burning terms (AIC= 781.0) (see Table 12). The second (Δ_i= 0.3) and third (Δ_i= 0.7) best ranked models both included density dependence and the burning perimeter in year t-1 for both constant and all years, but the effect of this was weak when the models were run without density dependence, ranked (Δ_i= 5.0) and (Δ_i= 2.4) respectively.

Table 12 Statistics illustrating the performance of the models in predicting grouse productivity in relation to density dependence and the heather burning variables. Where IF=inflation factor, C=constant, D=density dependence, y=years, BP_1=perimeter of heather burned in year category (BP_1=perimeter of heather burned in year t), BA_1=area of heather burned in year category. Models highlighted in bold identify the three best ranked (Δi) models.

Model	Log-likelihood	K	AIC	Δ_i
$IF + C$	-393.41	4	794.8	13.80
$IF_y + C_y$	-385.77	10	791.5	10.50
$IF + C + D$	**-385.51**	**5**	**781.0**	**0.00**
$IF_y + C_y + D_y$	-383.40	11	788.8	7.80
$IF + C + D + BP_1$	-389.42	6	790.8	9.80
$IF_y + C_y + D_y + BP_1$	-383.13	12	790.3	9.30
$IF + C + D + BP_2$	**-384.65**	**6**	**781.3**	**0.30**
$IF_y + C_y + D_y + BP_2$	**-378.85**	**12**	**781.7**	**0.70**
$IF + C + D + BP_3$	-389.50	6	791.0	10.00
$IF_y + C_y + D_y + BP_3$	-383.29	12	790.6	9.60
$IF + C + D + BP_1 + BP_2 + BP_3$	-383.86	8	783.7	2.70
$IF_y + C_y + D_y + BP_1 + BP_2 + BP_3$	-378.17	14	784.3	3.30
$IF + C + D + BP_2 + BP_3$	-384.64	7	783.3	2.30
$IF_y + C_y + D_y + BP_2 + BP_3$	-378.84	13	783.7	2.70
$IF + C + BP_1$	-392.88	5	795.8	14.80
$IF_y + C_y + BP_1$	-385.24	11	792.5	11.50
$IF + C + BP_2$	-388.02	5	786.0	5.00
$IF_y + C_y + BP_2$	-380.72	11	783.4	2.40
$IF + C + BP_3$	-393.41	5	796.8	15.80
$IF_y + C_y + BP_3$	-385.31	11	792.6	11.60
$IF + C + BP_1 + BP_2 + BP_3$	-386.48	7	787.0	6.00
$IF_y + C_y + BP_1 + BP_2 + BP_3$	-379.79	13	785.6	4.60
$IF + C + BP_2 + BP_3$	-387.96	6	787.9	6.90
$IF_y + C_y + BP_2 + BP_3$	-380.53	12	785.1	4.10
$IF + C + D + BA_1$	-389.52	6	791.0	10.00
$IF_y + C_y + D_y + BA_1$	-383.16	12	790.3	9.30
$IF + C + D + BA_2$	-387.00	6	786.0	5.00
$IF_y + C_y + D_y + BA_2$	-381.77	12	787.5	6.50
$IF + C + D + BA_3$	-388.81	6	789.6	8.60
$IF_y + C_y + D_y + BA_3$	-382.2	12	788.4	7.40
$IF + C + D + BA_1 + BA_2 + BA_3$	-389.79	8	789.4	8.40
$IF_y + C_y + D_y + BA_1 + BA_2 + BA_3$	-380.53	14	789.1	8.10
$IF + C + D + BA_2 + BA_3$	-386.64	7	787.3	6.30
$IF_y + C_y + D_y + BA_2 + BA_3$	-380.43	13	786.9	5.90
$IF + C + BA_1$	-393.21	5	796.4	15.40
$IF_y + C_y + BA_1$	-384.74	11	791.5	10.50
$IF + C + BA_2$	-391.58	5	793.2	12.20
$IF_y + C_y + BA_2$	-384.98	11	792.0	11.00
$IF + C + BA_3$	-392.16	5	794.3	13.30
$IF_y + C_y + BA_3$	-384.27	11	790.5	9.50
$IF + C + BA_1 + BA_2 + BA_3$	-401.68	7	817.4	36.40
$IF_y + C_y + BA_1 + BA_2 + BA_3$	-389.21	13	804.4	23.40
$IF + C + BA_2 + BA_3$	-390.63	6	793.3	12.30
$IF_y + C_y + BA_2 + BA_3$	-383.90	12	791.8	10.80

4.4 Discussion

In this Chapter I demonstrated the application of a supervised classification technique to map with accuracy and precision sufficient for grouse studies, the components of the heather moorland habitat mosaic created by heather burning at a landscape scale. This data was used to assess relationships between the habitat and grouse variables. Spatial analysis across all moors in 2000 found that the highest post-breeding grouse densities were associated with management units which had a high proportion of heather in the building phase.

Annual mapping of heather burning and collection of grouse data on Eggleston between 2000 and 2005 facilitated an assessment of the temporal effects of heather burning on grouse productivity. Modelling of the data identified that density dependence, rather than the heather burning parameters was the most important determinant of grouse productivity.

4.4.1 Mapping heather moorland

The success of the Landsat ETM+ data in this application is due to a number of factors. In the first case the spectral characteristics of the heather moor components of interest in this study were distinctive enough to be used for the identification of individual types. Secondly the spatial resolution of 30 m was appropriate for spatial patchiness observed in these moorlands. It is evident from this and other studies in the United Kingdom that common moorland vegetation types (Buchanan *et al.* 2005) and heather vegetation biomass (Egan *et al.* 2000) can be mapped accurately using earth observation techniques. The accuracy of the maps produced in this and the other studies mapping moorland habitat mosaics (Buchanan *et al.* 2005; Egan *et al.* 2000) are clearly dependent upon the quality of the training site information, the spectral signatures developed, and the level of information on the habitat classes required from the final image. The technique has been shown to be adequate for identifying broad moorland habitat types, but may not be suitable for identifying niche vegetation communities within the sward.

Satellite remote sensing offers a rapid means of data collection for assessing heather habitat at a grouse moor spatial scale, which though available through more conventional methods such as air photography and field survey are both inherently labour intensive and costly. Satellite-based earth observation applications are now widely used in ornithology to evaluate habitats and bird/habitat relationships at landscape or ecosystem scales (Gottschalk *et al.* 2005). Earth observation is an invaluable tool for conservationists to monitor habitats and to inform management strategies, particularly for the assessment of relatively inaccessible areas. For example, earth observation has been used to assess ice cover on rivers in Canada to assess habitat availability for the threatened harlequin duck *Histrionicus histrionicus* (Thibault *et al.* 1998) and to map the distribution of adelie penguin *Pygoscelis adeliae* rookeries in Antarctica (Schwaller *et al.* 1989).

During the study, heather burning management on Eggleston moor has changed radically from a strategy of few large fires to more frequent smaller fires. The management change was due to a number and combination of factors. In 1999 the head gamekeeper retired and was succeeded by his son. Initially long strips were burned to break up large tracts of mature heather, these established fire breaks enabled better control of heather burning as there was an edge of short vegetation to burn to. A further change in burning management resulted following the purchase of mowing equipment in 2001, with two metre wide strips cut around areas of heather prior to burning, to act as fire breaks which further increased both the control and the efficiency of burning. This development in heather burning management has potential repercussions for the suitability of Landsat ETM+ to map heather moorland as if the size of fires became less than 30 m by 30 m it may mean a loss of resolution and the method may not be suitable to distinguish between heather classes. Earth observation technology continues to develop at pace with the launch of the Quickbird satellite in October 2001 (www.digitalglobe.com), which collects high resolution data (61 cm class panchromatic and 2.5 m multi-spectral stereoscopic data) over a large field. Instruments on this platform provide high resolution multi-spectral data for civilian applications: for instance, it has been used in agriculture to assess crop growth and harvests (Yang *et al.* 2006) and to assess lake water clarity, distribution of aquatic vegetation and the area of urban impervious surface area which effects storm water run off and surface water pollution (Sawaya *et al.* 2003). These developments will provide opportunities for exploring fine scale relationships between habitat and animals at landscape and ecosystem scales.

4.4.2 Effects of heather management on red grouse

The temporal analysis of the effects of heather burning on found that density dependence was a more important factor effecting grouse productivity than the heather burning variables. It is likely that the model was unable to detect any effect as heather burning was widely practised across the study area and therefore there was not enough variation within the sample to detect changes.

Rotational heather burning to create a mosaic of different heather ages is widely recognized as a management tool to maximize red grouse densities (Lovat 1911; Miller *et al.* 1970; Picozzi 1968). Although heather is an important component of red grouse diet (Savory 1978) and their presence or absence is dependent on heather, they have been estimated to consume only 2%, up to a maximum of 10% of the total annual production of heather shoots and flowers on a heather dominated grouse moor in North East Scotland (Savory 1978). On moors where heather cover is abundant, such as this study area, it is unlikely that grouse breeding densities could be limited by the total quantity of food present. It is the quality of food which is a more likely explanatory variable of grouse breeding density. In this study, I found that across moors in 2000, the highest pre-breeding densities of grouse were associated with management units where the heather sward had a high proportion of heather in the building phase, five to 40 cm high (regenerating heather plus building heather). This is biologically plausible as grouse are selective foragers, spending most of their time foraging on heather in the ten to 37 cm high category (Savory 1978). Grouse show seasonal preferences for different heather ages, with heather aged four to eight years old preferred in winter and heather aged two to five years old preferred in the spring (Palmer & Bacon 2001; Savory 1978). In the winter and spring, grouse select heather with a high nutrient content, particularly nitrogen and phosphorous (Moss 1972). A high proportion of heather in the building phase will provide an abundance of high quality feeding habitats for grouse through the winter and importantly when females are seeking to gain breeding condition in the spring. It is important to note that red grouse settling patterns in spring are clearly affected by other factors such as kin-selection (MacColl *et al.* 2000), losses through parasitism (Potts *et al.* 1984), predation (Redpath & Thirgood 1997) and harvesting rates.

