Modelling the spatial and temporal dynamics of upland birds in Scotland

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Abstract

Population numbers change in space and time. The construction of models to investigate the spatial and temporal dynamics of populations may offer a means to identify the processes driving this change. In this thesis, we make use of models to examine the population ecology of three species of upland birds: red grouse, meadow pipit and capercaillie.

Populations of red grouse in the British Isles exhibit cyclic fluctuations in abundance. Time series data from 287 grouse moors across the United Kingdom were analysed to investigate co-variation in these fluctuations. Results indicate high levels of synchrony between populations on neighbouring moors, with synchrony declining with increasing intermoor distance. At distances greater than 100km, populations exhibit only weak synchrony. Synchrony is shown to be a product of strong coupling events, which occur on average every one in six years. In the absence of such events, synchrony is shown to dissipate within three years. Further, we present evidence which suggests this coupling is driven (at least in part) by dispersal between populations. The density dependent structures are also found to be sufficiently homogeneous to allow correlations in climate to synchronise dynamics, but examination of three climate variables failed to detect a relationship.

We also studied the population dynamics of meadow pipits in upland grassland ecosystems. Data, collected as part of an ongoing grazing field experiment, were analysed to construct a Bayesian model of population growth, and predict the effect of grazing intensity on meadow pipit populations. Results suggest grazing has a significant impact on population growth. Grazing may act to improve meadow pipit foraging efficiency and thus productivity.

Finally, a spatially explicit population viability model was constructed to predict changes in the future abundance and distribution of capercaillie. Published estimates of key demographic variables were drawn from the literature to parameterise the model. The spatial structure of the population was inferred from spatial data, documenting the extent and configuration of remnant pine woodlands in Scotland. The model predicts a low probability of extinction for capercaillie in

the future, and offers insights into key processes affecting the distribution and abundance of this species.

The development of these models has advanced our understanding of the environmental processes driving changes in the spatial and temporal dynamics of these species. The results of these studies may be useful in anticipating the future consequences of various drivers of change on the ecology of upland species.

Candidate's declaration

I declare that the work recorded in this thesis is entirely my own, except where otherwise stated, and that it is also of my own composition. Much of the material included in this thesis has been produced in co-authorship with others, and my personal contribution to each chapter is as follows:

> Chapter 2. Kerlin, D.H., Haydon, D.T., Miller, D., Aebischer, N.J., Smith, A.A. and Thirgood, S.J. Spatial synchrony in red grouse population dynamics. *Oikos*, 116:2007-2016. Data collection and compilation facilitated by NJA and AAS. Initial concept developed by DTH, SJT and DHK. Analysis conducted and manuscript drafted by DHK. GIS assistance provided by DM. Final draft enhanced by DTH, SJT and AAM.
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Chapter 6. Initial concept developed by DHK, with input from DTH and SJT. GIS assistance provided by DM. Analysis conducted and manuscript drafted by DHK. Final draft enhanced by DTH, SJT, DRM.

I further declare that no part of this work has been submitted as part of any other degree.

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1 General introduction

1.1 Models in population ecology

Patterns in the distribution and abundance of species are governed by processes operating in space and time. Investigations into patterns in the abundance and distribution of populations have stimulated the development of biological experiments, and mathematical models to describe these patterns. Temporal changes in species abundance have been a focus of population ecology since the origins of the discipline (Kingsland 1995; Turchin 2003). Initial studies were motivated by entomology; insect outbreaks (spruce bud moth *Zeiraphera canadensis*, and forest tent caterpillar *Malacosoma disstria* in particular) in the 1920s and 1930s led to an increased desire to understand the dynamics of insect populations, and the complex causes of these outbreaks (Kingsland 1995). Studies by Charles Elton and Mary Nicholson, on fur returns for Lynx in Canada (1942) drew attention to the importance of understanding the drivers of temporal changes in other single species systems, both for economic reasons, and for the insights such study could offer into evolutionary theory (Kingsland 1995).