Although heather makes up 90% of the diet of red grouse (Jenkins *et al.* 1963; Wilson 1911) and provides a key habitat throughout the year, other moorland habitats are also important, e.g. wet, boggy ground and heather and grass mosaics, where invertebrate food are more abundant which are favoured by broods (Savory 1977). Although chicks forage on heather from the first day after hatching, invertebrates, particularly craneflies

Tipulidae can be an important determinant of their growth rates and survival (Park *et al.* 2001). On blanket bog, craneflies are also eaten by adults and may be an important determinant of breeding condition and success (Butterfield & Coulson 1975). Cotton grass is also a characteristic species of blanket bog habitats and the flowers in early spring are a protein rich food (Trinder 1975), sought out by red grouse females and other upland herbivores seeking breeding condition (Baines 1994).

It is clear that red grouse utilize all ages of heather available to them, with nest sites selected in areas of predominantly taller heather than the surrounding vegetation (Campbell *et al.* 2002), which is also important for shelter and provides a food source during periods of deep snow. The open areas created by new fires, have been reported to be avoided as they offer no food source or cover (Palmer & Bacon 2001; Savory 1978). From personal observations and from communications with colleagues (D. Newborn pers comm.) grouse prefer to use these open areas as roost sites as they can see and hear predators approaching.

Heather burning is an important component of grouse moor management to produce harvestable surpluses for driven shooting, which underpins the economics of grouse moor management, which has wide conservation benefits for a suite of ground nesting birds (Tharme *et al.* 2001). There is though concern from conservation bodies regarding the intensity of burning management on the structure and diversity of moorland vegetation communities (Yallop *et al.* 2006) and the potential impacts on global warming (Garnett *et al.* 2000). To maintain heathland communities a degree of burning management is widely acknowledged as a beneficial conservation tool (Allchin *et al.* 1996; Gimingham 1992) and therefore a balance between grouse moor management and conservation requirements is required for the future management of the English uplands.

In conclusion, the study illustrates that this earth observation technique is an appropriate technique for mapping heather moorland habitat mosaics. This habitat data in combination with the annual mapping of heather fires and the collection of data on the distribution and abundance grouse across the study area using distance sampling (Chapter 3) allows spatial scale comparisons between grouse abundance and habitat to be made at landscape scales.

CHAPTER 5

Dispersal by juvenile red grouse

Abstract

I used radio telemetry to investigate the timing, frequency and distances of dispersal in 146 juvenile red grouse (116 females, 30 males) on the North Pennines study moors between 1999 and 2002. A third of the radio tagged birds were shot. Disturbance on shoot days resulted in radio tagged birds being shot more than twice the distance from the catch location than to the last location alive, therefore shot birds were excluded from the dispersal analysis. Dispersal distance differed significantly between sexes, with juvenile females dispersing on average 861 m (range 50 m to 4660 m) and juvenile males on average 343 m (range 90 m to 660 m). Dispersal distances were not related to either pre-dispersal grouse densities in summer or with grouse densities in the following spring. The mean date of dispersal for juvenile females was 6th October ($\pm$4 days SE), with only one record of spring dispersal (14th March) by a female of 1490 m.

The low dispersal distances recorded has repercussions for grouse moor management,as population growth is not limited by dispersal, which has implications for disease and harvest management strategies.

5.1 Introduction

Natal dispersal is defined as the movement between the place of birth and the place of breeding, or where an animal settled and would have bred if it had not died (Greenwood & Harvey 1982). This permanent movement of individuals from natal areas to locations where they breed is observed in most vertebrate species (Greenwood 1980). Studies have shown dispersal to be triggered by intrinsic factors, such as juveniles reaching a certain physical size (Holekamp 1986), an individuals development (Macri *et al.* 2002), or increasing activity levels (Ritchison *et al.* 1992). Dispersal by birds and mammals has also been shown to be influenced by extrinsic or environmental factors, such as avoiding inbreeding, competition for mates and food resources (Clutton-Brock 1989; Dobson 1982; Dobson & Jones 1985; Wolff 1993). The hypothesis to avoid inbreeding suggests that this is best achieved by the complete dispersal of one sex regardless of population density (Dobson 1982; Pusey 1987). Dispersal is recognised as a risky behaviour, with associated costs to survival or fecundity (Bengtsson 1978). Reduced survival rates as a consequence of dispersal may be associated with unfamiliar habitats and increased vulnerability to predators and the ability to source food, while an increased rate of movement may increase energy expenditure and exposure to predation (Gaines & McClenaghan 1980; Johnson & Gaines 1990; Plissner & Gowaty 1996; Small 1993; Waser *et al.* 1994).

The distances and frequency of dispersal show variation between individuals within a species and vary widely between species (Paradis *et al.* 1998; Sutherland *et al.* 2000; Swingland 1983). Information on the distances and frequency of dispersal are of interest to biologists as it is a fundamental element of population dynamics (Arcese 1989), which can influence population growth and spread (Hengeveld 1994; Paradis *et al.* 1998; Sutherland *et al.* 2000) and with it gene flow (Neigel & Avise 1993) and spread of disease (Smith *et al.* 1996). In many species the frequency of dispersal decreases with increasing distance (Taylor 1980), with short and frequent dispersal distances affecting age and sex structure and abundance of populations. The less frequent long dispersers are important for invasion, colonisation processes (Murray 1967; Shaw 1995) and the genetics of populations (Ibrahim *et al.* 1996).

In red grouse, parasitism by intestinal trichostrongyle worms is an important aspect of grouse populations (Potts *et al.* 1984), but so may dispersal. If juvenile dispersal is density-dependent, increased distances and rates of dispersal at increased density may limit population growth. Similarly if dispersal is independent of density as recorded in many other grouse species such as the blue grouse *Dendragapus obscurus* (Hines 1986), spruce grouse *Falcipennis canadensis* (Keppie 1979) and willow grouse (Smith 1997) it may not limit population growth.

A previous study by Jenkins *et al.* (1963) investigated dispersal in red grouse in the Scottish Highlands through ringing chicks and examining ring recoveries. This study did not examine between sex differences in dispersal, the timing of dispersal and was biased by the fact that the majority of recoveries were killed by shooting. In this Chapter I used radio telemetry to investigate the timing, frequency and distances of dispersal in juvenile red grouse and to test the hypothesis of whether dispersal is influenced by grouse density by tagging individuals in areas of known high and low grouse density. Detailed knowledge of these factors has important repercussions for grouse moor management and shooting strategies.

5.2 Methods

Dispersal in juvenile red grouse was studied between 1999 and 2002. A total of 146 juveniles (116 females, 30 males) were located at night whilst roosting, using a high-powered lamp and a hand-held net. In 1999, 61 juveniles (40 females and 21 males) were caught and tagged between the 9th and 13th September, when they were 14 to 16 weeks old. To ensure that any early dispersal was not missed, grouse were tagged earlier in 2000 and 2001, with 26 juveniles (21 females and five males) caught on either the 3rd or 4th August in 2000 and 59 juveniles (55 females and four males) caught between the 25th and 27th July in 2001, when they were eight to 12 weeks old. Capture sites of the juveniles were probably close to the nests from which they hatched, as a study of 38 radio tagged broods on the same study area in summer 2000 found that after eight weeks, broods on average were only 182 m ($\pm$29 SE) from their nests. Individuals were fitted with 15 g necklace radio transmitters, supplied by Biotrack Ltd. Catch sites and subsequent locations were recorded using a hand-held Magellan GPS 300 (Global Position System) navigator with accuracy, particularly prior to 2000, confirmed by checking the position on OS 1:25000 maps. Birds were flushed at least fortnightly with regular searches for missing/dispersing birds conducted from high points in the vicinity of the study area. The study was conducted in parallel with a black grouse radio telemetry study in the North Pennines (Warren & Baines 2002), with missing individuals of both species searched for routinely during fieldwork which covered a radius of some 60 km of suitable habitat from the study moors.

To assess whether dispersal varied according to density, I collected estimates of grouse density both within the natal area of each tagged grouse prior to dispersal and at the site where it subsequently bred the next spring following dispersal. From 2000 to 2002, grouse abundance across the study area pre-breeding in spring and post-breeding in summer (interrupted owing to Foot and Mouth Disease in spring 2001) was surveyed using a line-transect distance sampling methodology. Maps of grouse spatial distribution were generated using Kriging for spring and summer 2000, summer 2001 and spring 2002 (see Chapter 3).

In September 1999, with no prior information available on grouse density, juveniles were caught and tagged within a 3 km^2 area at the centre of the study area. In the subsequent years, maps of spatial abundance for that summer were used to identify areas of high and low grouse abundance in which to catch and tag juveniles. In August 2000, using the map of spatial abundance for summer 2000, 17 juveniles were caught in an area of high summer abundance (>30 grouse per km^{-1}) and nine in an area of low summer abundance (<20 grouse per km^{-1}). In late July 2001, 25 juveniles were caught in an area of high summer abundance (>40 grouse per km^{-1}) and 34 in an area of low summer abundance (<20 grouse per km^{-1}).

Harvesting by driven shooting commenced annually on August 12th and finished on or before 10th December. On shooting days birds may be driven and subsequently shot outside their home ranges. I examined the effects of disturbance during shoot days by comparing distances between tagging locations and the points where birds were shot, with both the dispersal distance of the survivors and with the distance between the tagging location and the last location alive for those birds that were shot.

5.2.1 Statistical analysis

Nine individuals were excluded from the analysis, due to radio transmitters falling off within the first month after capture. To avoid any bias which may be caused by capture and handling, four birds which died within the first two weeks after capture were also removed from the analysis. There was no accurate information on the distance between the catch site to the location where they were shot for eight individuals and these were also excluded. During the study there were only two individuals which were 'lost' and whose outcome could not be verified and these were also excluded from the analysis.

From the original 146 radio-tagged individuals, 123 survived long enough to measure the timing and distance of dispersal. The natal dispersal distance was defined as the straight-line distance between the capture point as a juvenile in August/September and either the centre of the home range in the autumn (flush point data until the end of November) or the following spring (nest site for females) for those that survived. The centre of the home range was quantified using minimum complex polygons (MCP) (Mohr 1947). For birds that were shot, shooting dispersal was defined as the straight-line distance between capture point and point of death. Distances were all log transformed before analysis to normalise the distribution and standardise the variance. To determine whether there were differences between the natal dispersal distances calculated in the autumn and the ones calculated in the following spring, data from individuals for which both measures were available were analysed using a paired t-test. To test for differences in natal dispersal distances in relation to year and sex, a General Linear Model was used with natal dispersal distance as the dependent variable and year and sex as the categorical independent variables. Birds that were shot were analysed in the same way, though to distinguish whether birds which were shot later in the season had dispersed, a date term, the number of days after August 12th that the bird was shot, was included as a continuous variable. To assess whether movements were influenced by disturbance on a shoot day, where grouse can be driven up to 5 km (Jenkins *et al.* 1963), the distances from the catch to place where each bird was shot were compared with the distances from catch site to the last recorded location when alive by a paired t-test. To test for the effects of pre-dispersal grouse abundance in summer on the dispersal of females, a categorical variable indicating high or low density was added to the model (data restricted to birds dispersing in 2000 and 2001). To test for the effects of pre-breeding abundance in the subsequent spring on female natal dispersal distances, a continuous variable measuring spring grouse density in a 500 m radius around the nest or centre of the territory was added to the model (restricted to birds dispersing in 1999 and 2001).

The date of dispersal by females was taken as the mid-point date between the date of leaving the natal home range and the date of settling in the territory in which they subsequently bred. It was not feasible to estimate the timing of male dispersal as we could not distinguish the date of dispersal, due to the small distances from their tagging location recorded in males. The timing of dispersal for females was assessed only for those birds which dispersed further than the mean distance to differentiate between true dispersal and non-dispersive movements within the home range. Differences in the timing of dispersal between years were tested by ANOVA.

5.3 Results

5.3.1 Spatial Interpolation

The distribution of grouse in spring 2000 is illustrated in Chapter 3, Figure 9. The variograms for summer 2000, summer 2001 and spring 2002 were fitted with spherical models; summer 2000, had a nugget of 0, a sill of 220 and a range of 500; summer 2001 had a nugget of 0, a sill of 280 and a range of 900; with spring 2002 having a nugget of 0, a sill of 25 and a range of 1200. The interpolated grouse distribution maps for summer 2000, summer 2001 and spring 2002 are illustrated in Figure 28, Figure 29 and Figure 30, respectively.

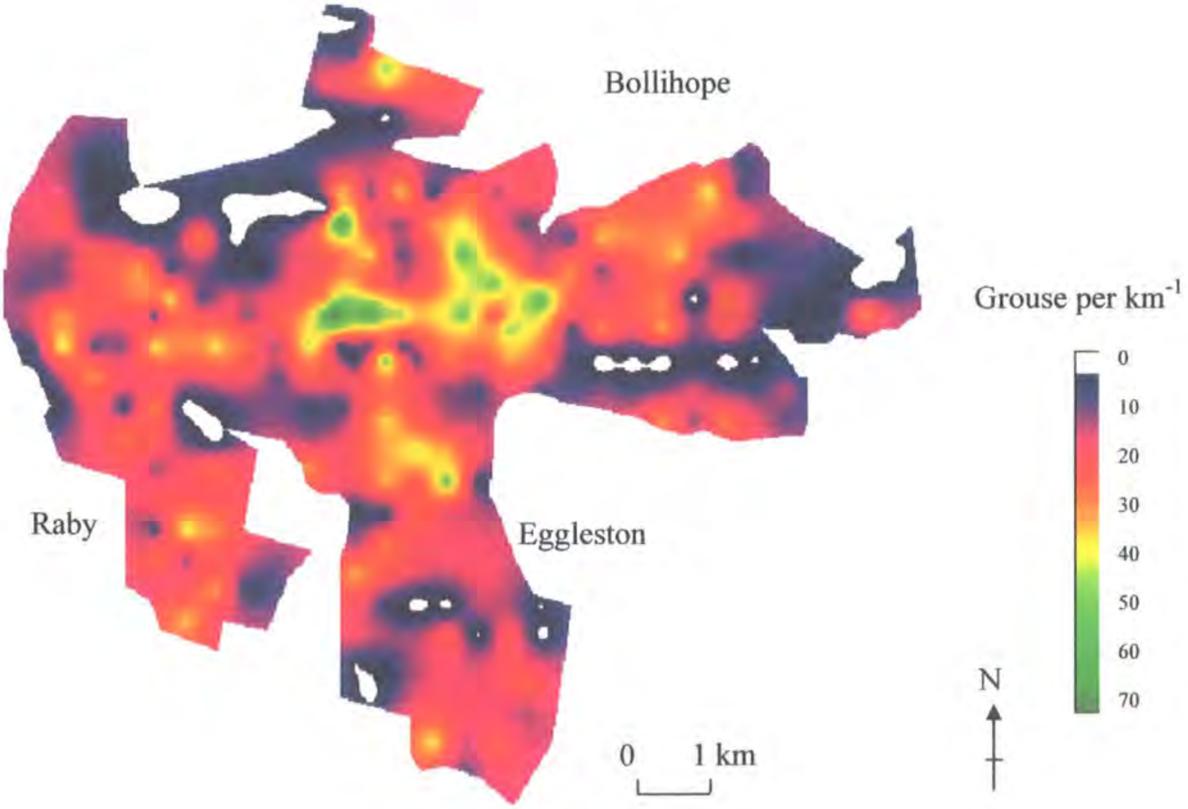


Figure 28 The spatial distribution of grouse across the Bollihope, Raby and Eggleston study areas in summer 2000.

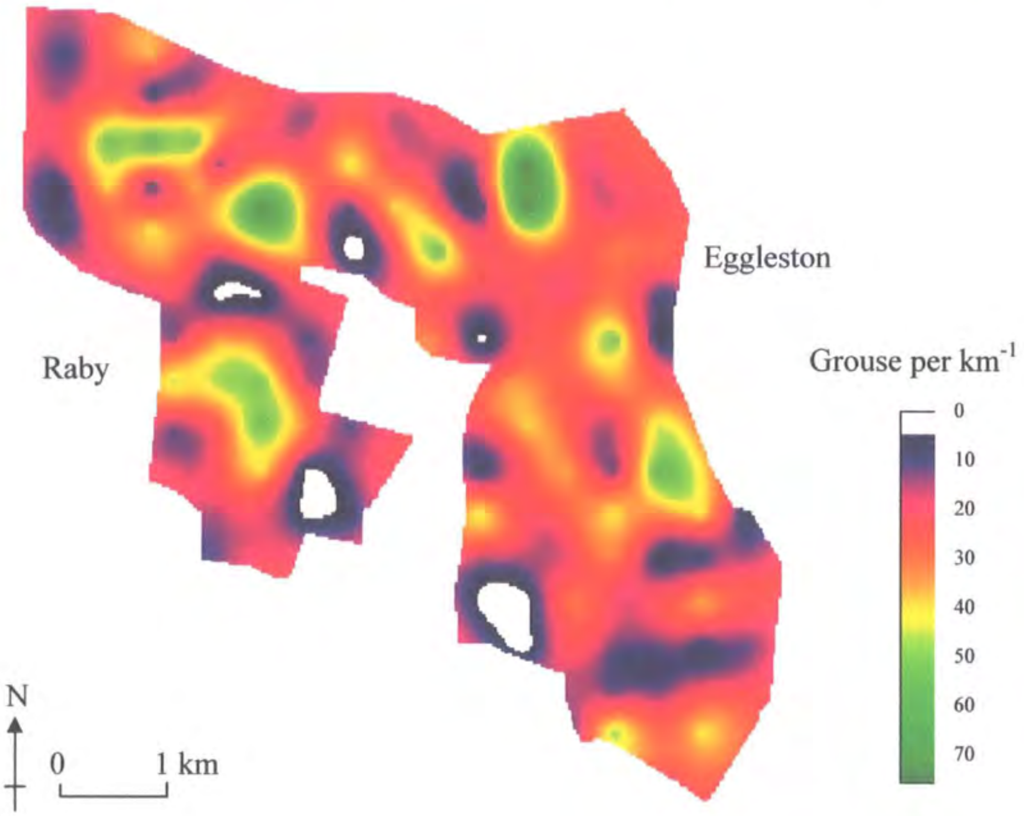


Figure 29 **The spatial distribution of grouse across the Raby and Eggleston study area in summer 2001.**

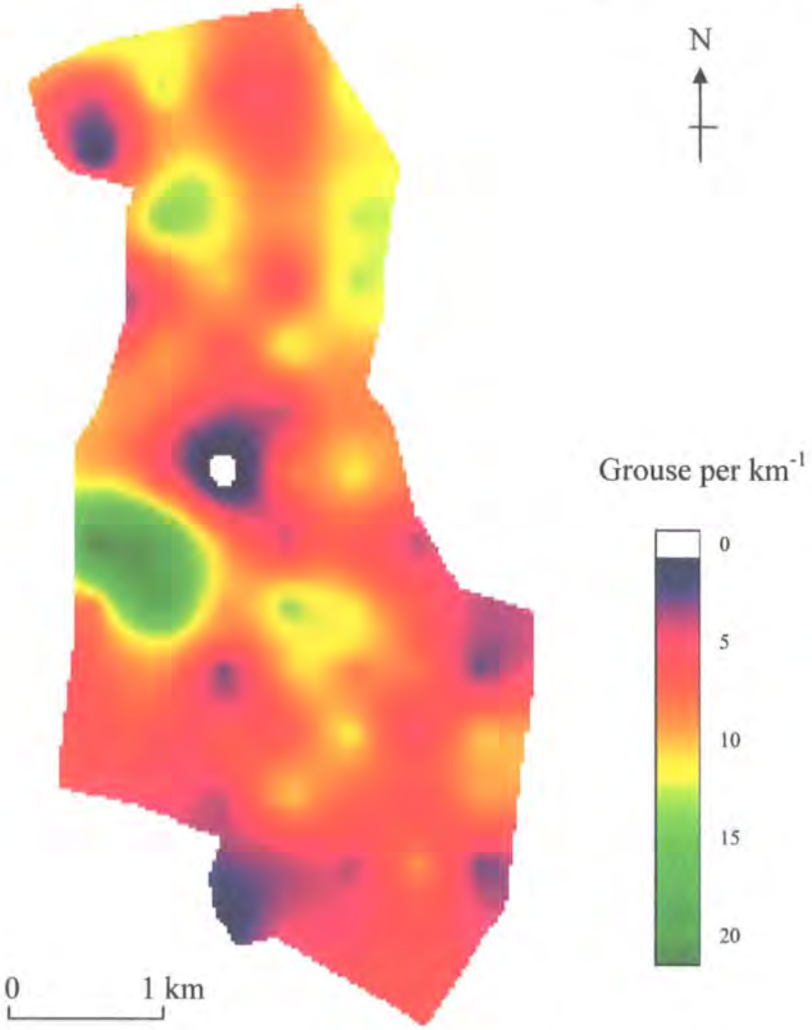


Figure 30 The spatial distribution of grouse on the Eggleston moor in spring 2002.