The importance of the spatial dynamics of a population was first demonstrated in 1958, in a series of experiments which demonstrated that the temporal dynamics of a population were in part dependent on the spatial organisation of the environment (Huffaker 1958; Renshaw 1991). The increasing relevance of spatial dynamics and the distribution of species through space, to island biogeography theory and the conservation of fragmented landscapes, prompted the further development of a range of models, aimed at describing patterns in the distribution of populations, and the movements of individuals between these populations (Crooks and Sanjayan 2006; MacArthur and Wilson 1967; Morris and Doak 2002).

Mathematical models can be used to describe the variation and co-variation observed in these patterns, investigate the processes driving the development of these patterns, and predict future dynamics of populations. Outputs of modelling studies can offer instructive insights and subsequently increase our understanding of the processes driving these patterns. The general aim of the current research has been the development and application of a variety of modelling techniques to single species systems in the Scottish uplands. The use of these models can help address important ecological questions, and will hopefully inform future research and management decisions in these upland habitats.

1.2 The Scottish uplands

The Scottish uplands can be broadly defined as those areas of Scotland above the limits of enclosed farmland. Major upland habitats include dwarf shrub heaths, grasslands and remnant patches of Caledonian pine woodland (Pearsall 1950; Ratcliffe 1977). Collectively, these areas form the largest extent of undeveloped wildlife habitat remaining in Britain (Ratcliffe 1977).

Scottish commitments to protecting and enhancing biodiversity under international agreements and national legislation have increased the need for further investigations into upland biodiversity in order to safeguard these habitats into the future. In order to deliver the environmental outcomes required, there is an increasing need to develop an understanding of the population ecology of existing species.

The principle aim of the current research is to advance our understanding of the population dynamics of three upland bird species, and the impacts of policy and land-management practices on these dynamics. In particular, we will focus on three upland ecosystems of Scotland: heather moorland, upland grassland and remnant pine forest habitats. Within these ecosystems, we will examine aspects of the population ecology of three major upland bird species: red grouse (*Lagopus lagopus scoticus*), meadow pipits (*Anthus pratensis*) and capercaillie (*Tetrao urogallus*). These three species have been selected for study for a number of reasons. Each species is characteristic of a particular upland habitat, and in the case of red grouse and capercaillie, highly dependent on that habitat for the future persistence of the species. However, most crucially, each species has been the subject of intensive study for significant periods of time, and as such, a significant body of data are available for analysis. For example, in the case of the red grouse, landowners and gamekeepers have been keeping detailed records of grouse shooting bags for nearly two centuries, for populations located across the country.

1.3 Synchrony in red grouse

1.3.1 Red grouse and heather moorland

Upland heather moorland, one of the more distinctive habitats found in Europe (Thompson et al. 1995a), is a dwarf-shrub heath ecosystem with few extensive areas remaining outside Great Britain (Mackey et al. 1998). It therefore has considerable nature conservation, aesthetic and economic value (Atkinson et al. 2002; Thompson et al. 1995a). Heather moorland is characterised by common, or ling heather (*Calluna vulgaris*), the staple food resource of the red grouse (Ratcliffe 1977). Originally a feature of exposed coastal areas and alpine regions of Britain (i.e. areas at high altitude above the tree-line), a significant proportion of current heather moorland coverage extends through sub-montane regions, and was created where humans have modified moorland areas over thousands of years to provide habitat and palatable fresh heather for domestic stock (Atherden 1992; Mackey et al. 1998). Moorland is thus regarded as a ‘cultural landscape’ such that it has largely developed in areas of former forest, which has been cleared by human activity (Gimingham 1995).

Red grouse were initially regarded as a secondary inhabitant on many hill farms, though they were present in significant numbers. From 1850 however, the increasing accessibility to the Scottish uplands (driven by the growth of the railway system), and the development of improved guns and ammunition, resulted in increased popularity of grouse-shooting (Atherden 1992). Large parts of Scotland were bought up and transformed into sporting estates for the purpose of shooting red grouse and black grouse. Ownership of a sporting estate in the uplands even became an important status symbol for the aristocracy of England and Scotland after Queen Victoria’s acquisition of Balmoral in 1848 (Dixon 2002). At this time, moorland areas tended to have greater value as sporting estates then as areas to graze livestock, thereby resulting in a dramatic increase in the number of sporting estates and subsequent growth of heather land cover (Mackey et al. 1998). However, there is a natural tendency for areas of heather to, over time, become dominated by other species. To provide ideal habitat for red grouse to support shooting, moorland is therefore heavily influenced by management, and “maintained by a combination of muirburning – burning the heather in small patches to create a mosaic of heather ages – and grazing by sheep and deer, which prevent succession to scrub and woodland" (Dixon 2002).

In recent years, there has been a marked decline in the economic benefits of grouse moor management practices. "Losses are incurred by 75% of Scottish grouse moors, and were grouse shooting regarded as a purely commercial activity, this would be cause for concern" (McGilvray and Perman 1992). Many of the current benefits of grouse moor ownership are instead non-economic (e.g. prestige, pleasure, business opportunities). Additionally, sheep farming and forestry are often heavily dependent on subsidy payments. Yet, despite the crucial role grouse moor management plays in the conservation and maintenance of natural habitats in the uplands grouse moors generally do not receive such support (Hudson 1992). A decline in grouse moor management practices, as grouse shooting becomes increasingly less viable, may have profound effects on the upland landscape. Mounting evidence suggests moorland land cover is already decreasing, with 70% considered to be at risk, and 50% of the remainder in poor environmental condition (Thompson et al. 1995a). Without management, sub-montane heather moorland would revert to woodland or convert to acid grasslands (Mackey et al. 1998), with important consequences for moorland dependent species.

Red grouse are a key species in heather moorland habitats, and the cyclic dynamics observed in red grouse populations can have dramatic consequences for the viability of these estates. This has stimulated considerable research effort, focused on determining the causes of these fluctuations. A study of the population ecology of red grouse may offer valuable insight into the effects of change in this habitat.

1.3.2 Cycles in natural populations

Cyclic dynamics have been observed in a wide range of species, including a range of northern mammals (Krebs et al. 1995; Lindström et al. 2001), and birds of the grouse family (Tetraonidae) (reviewed by Moss and Watson 2001). The cyclic dynamics of such populations have been of interest to ecologists for decades (Turchin 2003). The empirical study of cyclic population dynamics is generally accepted to have begun with the work of Charles Elton on the population dynamics of a variety of species, predominantly lemmings (*Lemmus lemmus*) in Scandinavia (Elton 1924; Lindström et al. 2001; Turchin 2003).

Cyclic behaviour is attributed to a range of factors, including variation in the environment, consumer-resource interactions and direct and delayed density dependence (Kendall et al. 1999; Turchin 2003). Cycles in the abundance of lemmings have been linked to winter weather and snow conditions, and the effects of density dependence on the net population growth rate (Elton 1924; Kausrud et al. 2008). Analysis of muskrat (*Ondatra zibethicus*) and mink (*Mustela vison*) fur records from Canada reveal fluctuating dynamics, likely driven by a predator-prey relationship between the two species, with muskrat cycling 1-2 years ahead of the mink (Viljugrein et al. 2001). Snowshoe hare (*Lepus americanus*) populations have been shown to cycle with a 10-year period, with cycles linked to food availability, and predator-prey interactions with the Canadian lynx (*Lynx canadensis*) (Krebs et al. 1995; Vik et al. 2008).

Evidence from northern Europe suggests a number of species closely related to red grouse also exhibit cyclic fluctuations in abundance. Capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*) and hazel grouse (*Bonasa bonasia*) all fluctuate with a periodicity of approximately 6-7 years (Moss and Watson 2001).

1.3.3 Cycles in red grouse

The cycles observed in red grouse dynamics have been the focus of scientific investigations for more than fifty years, and consequently, a significant body of long-term abundance data is available. Two schools of thought have developed, which attempt to explain the observed dynamics. First, fluctuations may be driven by infections of the nematode *Trichostrongylus tenuis* (Hudson 1992; Hudson et al. 1998). A number of studies have demonstrated a link between *T.tenuis* and demographic performance of red grouse. In particular, high parasite burdens have been shown to reduce breeding performance and adult survival (Dobson and Hudson 1992; Hudson et al. 1992). Experimental reductions in parasite burden, using anti-helminthic treatments, have been shown to prevent crashes in populations of red grouse, providing strong support for this hypothesis (Hudson et al. 1998). Red grouse population fluctuations may be generated as the nematode mediates reductions in female fecundity and increased mortality when grouse are present at high densities.