5.3.2 Radio telemetry

In 1999 when juveniles were tagged at 14 to 16 weeks, only 1.6% of juveniles lost their tags, but in 2000 and 2001 combined, when juveniles were only eight to 12 weeks old, 9.4% lost their tags.

For the 57 individuals which survived through to the following spring there were no differences in the distances between catch location and the autumn home range or the following spring home ranges (t_{56}=-0.12, p=0.906). There were no differences between females only (t_{39}=-1.28, p=0.208) or males only (t_{16}=1.09, p=0.292). There were no significant interactions between sex and year in autumn dispersal distances ($F_{1,55}$=1.03, p=0.315). Therefore the individuals which settled in the autumn, but did not survive the winter were included in all analysis.

During the shooting season 32% of the radio tagged birds were shot. For shot birds the mean distance between the catch site and the place where shot was twice the natal dispersal distances of the survivors ($F_{1,118}$=16.02, p=<0.001), being 1547 m ±250 SE for shot juvenile females (n=33) and 690 m ±178 SE for shot juvenile males (n=6). There was no measurable effect of birds shot later in the season having dispersed ($F_{1,36}$=0.27, p=0.607) or any interaction between shot and days since August 12th ($F_{1,35}$=0.003, p=0.954). For shot birds the distance between the capture location and the place where shot was more than twice the distance (t_{32}=-5.97, p=<0.001) of that between the capture locations and the last location alive, 527 m ±100 SE (n= 29) for females and 264 m ±113 SE (n= 5) for males. Shot birds were therefore excluded from the dispersal analysis.

For unshot birds there were no significant interaction between sex and year ($F_{2,81}$=0.50, p=0.611). Dispersal distances differed significantly between sexes ($F_{1,80}$=4.10, p=0.046), but not between years ($F_{2,80}$=0.39, p=0.680). Therefore the data were pooled across years. The mean dispersal distance by juvenile females (n=63) was 861 m (±120 SE), ranging from 50 m to 4660 m (Figure 31). For juvenile males (n=21) the mean dispersal distance was 343 m (±31 SE), ranging from 90 m to 660 m. Female dispersal distances were not related to either pre-dispersal density in summer ($F_{1,30}$=1.87, p=0.181) or with density in the following spring ($F_{1,50}$=0.01, p=0.928).

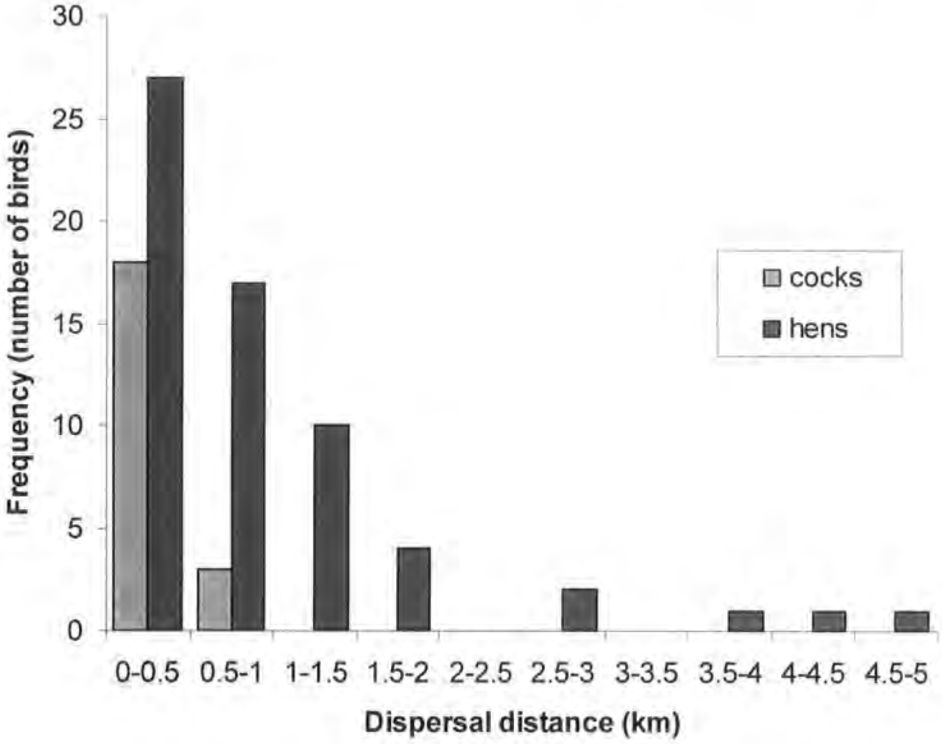


Figure 31 The distribution of dispersal distances by juvenile male and female red grouse 1999-2001 (n=84).

The mean date of the autumn dispersal for juvenile females was 6th October (±4 days SE) (Figure 32) and this did not differ significantly between years ($F_{2,20}$=0.46, p=0.636). During the study there was only one record of spring dispersal (14th March) by a female of 1490 m.

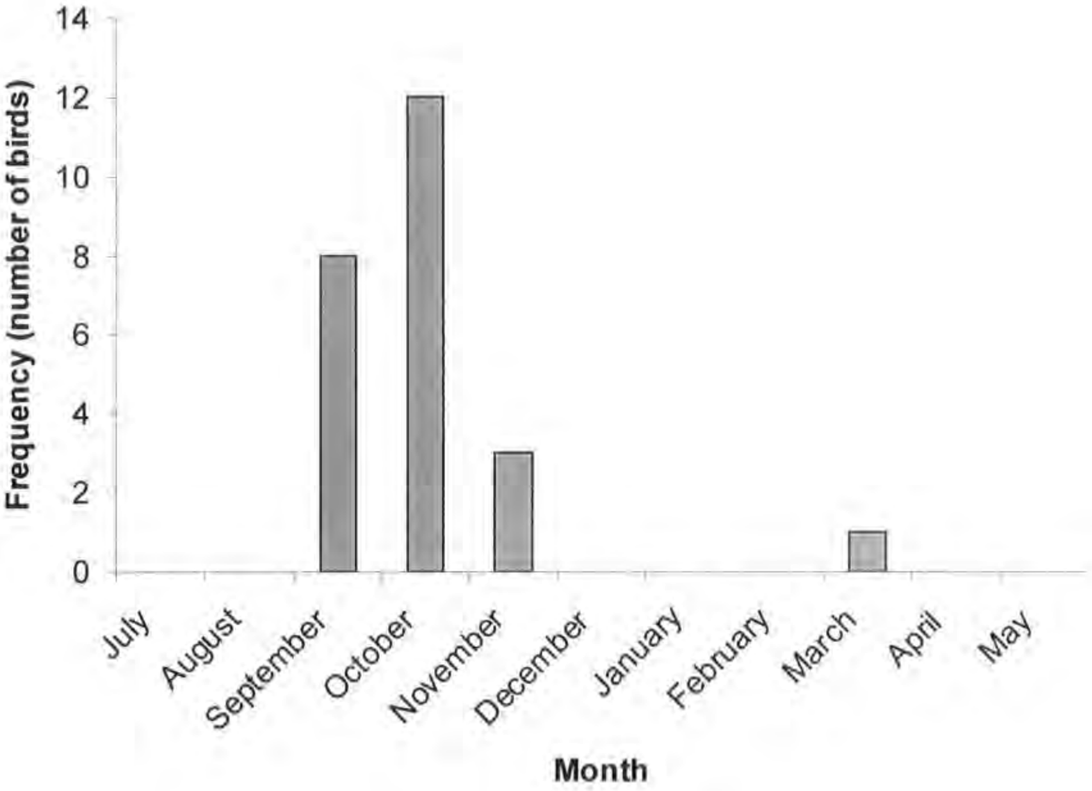


Figure 32 **The timing of dispersal by juvenile female red grouse 1999-2001 (n=24).**

5.4 Discussion

The main findings in this Chapter are that dispersal in red grouse is female biased, with females dispersing on average 861 m in comparison to the average distance of 343 m recorded in males. Juveniles began dispersing following independence from family groups in September with the average date of dispersal being the 6th October. Female dispersal distances were found to be both independent of both summer grouse densities and densities the following spring.

This Chapter confirms that red grouse are highly sedentary. The juvenile dispersal distances were similar to those found by Jenkins (1963) whereby of 793 ringed juvenile grouse recovered (ringed as chicks), 84% were within 1.5 km of the ringing location and 94% within 5 km, with one hen moving 42 km. The sample size is approximate ly seven times larger than this study and this may explain why I have not recorded any long dispersers. During the study only two individuals were not recovered and although I cannot discount that some of these individuals may have dispersed a long distance, I deem this to be unlikely due to a number of factors. The study was run in tandem with a study on black grouse with a wide search area (c. 500 km^2) and the landscape of the North Pennines is favourable to radio telemetry with a good road network and rolling landscape. The other more feasible reasons for the failure to locate these individuals are the failure of radio transmitters due to a technical fault or direct damage by shooting and the bird not being recovered. Another explanation is that grouse predated by stoats are often cached underground and these are very difficult to locate and retrieve.

It has been observed in other studies that long-distance dispersal occurs regularly but at a relatively low frequency (Murray 1967; Paradis *et al.* 1998). These long distance dispersers have been shown on theoretical grounds to be important in invasion processes (Shaw 1995) and the genetic structuring of populations (Ibrahim *et al.* 1996). An example of this has been recently observed in willow ptarmigan in Alaska where flocks of birds have been seen at sea, eight to 17 km from land (Zimmerman *et al.* 2005). This may have been a one off event, but shows that grouse have the potential to disperse long distances if required.

The female biased dispersal behaviour of red grouse has been demonstrated in other grouse species; willow grouse (Smith 1997), white-tailed ptarmigan (Giesen & Braun 1993), ruffed grouse *Bonasa umbellus* (Small & Rusch 1989) and black grouse (Caizergues & Ellison 2002; Warren & Baines 2002). Natal dispersal strategies of red grouse differed from those reported in willow ptarmigan in Norway (Broseth *et al.* 2005) where no significant differences between sex in natal dispersal distances were recorded. These results may have been confounded by low sample sizes, but the three longest dispersers (six to eight km) where the sex was known were all males. Autumn densities on the Norwegian study areas were estimated at 22 (18.9 to 25.1) birds per km^2 which is at least ten-fold lower than those recorded on the North Pennines study moors. The differing dispersal strategies in male willow ptarmigan may be due to other factors such as the limited availability of food resources and competition for territories.