Alternatively, it has been proposed that fluctuations are generated by delayed density-dependent changes in aggression and the rate at which young males are recruited into the population (Moss and Watson 1985; Moss et al. 1996). Population density is determined by the mean territory size of male grouse. Experimental manipulation of testosterone levels in male grouse suggested increased male aggression results in increased mean territory size and therefore reduced breeding densities (Moss et al. 1994). Further, kin are less aggressive towards kin (Watson et al. 1994). However, at high densities, clusters of closely related individuals break-up, resulting in the break-down of kin groups, increased aggression between neighbours, and a general reduction in breeding densities (Watson and Moss 2008).

More recent work has offered a synthesis of these two hypotheses. Under conditions of high grouse density, elevated testosterone levels and associated increases in male aggression were observed. Increased testosterone may lead to suppression of the grouse immune system, and result in increased nematode-induced mortality (Mougeot et al. 2005; Redpath et al. 2006).

While the cyclic dynamics of individual populations of red grouse have been extensively studied, patterns of synchrony between populations have been observed, but rarely investigated in any detail.

1.3.4 Synchrony in natural populations

Synchrony has been observed in a wide variety of taxa, including mammals (Lindström et al. 2001), fish (Freon et al. 2003) and insects (Esper et al. 2007). Extensive studies have also reported synchrony in species of close relation to the red grouse, black grouse, capercaillie, rock ptarmigan (*Lagopus mutus*) and hazel grouse (Cattadori et al. 2000; Lindström et al. 1996). In many cases, this synchrony is not limited to a single species; Finnish populations of capercaillie, black grouse and hazel grouse all exhibit dynamics that suggest synchrony between species (Ranta et al. 1995b). Identifying the processes driving synchrony in natural populations has become an increasingly important issue in ecology, as the persistence of metapopulations has been shown to decrease as synchrony increases (Harrison and Quinn 1989).

Two general mechanisms have been espoused in the scientific literature to explain patterns of synchrony: biotic coupling between populations, and abiotic correlations in climate. Theoretical studies have demonstrated that synchrony in population cycles can be induced by the dispersal of individuals between populations in the absence of abiotic processes (Bjørnstad 2001; Liebhold et al. 2004). As individuals disperse from regions of high density, they synchronise local dynamics by increasing abundance in adjacent populations (Swanson and Johnson 1999). Alternatively, synchronous dynamics may be the result of abiotic factors. Moran (1953) demonstrated that if populations have the same intrinsic linear, delayed density-dependent structure (DDS), the correlation between populations would exactly equal the correlation between environmental perturbations experienced by different populations - the Moran effect. The Moran effect has been reported across a range of taxa, including great gerbils (*Rhombomys opimus*) (Kausrud et al. 2007), great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) (Saether et al. 2007), and species of freshwater fish (Tedesco and Hugueny 2006). Models describing synchrony between capercaillie, black grouse and hazel grouse in Finland were shown to exhibit synchronous dynamics if a stochastic event, characterised by breeding failure, was applied to the model at a given average interval (Ranta et al. 1995b); this stochastic event was interpreted as a climate perturbation, acting to couple the dynamics of otherwise uncoupled species.

Disentangling the drivers of synchrony in these populations, be they biotic or abiotic, is often difficult. In a study examining synchrony in 22 regions of synchrony observed in 7 mammalian species, the most likely synchronising agent (dispersal or climate) could only be identified in 10 of 21 cases (Swanson and Johnson 1999). Often, unless one of these processes can be completely excluded, the results are ambiguous. For example, Soay sheep (*Ovis aries*) occupying different islands in the St. Kilda archipelago display synchrony in abundance that can only be attributed to the Moran effect, as the sheep are unable to disperse between islands (Grenfell et al. 1998). Similarly, synchrony in Canadian lynx are attributed to correlations in environmental conditions, as the cycles occur over wider distances than would be expected from dispersal (Moran 1953). Population dynamics suggest a regional structure, with lynx grouped into three geographically distinct metapopulations, each experiencing different correlated climate patterns (Stenseth et al. 1999). However, recent evidence suggests that the genetic structure of lynx populations is broadly reflective of the geographic structure of these metapopulations (Rueness et al. 2003), suggesting dispersal may in fact play a significant role in driving synchrony in the species.

While biotic factors such as dispersal can induce synchronous dynamics, clear examples from natural populations are more difficult to find. In particular, populations synchronised by dispersal are expected to be characterised by a decrease in synchrony as inter- population distance increases, and the intensity of dispersal between populations decreases (Swanson and Johnson 1999). However, locally correlated climate patterns may produce a similar picture (Lindström et al. 1996). Further, if the degree of similarity in the DDS of populations decreases with increasing distance, synchrony would also decline. It is often therefore difficult to disentangle the drivers of synchrony (Ranta et al. 1995a).

1.3.5 Synchrony in red grouse

Much of our understanding of the dynamics of red grouse has been inferred from studies examining the phenomenon in related species. In one of only a few papers that discuss synchrony in red grouse, Cattadori et al. (2005) suggest that synchrony may be a result of correlations in rainfall and temperature generating synchronous outbreaks of parasitic nematodes (*T. tenuis*). However, Cattadori et al. (2005) considered only a small subset of populations in the northeast of England, and no studies have examined the nature of coupling across the species range. In an attempt to address the current deficit in our knowledge of the population dynamics of red grouse, aspects of synchrony are examined in Chapters 2-4. A more detailed and focused study of synchrony in red grouse is of value in extending our understanding of these patterns of co-variation, and the drivers of this synchrony, in the species.

Chapter 2 details investigations into general patterns of synchrony in red grouse. Harvesting records, indexed as the number of grouse shot per year, were utilised to provide an indirect measure of grouse abundance. Additionally, we introduced two new variables, neighbourliness and local synchrony. Neighbourliness provides a measure of the local density of moor locations, and the extent to which a given moor is located within a cluster of other nearby moors. Local synchrony quantifies the degree to which each moor time-series is generally in synchrony with time-series from other nearby moors. Analysis of the relationship between neighbourliness, local synchrony and other covariates can be used to determine significant predictors of patterns of synchrony in red grouse.

Chapter 3 examines synchrony in red grouse by applying a discrete Markov model that describes the trajectory of a population as it cycles through four possible states: trough, increasing, peak and decreasing. By describing the mechanics by which a regional group of populations cycle through these four states, we are able to determine the degree of independence between these cycles, and whether coupling is present. This model can be used to identify ‘collective forcing events’, during which the dynamics of red grouse populations are coerced into a state more synchronous than would be expected under the assumption of independent dynamics. The use of such a mechanistic model allows us to identify the nature of synchrony in red grouse, and determine if the coupling necessary to drive synchrony is weak or strong, and whether such coupling is intermittent in nature, or constantly applied to populations.

Chapter 4 investigates the drivers of synchrony in red grouse. In particular, we develop models to examine the relative importance of biotic coupling between populations (i.e. dispersal), and abiotic process, such as correlated climatic fluctuations. Initially, we examine the density dependent structure of red grouse populations, to determine whether they are sufficiently similar to exhibit co-variation under correlated climatic conditions. The density of grouse in the landscape surrounding two grouse moors is used as a proxy measure for the degree of dispersal between two populations. A randomisation technique is used to analyse bootstrapped samples of our data, to determine the relationship between density, climate and synchrony, and identify the significant drivers of synchrony in red grouse.

1.4 Meadow pipits and grazing

1.4.1 Land-use and bird declines

Farmland birds in the United Kingdom have displayed significant declines in abundance in recent decades (Fuller et al. 1995). Numerous studies have demonstrated that changes in agricultural management and practices have played a significant role in these declines (Chamberlain et al. 2000; Newton 2004; Robinson and Sutherland 2002). Intensification of agriculture from 1962-1995, including increased crop and grass production, has been correlated with bird declines (Chamberlain et al. 2000). This intensification has been linked to reductions in breeding performance, particularly due to the effects of increased pesticide use (Morris et al. 2005). Additionally, changes in the timing of agricultural activities, in particular the introduction of autumn sown crops, have reduced the availability of winter food and subsequently led to increased winter mortality in many species (Newton 2004; Siriwardena et al. 2008).