The dispersal behaviour of red grouse differed markedly from that of black grouse in the study area, where the mean natal dispersal distances of juvenile black grouse females were recorded at 9.3 km (Warren & Baines 2002), up to a maximum of 27 km. These differences in dispersal distances between species may be explained by the different mating systems, i.e. territorial pairing in red grouse (Hudson 1992) and the lekking system of one cock, many hens in black grouse (De Vos 1978). It is therefore likely that because red grouse are found at autumn densities, ten-fold higher than black grouse densities the juvenile females need only disperse a relatively short distance crossing a number of territories to select a mate which is not a directly related sibling.

The limited frequency and distances of dispersal recorded in red grouse in this study means that management for red grouse has to be considered at a landscape scale, with connectivity of heather moorland habitats necessary to allow dispersal between sub-populations. This is recognised as a problem for black grouse in northern England with sub-populations becoming fragmented and isolated from one another due to the loss and degradation of suitable habitat mosaics (Warren & Baines 2004). Black grouse have a greater dispersal capacity than that recorded in red grouse (Warren & Baines 2002), therefore future management of red grouse has also to consider the connectivity of heather moorland habitats at a landscape scale to allow natural dispersal processes.

Most grouse species studies have found dispersal distances and frequency to be independent of density, i.e. blue grouse (Hines 1986), spruce grouse (Keppie 1979) and willow grouse (Smith 1997). In this study, both dispersal distances and rates were independent of both start and end indices of grouse abundance. This fits with the two hypotheses that try to explain grouse cycles, the parasite hypothesis (Hudson *et al.* 1992) and the kin selection hypothesis (Moss & Watson 1984). The low dispersal distances for juvenile males (mean 343 m), fits with the kin selection hypothesis, whereby the highly sedentary behaviour of new male recruits, causes them to settle near to their fathers and creates clusters of related territory owners (Watson *et al.* 1994). Density independent dispersal by juvenile females means that the population growth is not regulated by increased dispersal at high densities and cannot therefore account for population cycles. This lack of dispersal by both males and females, in conjunction with the kin selection hypothesis is important in the parasite hypothesis, as population growth is not limited by dispersal, growing to high densities whereby the density dependent effect of the parasitic nematode *Trichostrongyle tenuis* causes such dramatic crashes in the population (Potts *et al.* 1984).

Juvenile red grouse begin dispersing following independence from the family groups from September through to early November. This has potential repercussions for harvest management, as shooting late in the shooting season after birds have dispersed may impact on subsequent breeding densities as birds have already taken territories.

This may be an important opportunity for extending harvest programmes to regulate density to combat density dependent stronglyosis disease outbreaks.

This information on dispersal in juvenile red grouse is very important to grouse moor managers as it confirms that red grouse are in general sedentary which has repercussions for harvest management and disease prevention. A well organised shooting programme, based on July counts may have an important role in limiting population growth and therefore in managing disease. Shooting plans which concentrate on high density areas and take into account the fact that grouse have settled onto breeding territories by mid-November, may be a important tool in combating the disease strongylosis by regulating breeding density.

CHAPTER 6

An investigation of the role of shooting on red grouse population dynamics on the study moors and in other UK regions

Abstract

I evaluated the population processes of red grouse on the North Pennines study moors and assessed differences in the causes of mortality recorded from radio telemetry studies in the North Pennines, England; the Langholm moors in the Scottish Borders and from moors in the Scottish Highlands. Estimates of grouse density on the North Pennines study moors in 2000 were calculated both in spring and in summer using the distance sampling method. Density estimates and breeding success were compared with information on the age structure of the harvest and nematode worm burdens collected from shooting days on the same areas across the study area. Estimates of grouse density in spring and summer for each moor (2000 to 2005) were compared with breeding success, harvest rates and over-winter losses for each moor.

On the North Pennines study moors, juveniles comprised 74% of the harvest, with the proportion of young grouse harvested positively associated with breeding success. Worm burdens were ten-fold higher in adults than juveniles and worm burdens differed between management areas. Recorded spring densities were on average 131 (±15 SE) grouse per km^2, ranging from 81 to 215 grouse per km^2. On average, 88% of adults survived the breeding period, with productivity averaging 5.2 (±0.4 SE) chicks per hen, with an average 84% of hens with broods. A strongylosis disease outbreak in 2005 severely reduced survival rates and breeding success. The density of grouse shot was positively correlated with both summer densities and breeding success. On average, 41% of the post-breeding summer moor population were shot, ranging from 66% in 2003 to zero shot in 2005, as a result of the strongylosis induced population crash in that spring.

The cause of death of radio-tagged grouse varied between regions. Shooting explained 61% of all deaths on the North Pennine moors, in contrast to the Langholm moors, where predation, particularly by raptors explained 74% of losses.

6.1 Introduction

Population size of species is determined by the balance between gains from breeding, immigration and losses from mortality and emigration. To maximise harvestable surpluses of red grouse for driven shooting, grouse moor managers aim to increase the equilibrium density (Redpath & Thirgood 1997). This is the point where gains through breeding and immigration equal the losses through mortality and emigration. This is achieved by employing gamekeepers to control the predators of red grouse, to improve habitat quality through rotational heather burning (Miller *et al.* 1966; Picozzi 1968) and through the control of the parasitic nematode worm *Trichostrongylus tenuis* (Newborn & Foster 2002).

Both density dependent and density independent processes, such as habitat quality, climate, parasites, predation and competition act on grouse populations at any one time. The importance of these processes varies both spatially and temporally. To effectively manage red grouse populations it is important to determine which of the vital rates influence the growth of the population. Survival rates through the breeding period and over-winter can be important determinants of population growth, as can breeding productivity. Factors which limit population growth such as predation and disease are also important (Newton 1994).

Red grouse populations demonstrate cycles, with density dependent strongylosis disease outbreaks reducing fecundity and survival (Hudson *et al.* 2002). In non-harvested grouse populations, predators play an important role in population cycles, with the abundance of gyrfalcon *Falco rusticolus* has been shown to be an important factor in the population cycles of rock ptarmigan in Iceland, with predation rates highest in the decline stages and low years of the population (Nielsen 1999). In Scotland, raptors, specifically hen harrier *Circus cyaneus* and peregrine falcon *Falco peregrinus*, have been shown to limit population growth and dampen cycles in red grouse populations to such a low level that driven grouse shooting became uneconomic (Thirgood 2000). Predators also play important roles in the population cycles of snowshoe hare (Krebs *et al.* 1995), lemmings (Gilg *et al.* 2003) and voles *Microtus agrestis*, *Microtus rossiaemeridionalis* and *Clethrionomys glareolus* (Norrdahl & Korpimaki 1995).

In this Chapter I tested the hypothesis "could shooting be used as a tool to control population cycles in grouse through limiting population growth". To test this hypothesis

I investigate the role of shooting on grouse populations on the study moors in northern England spatially across all moors in 2000. Shoot days were attended across the study moors and drive specific bag information gathered on age and parasite burdens which were compared with grouse density estimated from the distance sampling method (Chapter 3). I assessed this temporally from 2000 to 2005, with harvest bags collected annually and compared with density estimates and breeding success data collected using the distance sampling method.

To place these results in context with grouse populations in other regions of the United Kingdom where the intensity of management differed, I compared and contrasted the causes of mortality from radio tagged individuals in northern England (Chapter 5) with data from two other radio telemetry studies conducted during a similar time frame in Scotland, at the Langholm moors in the Borders (Redpath & Thirgood 1997) and from population dynamics studies conducted in the Highlands (Campbell *et al.* 2002).

6.2 Methods

6.2.1 Population dynamics on the North Pennines study moors

Red grouse density in spring, summer and breeding success (chicks per hen), were surveyed using the distance sampling method (see Chapter 3). Data were collected in spring and summer on Eggleston, Raby, Bollihope and Edmondbyers moors in 2000, Eggleston and Raby moors in summer only in 2001, and in spring and summer from Eggleston moor 2000-2005. The total numbers of grouse shot during the shooting season (12th August to December 10th) were collected from each of the moors.

To assess the age structure of grouse harvested and nematode worm burdens in relation to grouse density and breeding success, 22 shooting days were attended on the study moors in 2000. Information was collected on the numbers of grouse shot, the age structure of the bag and the worm burdens across the study area. Efforts were made to collect samples from each of the 23 management units across the study area (see Chapter 4, Figure 24). The age structure of the bag was recorded from 20 management units and worm burdens sampled from 16 of the management units. Shot birds were aged as juveniles or adults from their toenail scarring (scarred in adults) and by the condition and moult of primary feathers (Hudson & Newborn 1995). Worm burdens, were assessed from a minimum of five young and five old birds selected at random.

Strongyle worm burdens were assessed from one of the two blind ended caeca, using a standard technique (Hudson & Newborn 1995; Wilson 1983). One of the caecae was cut length ways into small pieces and washed thoroughly in an 800 μm mesh sieve on top of a 200 μm sieve, into which adult worms were collected. The contents of the second sieve were washed into a beaker and diluted to a volume of 300 ml with water. The number of worms within three 10 ml samples, were counted in a Petri dish placed on a dark background. The number of worms in a grouse was calculated by adding the three counts, multiplying by ten (up to 300 ml), and then multiplied by two as a grouse has two caeca. A geometric mean strongyle worm burden was calculated for each bird and a mean strongyle worm burden for adults and juveniles calculated for each management unit.

6.2.2 Causes of mortality in red grouse

Radio telemetry was used to determine the cause specific mortality factors, as the tagged individual can be located after death and a cause ascertained (Heisey & Fuller 1985). It is important however that the capture and attachment of a radio transmitter does not affect the probability of death as this can bias the results (Demers *et al.* 2003). In this study, necklace radio transmitters have been used which have been found to have no significant effect on survival rates of red grouse (Thirgood *et al.* 1995), albeit the power of the study to test for a significant effect was weak.