While farmland bird communities have displayed the most significant declines, and received the bulk of public attention, upland bird communities in Britain have also been subject to declines (Fuller and Gough 1999; Thompson et al. 1995b).

1.4.2 Upland grassland ecosystems

Grass dominated habitats (sheepwalk) have become widespread in large areas of the uplands after unmanaged exposure of dwarf-shrub heaths to grazing and burning impacts (Ratcliffe 1977). These areas typically resulted from a greater degree of human impact than on moorland counterparts. The first major increase in grassland in Britain occurred in the Iron Age (Atherden 1992); there is evidence from areas of North Yorkshire, Cumbria and southwards that woodland areas had been extensively cleared. In Scotland however, this clearing was delayed until after the Roman period. These grassland areas were created and are continually managed to provide improved grazing for sheep (*Ovis aries*).

Between 1950 and 1990, an increase in sheep numbers in Britain from 19.7 million to 41.2 million resulted in dramatic increases in grazing pressure (Fuller and Gough 1999). These increases were historically driven by a perceived need to increase agricultural production during the post-war reconstruction throughout Europe; “It is easy to understand why in the Treaty [of Rome] objectives of the Common Agricultural Policy (CAP), drawn up at a time when food shortages in western Europe were still a vivid memory, such emphasis was laid on increases in agricultural productivity” (Brown and Bainbridge 1995). To achieve increased agricultural output, production had been heavily supported through commodity programs, trade barriers, and (of more relevance to this thesis), through the use of subsidies (Legg 2000). Initially, this subsidy took the form of a production-linked payment, where subsidy payments were determined by tonnage with respect to crop production, or headage with respect to livestock production. This encouraged intensive agriculture, and overstocking in many areas, including the Scottish uplands. At one stage, “the only profit to the farmer came from headage payments, increasing the temptation to get as many mouths on the hill as possible” (Smout 2002). The Moorland Working Group (2002) concluded that such over-grazing contributed to a decline in the diversity and quality of upland habitats, and accelerated the conversion of heather moorland to grassland.

By the 1980’s however, increased productivity and efficiency had resulted in huge surpluses in agricultural production (Brown and Bainbridge 1995). The ‘cut-price’ disposal of unwanted surplus was damaging to world export markets, and to the credibility of the CAP. Additionally, under the terms of the Treaty of Amsterdam, policy makers within the European Union were obliged to recognise the impact of European policy on the environment (Brown and Bainbridge 1995). Under such influences, steps have recently been taken to reform the CAP. A key platform of this policy shift was the introduction of a single payment to farmers, based on acreage of agricultural land, to decouple subsidies from production; payments will also be dependent on meeting cross compliance conditions, including keeping land in good agricultural and environmental condition. Policy makers envisaged that such changes would lead to a reduction in intensive agriculture and overgrazing.

Farms in the Scottish uplands often operate at the margins of financial viability (Mowle and Bell 1988). Warren (2002) presents statistics which suggest that over 90% of income for farms in Least Favoured Areas (LFA’s) such as the Scottish uplands is provided through subsidy payments, and that hill-sheep farms in 1999-2000 operated at a loss. Farming interests in the uplands are heavily dependent on government assistance, and therefore operations are heavily influenced by the precise terms of any subsidy (Mowle and Bell 1988). Consequently, moves to a single payment system, and the decoupling of livestock numbers from payments, have resulted in dramatic declines in sheep numbers in Scotland since 1999 (Rural Policy Centre 2008). The impacts of such a decline may have profound effects on upland grassland areas, and the species dependent on these habitats.

1.4.3 Impacts of grazing on upland grasslands

Grasslands are an important upland community for a number of conservation significant species. In particular, grasslands provide ideal habitat for field voles (*Microtus agrestis*) and meadow pipits, which form the primary food resource of many upland raptor species, including the threatened hen harrier (*Circus cyaneus*). Additionally, sheepwalk provides habitat for threatened waders and other significant birds such as black grouse (*Lyrurus tetrix*). While grassland cover is not decreasing, grazing management, which has traditionally been an important driver of land-use change in upland habitats (Bignal and McCracken 1996), has been implicated in dramatic changes in vegetation structure. Associated declines have been observed in the abundance of upland birds (Thompson et al. 1995a), although the mechanisms driving such declines are poorly understood (Evans et al. 2005b; Evans et al. 2006b).

Declines in upland passerines prompted the establishment of a large-scale field experiment at Glen Finglas in central Scotland. The general objective of this project was to find evidence of a causal link between grazers, habitat and declines in bird populations. Interactions between mixtures of grazing herbivores, and vegetation structure were investigated in detail. Additionally, insect abundance and diversity was assessed via soil sampling, and sweep net/vacuum sampling of the above-ground fauna. Finally, avian and small mammal species were assessed Early results from this experiment have suggested grazing has a significant impact on vegetation structure and diversity, as well as aspects of the demography of meadow pipits (Evans et al. 2005b; Evans et al. 2006b), and on the abundance of certain arthropod groups (Dennis et al. 2008) and field voles (Evans et al. 2006a).

1.4.4 Impacts of grazing on meadow pipits

Chapter 5 details the development of models, making use of data collected as part of the Glen Finglas Project, to describe the responses of meadow pipit populations to changes in grazing pressure. We apply a Bayesian modelling framework to the analysis of data collected from the Glen Finglas Project. A Bayesian modelling framework was preferred to a standard frequentist approach, as we could incorporate *a priori* information, in the form of a wealth of information from previous studies, and it allowed the estimation of a number of key demographic parameters which had not been previously reported in the scientific literature. The generated models further allowed us to evaluate the effect of grazing management regimes on the dynamics of meadow pipit populations.

1.5 Population viability analysis of capercaillie

1.5.1 Scots pine woodlands in Scotland

Scots pine (*Pinus sylvestris*) is one of only three native coniferous species in Great Britain. In Scotland, it first appeared approximately 9,000 years ago in Wester Ross, and thereafter extended to the Cairngorms (Bennett 1995). The subsequent history of pine woodland in Scotland reflects the history of human impacts. By the eighteenth century, centuries of felling, burning and overgrazing had removed Scots pine from much of its former range (Watson and Moss 2008). In the late eighteenth and nineteenth centuries, new woods were planted. However the onset of two world wars resulted in much of this new timber being sacrificed to the war effort. Consequently, following the First World War, the Forestry Commission was established with a remit to plant more trees. However, surviving stands of Scots pine, compared with pinewoods from other parts of Europe, are fragmentary, both in extent and floristic integrity (Rodwell and Cooper 1995).

Fragmented landscapes, such as Scots pine woodland in Scotland, often pose significant problems for wildlife. Fragmentation not only reduces the total area of habitat available for a species, it also isolates remaining habitat and prevents the dispersal of individuals throughout the landscape (Crooks and Sanjayan 2006). Models describing the likely movements of reintroduced Eurasian lynx (*Lynx lynx*) through patches of woodland in Scotland concluded that while populations could persist in two core areas in Scotland (Highlands and Southern uplands), connectivity between these regions was too weak to allow an exchange of individuals (Hetherington et al. 2008). Studies in other species have also shown a dependence on, or a preference for, contiguous areas of woodland; fragmented forests may reduce dispersal, and increase mortality. Examples of such species include American black bear *Ursus americanus* (Kindall and Van Manen 2007) and European pine marten *Martes martes* (Pereboom et al. 2008).

Climate change may have a significant effect on this fragmented landscape. Upland species are particularly sensitive to changes in climate (Hughes 2000). For example, an upward shift in the distribution of alpine and arctic plants has been reported (Pauli 1996). While a solid understanding of the impacts of climate change on the distribution of bird species is still relatively undeveloped, there is considerable evidence of changes in the phenology of birds, particularly with respect to migration and nesting (Crick 2004). Future changes to climate may result in upland habitats contracting to higher altitudes, and consequently impact on the distribution of populations and the dispersal of upland birds.