The radio telemetry data used to assess the causes of mortality in red grouse are from the following study sites:

(1) The dispersal study (1999-2001) in the North Pennines, reported in Chapter 5.
(2) Holwick and Wemmergill Moor in the North Pennines (1995-2001) (Newborn & Foster 2002).
(3) Langholm Moor in the Scottish Borders (1994-1999) (Redpath & Thirgood 1997).
(4) Eight moors in the Scottish Highlands (1996-2003) (Campbell *et al.* 2002).

In northern England grouse moor management was the primary land use with full-time gamekeepers employed, in comparison to the Scottish Highlands where grouse moor management was a secondary land use and at Langholm where grouse moor management had ceased to operate.

When all the radio telemetry studies were combined a total of 1064 birds were tagged between 1994 and 2003. The age and sex of sample birds varied between studies, with the dispersal study biased towards juveniles caught in the summer, and the breeding success studies biased towards adult females, caught in the late-winter. Data from the North Pennines (1997-2001), which included the dispersal study reported in Chapter 5, were combined with the Holwick and Wemmergill study to provide data from 248 individuals, 115 caught as adults (all hens) and 133 caught as juveniles (72 cocks and 61 hens). Data from the Scottish Highlands (1996-2003) were available for 291 individuals, 253 adult hens and 38 juvenile hens. From the Langholm Moors (1994-1999), data were available for 525 individuals, 246 caught as adults (136 cocks and 110 hens) and 279 caught as juveniles (125 cocks and 154 hens).

In common across studies, red grouse were caught at night, from July through to March, whilst roosting, using a high-powered lamp and caught in a hand-held net. Birds were sexed and aged as either juvenile (less than one year old) or adults. They were fitted with 15 g necklace radio transmitters, supplied by Biotrack Ltd. Tagged birds were visited at least every two weeks and flushed, with searches for dispersing/lost birds conducted within a 50 km radius of the study areas.

The time of death of radio-tagged individuals was recorded as either the mid-point between the last time the bird was flushed and when it was found dead, or the exact date when an individual was shot.

The cause of death was ascertained from associated field signs and from the external and internal examination of the carcasses for either evidence of predation (e.g. talon, beak or teeth marks) or shooting related injuries following criteria described in (Corbet & Harris 1991; Cresswell & Whitfield 1994; Jenkins *et al.* 1964) and (Thirgood *et al.* 1998).

6.2.3 Statistical analysis

The relationship between strongyle worm burdens, age of red grouse and management unit on the North Pennines study area were considered using a General Linear Model.

The relationship between mean strongyle worm burdens in juveniles and adults and the age structure of the harvest were considered independently with spring and summer grouse density and breeding success using linear regression. Data were tested for normality and if not normally distributed were log transformed to normalise the data.

The relationship between spring and summer grouse density and breeding success, harvest rates (grouse shot per km^2 of managed moor) and over-winter mortality (changes in numbers between summer in 'year t' and spring 't +1') were considered using linear regression. Data were tested for normality and if not normally distributed were log transformed to normalise the distribution.

The causes of mortality were grouped into categories for analysis; predation by raptors, predation by mammals, shot, other (which included death by collision and disease) and unknown, where the cause of death could not be identified. Differences in the causes of mortality of grouse between region, age and season were tested by chi-square contingency table analyses.

6.3 Results

6.3.1 North Pennines study moors in 2000: age structure of the harvest and strongyle worm burdens in relation to grouse density and breeding success

Strongyle worm burdens were ten-fold higher ($F_{1,155}=59.72$, p=0.000) in adult grouse, mean 5342 (±369 SE) worms per bird than juveniles, mean 458 (±44 SE) and differed significantly between management units ($F_{15,155}=2.29$, p=0.006).

Mean worm burdens in adults were not related to spring density (y=0.16x +7.7, $r^2=0.06$, p=0.357, n=17), breeding success (y=0.07x +8.3, $r^2=0.01$, p=0.663, n=17) or summer density (y=0.18x +7.5, $r^2=0.05$, p=0.395, n=17). Mean worm burdens in juvenile grouse were positively associated with adult density in the spring (y=0.64x +2.84, $r^2=0.26$, p=0.038, n=17), but were not related to worm burdens in adults (y=0.31x +3.39, $r^2=0.03$, p=0.524, n=17), breeding success (y=0.00x +6.01, $r^2=0.00$, p=0.977, n=17) or total density in summer (y=0.51x +3.08, $r^2=0.11$, p=0.192, n=17).

Juveniles comprised 74% of the harvest, with the proportion of juveniles harvested positively associated with breeding success ($y=0.18x +0.07$, $r^2=0.27$, $p=0.022$, $n=20$).

6.3.2 North Pennines study moors: breeding densities, summer losses and breeding success

Spring densities were on average 131 (±15 SE) grouse per km^2, ranging from 81 to 215 grouse per km^2 (Table 13). The percentage of adults surviving through the breeding period, spring to summer, for the period 2000 to 2004 were on average 88%, with the exception of 2005 when an outbreak of strongylosis lead to a dramatic reduction in survival with only 21% of adults surviving this period.

Table 13 Estimates of red grouse densities in spring and summer for each moor and year calculated using distance sampling. Survival of adults during the breeding season and breeding success shown as numbers of chicks per hen and the proportion of hens with broods on the study moors 2000-2005 (FMD= Foot and Mouth Disease).

Estate	Year	Spring density (grouse/km^2)	Summer adult density (grouse/km^2)	Survival (%) between spring and summer	Breeding success (chicks per hen)	Percentage of hens with broods
Eggleston	2000	97.5	88.3	91	5.0	86
Raby	2000	81.0	96.3	119	5.3	86
Edmondbyers	2000	130.2	93.2	72	3.9	76
Bollihope	2000	138.6	104.9	76	4.9	81
Raby	2001	FMD	107.8	-	6.3	88
Eggleston	2001	FMD	106.7	-	7.4	95
Raby	2002	215.3	-	-	-	-
Eggleston	2002	192.8	101.0	52	5.2	87
Eggleston	2003	119.2	76.8	64	5.2	89
Eggleston	2004	120.9	109.9	91	5.2	86
Eggleston	2005	84.5	17.9	21	3.3	67

Breeding productivity across all moors averaged 5.2 (±0.4 SE) chicks per hen with an average 84% of hens with broods. The strongylosis population crash in 2005 reduced breeding success to a mean of 3.3 chicks per hen, with only 67% of encountered hens with broods. Breeding success was positively correlated with summer density

($y=0.30x -0.10$, $r^2=0.74$, $p=0.001$, $n=10$), but was independent of breeding densities measured in spring ($y=0.18x +0.68$, $r^2=0.09$, $p=0.475$, $n=8$).

6.3.3 Harvest rates

The density of grouse shot (grouse km^{-2}) was positively correlated with breeding success ($y=5.81x -4.89$, $r^2= 0.61$, $p=0.007$, $n=10$) and the density of grouse in summer ($y=2.54x -9.87$, $r^2=0.94$, $p=0.000$, $n=10$), but not with spring density ($y=2.92x -9.53$, $r^2=0.21$, $p=0.258$, $n=8$). On average, 41% of grouse in summer were shot, ranging from 66% to none shot in 2005 due to the strongylosis induced population crash in that spring (Table 14).

Table 14 Summer population estimates calculated using distance sampling and the annual harvest and the proportion of the population harvested.

Estate	Year	Total summer population (95% confidence limits)	Harvest (total numbers of grouse)	(%) of population harvested (including 95% confidence limits)
Edmondbyers	2000	7477 (6136-9111)	1759	23.5 (19.3-28.7)
Bollihope	2000	13546 (10869-16882)	4527	33.4 (26.8-41.7)
Raby	2000	7147 (5726-8921)	3512	49.1 (39.4-61.3)
Raby	2001	8963 (7049-11396)	4217	47.0 (37.0-59.8)
Eggleston	2000	5319 (4248-6661)	2079	39.1 (31.2-48.9)
Eggleston	2001	9443 (7507-11879)	3600	38.1 (30.0-48.0)
Eggleston	2002	6830 (5274-8847)	4068	59.5 (46.0-77.1)
Eggleston	2003	5299 (4210-6671)	3512	66.2 (52.6-83.4)
Eggleston	2004	8164 (6407-10403)	5168	63.3 (49.7-80.7)
Eggleston	2005	1026 (673-1566)	0	0

6.3.4 Over-winter losses

Over-winter losses on Eggleston moor were on average 66% (range 56% to 80%), with an average 83% (range 63% to 118%) of these losses explained by shooting (Table 15). Summer density explaining 85% of the variation in total over-winter losses ($y=1.28x - 2.07$, $r^2=0.85$, $p=0.080$, $n=4$) and accounted for 77% of the variation in the unexplained winter losses ($y=2.59x -11.49$, $r^2=0.77$, $p=0.121$, $n=4$).

Grouse density in spring 't +1' was not correlated with grouse density in the previous summer 'year t' ($y=0.44x +2.22$, $r^2=0.10$, $p=0.678$, $n=4$).

Table 15 Over-winter losses explained by shooting and unexplained losses in relation to summer (year t) estimates and the following spring density (year t+1) calculated by distance sampling.

Estate	Year (t)	Mean summer density (grouse/ km^2)	Harvest (grouse/ km^2)	Density post-harvesting (grouse/ km^2)	Mean spring density (year t+1) (grouse/ km^2)	Over-winter loss per km^2 (spring t+1– summer (%)	Unexplained winter losses per km^2 (harvest–over winter loss) (%)
Raby	2001	433.0	203.7	229.3	215.3	217.7 (50)	-14.0 (3)
Eggleston	2001	491.8	187.5	304.3	192.8	299.0 (61)	-111.5 (23)
Eggleston	2002	355.8	211.9	143.9	119.2	236.6 (66)	-24.7 (6)
Eggleston	2003	276.0	182.9	93.1	120.9	155.1 (56)	+27.8 (10)
Eggleston	2004	425.2	269.2	156.0	84.5	340.7 (80)	-71.5 (17)

6.3.5 Radio telemetry estimates: causes of mortality

The cause of death varied significantly between region (X^2_8=360, p=0.000), with mortality due to shooting explaining 61% of all deaths on the North Pennine moors, compared to only 2% at Langholm and 9% on the Scottish Highlands moors (Table 16). Predation, particularly by raptors explained 74% of losses at Langholm in comparison to 37% of losses in the Scottish Highlands and 6% of losses in the North Pennines.

The cause of death varied significantly between age (X^2_4=32.3, p=0.000), with 22% of juveniles shot compared to 10% of adults. Cause of death also differed between season (X^2_4=97.5, p=0.000) due to no losses to shooting during the summer.

In the North Pennines the main natural predators were the stoat (14%), peregrine (6%), fox (4%) and badger *Meles meles* (1%), while collisions with stock fences, motor vehicles and losses to the disease, strongylosis accounted for a further 6% of all deaths. It is important to note that the low recorded losses to strongylosis were due to the radio telemetry study being undertaken between 1999 and 2001, a population building phase. Losses to strongylosis would have been considerably higher, if the study had been undertaken in 2005, when a strongylosis disease crash caused estimated 79% losses between spring and summer counts.

Table 16 A summary of the causes of mortality of adult and juvenile red grouse from radio telemetry studies in the North Pennines, Langholm and Scottish Highlands.

Region	Age	Period (sample size)	Cause of death (%)				
			Shot	Raptor	Mammal	Other	Unknown
North Pennines	Adult	Summer (n=8)	0 (0)	2 (25)	5 (63)	0 (0)	1 (12)
	Adult	Winter (n=37)	27 (73)	0 (0)	2 (5)	3 (8)	5 (14)
	Juvenile	Summer (n=5)	0 (0)	0 (0)	3 (60)	0 (0)	2 (40)
	Juvenile	Winter (n=71)	47 (66)	5 (7)	13 (18)	4 (6)	2 (3)
Langholm (Scottish Borders)	Adult	Summer (n=112)	0 (0)	86 (77)	9 (8)	2 (2)	15 (13)
	Adult	Winter (n=125)	6 (5)	82 (66)	13 (10)	1 (1)	23 (18)
	Juvenile	Summer (n=79)	0 (0)	71 (90)	2 (3)	1 (1)	5 (6)
	Juvenile	Winter (n=58)	0 (0)	38 (66)	11 (19)	2 (3)	7 (12)
Scottish Highlands	Adult	Summer (n=84)	0 (0)	28 (33)	18 (21)	3 (4)	35 (42)
	Adult	Winter (n=55)	11 (20)	24 (44)	8 (14)	2 (4)	10 (18)
	Juvenile	Summer (n=10)	0 (0)	3 (30)	6 (60)	1 (10)	0 (0)
	Juvenile	Winter (n=9)	4 (45)	3 (33)	1 (11)	0 (0)	1 (11)

At Langholm the main predators were birds of prey accounting for 74% of all deaths, specifically hen harrier and peregrine, but also goshawk *Accipiter gentilis* and sparrowhawk *Accipiter nisus*. Other predators were fox (8%) and stoat (1%) with other recorded deaths through collisions with fences and motor vehicles (2%).

In the Scottish Highlands the main predators were birds of prey, accounting for 37% of all deaths, including hen harrier, peregrine falcon, golden eagle *Aquila chrysaetos* and buzzard *Buteo buteo*. Other identified predators were mammals (21%), which included fox, stoat and wild cat *Felis sylvestris*, with other recorded deaths through collisions with fences and motor vehicles (4%).

6.4 Discussion

On the North Pennines study moors, shooting harvests were positively correlated with breeding success and summer density, with juveniles making up 74% of the harvest. Strongyle worm burdens were tenfold higher in adults than juveniles. Shooting removed on average 41% of the estimated summer population, up to a maximum of 66% and accounted for on average 83% of the estimated over-winter losses. The causes of mortality varied between region with shooting being the main cause of death on the North Pennines study moors, this contrasted to the findings from the Langholm and the Scottish Highlands moors where predation by raptors was the primary cause of red grouse mortality.

Interestingly in spring 2005 when a strongylosis induced population crash occurred on the Eggleston study moor, the previous summer densities and harvest rates were broadly similar to those reported in autumn 2001, yet no strongylosis outbreak occurred in spring 2002. If strongylosis outbreaks are related to density then an outbreak in 2002 may have been predicted, consequently other factors which effect disease outbreaks such as the climate, which effects parasite infection (Connan & Wise 1994; Shaw *et al.* 1989) and the age structure of the population need to be considered. Parasite infections vary both seasonally and between years, with large increases in infection reported in the early spring (February and March) (Hudson *et al.* 2002; Moss *et al.* 1993) dependent on local climate factors, particularly moisture and temperature (Connan & Wise 1994; Shaw *et al.* 1989). Parasite burdens are also reported to increase as a bird ages (Potts *et al.* 1984; Wilson 1983), with adults on the North Pennines study moors host to ten-fold parasite burdens compared to juveniles. A skewed age structure of birds older than one year within the population may be a contributing factor to strongylosis induced disease crashes.

Shooting programmes to regulate breeding density and reduce parasite burdens within the population by selective harvesting of adults may be an appropriate tool to manage grouse populations. Driven red grouse shooting has developed through time to maximise the sporting potential of red grouse, not as a tool to manipulate breeding densities or the age structure within the population. It is evident that further research is required to analyse the effects of driven shooting on the demographics of grouse populations and whether hunting strategies can be modified to prevent disease outbreaks. Shooting programmes need to be carefully practised, as at low densities, harvesting has been shown to negatively impact on grouse population dynamics in areas where there is no management to increase density for sport shooting, (Ellison 1991; Smith & Willebrand 1999). Conversely at high grouse density, studies in North East Scotland have found that harvesting by shooting under exploited a population surplus (Jenkins *et al.* 1963).

Comparison of the causes of mortality show clear differences between the three regions in the United Kingdom. Predation by raptors was the primary cause of red grouse mortality both at Langholm and in the Scottish Highlands. This is analogous with findings from other Scottish studies (Hudson *et al.* 1997); and from studies on willow ptarmigan in Canada (Hannon & Barry 1986) and Sweden (Smith & Willebrand 1999); as well as studies on rock ptarmigan populations (Nielsen 1999). Interestingly, raptors play an important role in un-managed grouse population dynamics, for instance rock ptarmigan population cycles in Iceland are limited by gyrfalcon predation (Nielsen 1999). With population cycles of forest grouse (capercaillie *Tetrao urogallus*, black grouse, hazel grouse *Bonasa bonasia* and willow grouse) in Finland destabilised by goshawk predation (Tornberg *et al.* 2005). In the United Kingdom the Joint Raptor Study at Langholm in the Scottish Borders found that predation by raptors limited red grouse summer densities and prevented grouse cycles (Redpath & Thirgood 1997). This predation effectively ensured that summer densities were too low for driven grouse shooting and the employment of gamekeepers ended as grouse moor management was no longer a viable proposition.

For managed red grouse populations in the United Kingdom, there is a recognised conflict between grouse moor management interests and the conservation of Biodiversity Action Plan birds of prey, particularly hen harrier (Etheridge *et al.* 1997). The economics of grouse moors depend on income generated from driven shooting, if driven shooting cannot be provided, the infrastructure of the moor breaks down, with the loss of gamekeepers jobs (Redpath & Thirgood 1997). Loss of income from shooting in the past has seen the change of use of heather moorland from grouse moor to commercial forestry and to agriculture (Hudson 1992; Robertson *et al.* 2001). Today, in northern England, heather moorland is an internationally important resource, designated as a Special Protection Area, which supports international important populations of breeding birds particularly waders (Tapper 2005; Tharme *et al.* 2001). If grouse moors in the United Kingdom were to become uneconomic, there would be serious repercussions not only for landowners and the local economy, but also for the management of the characteristic habitats, species and landscapes.

CHAPTER 7

General Discussion

7.1 General Discussion

The key objectives of this thesis were to provide a greater understanding of grouse population processes at the moor scale to better inform grouse moor managers on management techniques. To achieve this I first demonstrated that a line-transect distance sampling technique is an appropriate method to survey grouse at a moor spatial scale. These estimates of grouse distribution and density at the landscape scale facilitated the other aspects of the thesis. Secondly I demonstrated that heather moorland habitat types can be surveyed using established earth observation techniques from satellite remote sensing. These data enabled the investigation of the spatial and temporal effects of heather burning on grouse productivity, the influence of density on juvenile dispersal and the effects of harvesting on grouse populations.

The first key finding was that the frequency and distances of juvenile dispersal were limited, female biased and independent of density, which means that population growth is not regulated by increased dispersal at high densities, which could lead to density dependent outbreaks of Strongylosis, which causes such dramatic crashes in the population (Potts *et al.* 1984). Secondly, shooting was found to be an important factor in grouse population dynamics in northern England accounting for on average 83% of estimated over-winter losses and therefore could be enhanced as a potential tool for limiting population growth and preventing disease outbreaks.

7.2 New techniques for monitoring red grouse

A fundamental of ecological research and the conservation and management of species is the collection of accurate estimates of population distribution and density. High quality ecological surveys which deliver accurate, repeatable, efficient and cost-effective surveys which can be disseminated and presented to decision makers are essential to future conservation management. It is widely recognised that to conserve biodiversity world-wide, landscape scale ecological monitoring to evaluate relationships between species and habitat are required to inform conservation policy and management, but examples are rare due to the cost constraints of such monitoring programmes (Carlson & Schmiegelow 2002).

The investigation of relationships between species and habitat at landscape scales has been limited not only by the availability, collection and processing of landscape scale habitat data, but also due to the similar limitations associated with the collection of animal data at extensive spatial scales. Information on the distribution of organisms at landscape spatial scales is inherently difficult to collect, but with the development of survey techniques such as distance sampling, suitable sampling techniques exist which can be modified to survey individual species or suites of species of interest. Birds have been the focus of many studies to identify relationships between species and habitats (Gottschalk *et al.* 2005) as they are relatively easy to identify, their biology is generally well researched and they are often good indicators of the health of ecosystems (Furness & Greenwood 1993).

The distance sampling technique applied in this thesis to survey red grouse provides a rapid, cost-effective and statistically sound technique for collecting data at the grouse moor spatial scale. This technique has similarly been adapted and used to survey a wide range of species which include reptiles (Anderson *et al.* 2001), birds (Casagrande *et al.* 1997), fish (Endsign *et al.* 1995) and mammals (Jachmann 2002). These developments in conjunction with advances in earth observation technology discussed in Chapter 4 will provide further opportunities for exploring relationships between habitat and animals at landscape and ecosystem scales. With the continuing advances in earth observation technology the limiting factor for many future studies investigating relationships between habitat and animals may not be the availability of habitat data at landscape spatial scales, but is more likely to be the availability of accurate animal distribution and density estimates at similar spatial scales. With this in mind, the distance sampling technique may become a more widely used technique to assess the distribution and density of species at landscape scales.

7.3 What new evidence does a landscape perspective provide?

Prior to this study, Game Conservancy Trust research on red grouse had concentrated on total counts of grouse both pre-breeding in spring and post-breeding in summer within 1 km^2 blocks. This technique provides useful information on annual variations in spring density and breeding success, enabling cyclic patterns and variations in breeding success to be investigated. It is evident from my surveys at a grouse moor scale that the 1 km^2 block is not representative of grouse density and breeding success at a grouse moor scale, which varies both spatially and temporally across the moor. Grouse are not evenly distributed across the moor and the reasons for this appear to be closely linked to the kin selection hypothesis (Watson *et al.* 1994). Grouse settlement patterns are driven by the highly sedentary behaviour of new male recruits, which settle near to their fathers, creating clusters of related males. My findings in Chapter 5 supported this with the limited dispersal reported in juvenile male grouse.

These findings have repercussions for grouse moor managers as many management decisions are taken at the moor level regarding harvest rates and parasite control. Due to variations in grouse density and parasite burdens across a moor, management decisions need to be considered at a finer scale. To achieve this grouse moor managers need to annually survey grouse at a drive level to estimate summer density and breeding success and develop harvest plans accordingly. Similarly to undertake successful parasite control, worm burdens need to be surveyed at the grouse drive level, rather than the moor level. Parasite control through direct dosing and/or the provision of medicated grit needs to be practised in relation to areas of high density and known high parasite burdens.

Grouse moor managers tend to only consider management for red grouse at the scale of the moor, but it is becoming increasingly apparent in ecological conservation that the management of species has to be considered at a landscape scale to allow for natural dispersal and movement of species (Warren & Baines 2004). The limited frequency and distances of dispersal recorded in red grouse in this study means that the connectivity of heather moorland habitats at a landscape scale is an important requirement for their future long term conservation and management.

7.4 Implications for red grouse management

On the study moors in northern England, grouse moor managers reduce the effects of the main extrinsic factors which limit population growth. This is achieved through employing gamekeepers to burn heather in rotation, to maximise habitat quality and to control the predators of grouse, to reduce losses through predation. Limiting the effects of these extrinsic factors in conjunction with the intrinsic factors of density independent limited dispersal distances as found in Chapter 5 and the kin-favouritism hypothesis, (Mountford *et al.* 1990; Watson *et al.* 1994) leads to rapid population growth. At high density, density dependent outbreaks of strongylosis are responsible for the distinct crashes observed in the grouse cycle. Following the catastrophic strongylosis disease crash seen in northern England in 2005, which was widespread across the majority of grouse moors, including the moors in this study, interest has been further focussed to control these disease outbreaks. As identified in Chapter 6, on the intensively managed moors in northern England shooting is the main cause of mortality in the population building phases. Therefore modifying harvesting could be a potential tool for dampening the observed population oscillations in red grouse. Research has shown that cycles can be dampened through parasite control methods (Hudson *et al.* 1998) and/or by manipulating grouse density (Moss *et al.* 1996). Disease control methods through direct dosing with an anthelminthic (Hudson *et al.* 1998) or through providing medicated grit (Newborn & Foster 2002) have proved to be effective at reducing parasite burdens, increasing survival rates and breeding success. They are however expensive, difficult to administer and used in isolation may not be the only solution to reducing the oscillations observed in grouse as, importantly they do not limit population growth. The density manipulation experiment (Moss *et al.* 1996) provided interesting results as reducing the density of males in spring, did not prevent the grouse cycle it just extended it, exactly what grouse moor managers are aiming to achieve.

7.5 Questions remaining

As reported in this thesis, shooting is a major cause of mortality of individual red grouse on the study moors in northern England. In some managed red grouse populations, such as my study moors in northern England, the activities of gamekeepers reduce predator density and consequently natural predators have little effect on red grouse population processes. As explained in Chapter 6, this contrasts with the major influence on other cyclic vertebrates (Krebs *et al.* 1995; Turchin 2003) and indeed, red grouse populations elsewhere in the United Kingdom (Redpath & Thirgood 1997). Therefore density manipulation through harvest management strategies, whether used as a single strategy or in combination with disease management programmes may be a practical tool to limit population growth. This, in turn will dampen the cyclic oscillations caused by density dependent disease outbreaks in managed red grouse populations.

It should be recognised that red grouse harvest strategies have developed to provide high quality, exciting sport shooting and not specifically as a tool to manage grouse populations. Although this harvesting method is effective at delivering required bags for paying customers, it is evident from our current knowledge of grouse population dynamics and behaviour that harvesting strategies could be improved and adapted as a management tool to dampen grouse cycles. In managed populations harvesting by hunting affects both the population structure and the behaviour of individuals (Hutchings

& Harris 1995; Solberg *et al.* 1999) and studies have shown that harvesting can be spatially uneven within populations (Broseth & Pederson 2000; Jonzen *et al.* 2001).

Harvests of grouse are set by the head gamekeeper, with many estates setting target harvests from the results of summer counts (K. Wilson pers comm). If estimates of density are below 60 birds per km^2 driven shooting is usually cancelled (Hudson 1992). Theoretically with these count data it should be possible to maintain grouse populations by harvesting. Currently little is known about the effects of driven shooting as a harvesting strategy on grouse population dynamics and this is an important gap in our knowledge. It is though evident that grouse like many other animals adapt their behaviour to hunting pressure. Examples are brown hare *Lepus europaeus*, which adapt their flushing behaviour (Hutchings & Harris 1995), white-tailed deer *Odocoileus virginianus* (Verkauteren & Hygnstrom 1988) and wildfowl (Madsen 1998), which seek refuge areas away from hunting. Grouse adapt to driven shooting, by aggregating into large groups, often consisting of more than 100 birds in relation to the numbers of days they are hunted (Hudson 1984). From my own observations and from discussions with gamekeepers it is also not uncommon for these large groups of birds to seek refuge on neighbouring ground where no shooting is taking place when disturbed by hunting. These are successful behavioural adaptations to shooting as the proportion of grouse shot from large groups is less than that from small groups (Hudson 1984). However, a consequence is that meeting harvest objectives becomes almost impossible when birds form these large groups.

7.6 Future directions

Despite behavioural responses by grouse to shooting, it is evident from the literature that harvest programmes could be adapted to reduce spring densities. The density manipulation experiments in North East Scotland, where territorial males were removed in the spring were successful at reducing density, with equal numbers of hens lost from the population (Moss *et al.* 1996). Therefore can harvesting programmes be adapted to limit population growth and dampen cycles? To address this hypothesis there are a number of questions which need to be explored. One fundamental question is the behavioural response of grouse to shooting. When grouse harvesting begins in August, is there a threshold level at which disturbance by shooting causes the family groups of grouse to form large aggregations, or is this just a factor of juveniles becoming independent from family groups and then forming these loose aggregations? If disturbance by shooting is not a factor, then to regulate population growth harvest targets need to be achieved early in the season prior to the formation of large aggregations. In theory this is a practical management technique, but other factors need to be taken into account. Harvest targets can be difficult to attain early in the season due to a number of reasons, the first is inclement weather such as mist and fog which causes shooting to be cancelled. Periods of hot weather also make harvesting difficult as juvenile grouse become difficult to flush and tire after their first flight, with only a small percentage of birds presenting themselves to be harvested. Another important consideration is the ability of the hunters which varies widely between individuals and can make the delivery of harvest targets difficult to achieve.

The behavioural response of grouse to disturbance on shoot days may also have important implications for meeting harvest targets. Further research is required here to assess whether the age structure of the harvest is related to the length or area covered by a grouse drive and/or the weather conditions on a shoot day. Studies need to investigate whether harvesting could be made more efficient by modifying drive length and area. To ascertain whether more, shorter drives are more effective than few, longer drives for harvesting grouse populations. Due to the practised methods of driving grouse, for instance they are commonly driven from one area to another and then back again, consideration of the effect of continuous driving also needs to be considered on the age structure of the harvest.

Selective harvesting by shooting may be an appropriate tool for controlling outbreaks of strongylosis. By selectively harvesting adult grouse which harbour more parasites than juveniles (Chapter 6) (Hudson 1992) and through regulating population growth by removing males from the breeding population. The hypotheses to test are, is it feasible through selective shooting or through the experimental removal of birds from the population to manipulate the age and sex structure of the population, to control disease outbreaks and more importantly could this be developed as a practical management technique.

The selective shooting of males only or adults only, by driven shooting is a potential feasible management option. Particularly for adult males as they often fly independent from larger groups (Hudson & Watson 1985), but when birds are in groups it is very difficult to differentiate between sex and age when flying directly at the observer/hunter.

It is though possible to identify grouse by sex and by age in early August when they are hunted using pointing dogs, as the adult birds often flush first. It may be feasible to shoot males only from the population in the autumn when males have selected territories.

My work has raised the possibility that removal of territorial males in the winter period from high density clusters could be used as a practical tool for manipulating population density and thereby reducing density dependent disease crashes. Hypotheses to experimentally test would be in the first instance to test whether targeted harvesting of adults and males only by shooting is an appropriate and practical tool which can be incorporated into management regimes. Shooting grouse over pointing dogs has been developed to harvest grouse at low density and although feasible at high density this method may conflict with driven harvest programmes and be at an insufficient scale to effect population dynamics. Selective harvesting post dispersal may be a more effective management technique and this needs to be tested experimentally. Important factors to consider are when does the removal of male grouse effect settling patterns and subsequent spring breeding densities? Does the removal of adult grouse affect parasite burdens in the population? Does the removal of males lead to equal numbers of females being lost from the population and if so, do these females move to find single males in other areas, or are they lost from the breeding population altogether? If this method proves effective it may be appropriate to consider extending the grouse shooting season beyond the traditional end of the season on December 10th to allow targeted harvesting of areas of high grouse density to prevent disease crashes.

The causes of population cycles in red grouse and other species will continue to prompt much debate and it is clear that there are complex mechanisms and interactions involved which cause these cycles in birds and animal species. It is evident from this study that harvesting by shooting has an important role to play within the population dynamics of managed grouse populations and this study has lead to further research into this topic.

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