Additionally, while the establishment of the Forestry Commission promoted massive growth in the forestry industry, the rise of new commercial plantations has failed to have a positive impact on many native forest species, including capercaillie (Tapper 1992). Capercaillie is the largest of the grouse species, and their large size demands extensive tracts of habitat (Watson and Moss 2008). They show a strong preference for mature pine woodland, with an open structure which permits light to penetrate and stimulate a rich shrub and herb understory (Tapper 1992). However, modern commercial timber plantations are densely packed, to optimise stem form, taper and grain angle, and produce a strong, good quality timber (Petty 1995). Additionally, the forestry industry has also experienced a shift towards planting lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*), species that provide inferior quality habitat, often shading out blaeberry (*Vaccinium myrtillus*), an important component of the summer diet of capercaillie (Watson and Moss 2008). Unfortunately, old forest has been cut down in the past to give way to these more profitable commercial stands (Tapper 1992).

Modern commercial plantations do not provide optimum habitat for capercaillie. As a result of such changes in forestry, and the associated loss of preferred habitat, during the 1990s, the species experienced declines that would have led to extinction by 2015 (Watson and Moss 2008). While these trends have recently halted, capercaillie remains a species of conservation interest, and is currently listed under Annex 1 of the European Directive for the conservation of wild birds (79/409/EEC).

1.5.2 Population viability analysis

Population viability analysis (PVA) is one of a number of methods developed to assess the status of species and quantify extinction risk and address a range of additional questions concerning the conservation status and management of a given species (Morris and Doak 2002). A key component of many of these analyses is a sensitivity analysis (after Caswell 1978). These analyses examine the sensitivity of the growth rate of a population to small perturbations in demographic parameters, to identify the relative importance of each parameter to the population growth rate and thus the age specific demographic parameters that most affect population growth (Caswell 1978, de Kroon et al. 2000, Fefferman and Reed 2006). Spatially–explicit PVA methods also allow analysis of changes in the distribution of species, and the significance of extinction, colonisation and turnover in metapopulations.

PVA models were initially developed to assess extinction risk, and estimate minimum viable population sizes of Grizzly bears (*Ursus arctos horribilis*) in Yellowstone National Park (Mann and Plummer 1999). PVA models have subsequently been applied to a range of species of conservation interest. Island fox (*Urocyon littoralis*) populations on Santa Catalina Island have been dramatically affected by a recent outbreak of canine distemper virus. A PVA model was developed to assess the extinction risk of the population, and suggest recovery actions; key outputs of this analysis informed decisions regarding future translocation programs and management of risks to the population (Kohmann et al. 2005). Future viability of sea turtle populations were assessed by examining demographic parameters associated with the dynamics of the population; enhancing survival rates in the early life stages was suggested as an important management objective to compensate for mortality in other age classes (Mazaris et al. 2005). Sensitivity analysis of greater prairie-chickens (*Tympanuchus cupido*) and red-cockaded woodpeckers (*Picoides borealis*) was used to compare alternative management strategies to increase population size (Fefferman and Reed 2006).

Additionally, the application of PVA models is not just restricted to species of conservation interest. There are also applications for monitoring the spread of invasive species. The spread of the Colorado potato beetle (*Leptinotarsa decemlineata*) through Europe was investigated using PVA methods. The Colorado potato beetle is a significant pest of potato crops, and PVA methods were used to assess the effectiveness of current control strategies (Valosaari et al. 2008).

Despite the perceived benefits of PVA modelling, and their wide use, some caution is required when interpreting the outputs of models. In particular, PVA models are highly data dependent; the accuracy of the inputs is reflected in the degree of confidence in the outputs (Beissinger and Westphal 1998). Accuracy and confidence in the results also decrease with increasing length of model projection. Additionally, these methods cannot deal with unanticipated scenarios, the ‘unknown unknowns’ that may affect populations in the future.

Although these models have limitations, they fulfil a crucial role in endangered species management by providing a quantitative framework to: a) test and compare potential options for species management, b) determine the minimum population size required for viable reintroduction programs, and c) examine the impacts of habitat loss or changes to habitat reserves (Morris and Doak 2002).

1.5.3 Capercaillie population viability analysis

In chapter 6, we develop a spatially explicit PVA model of capercaillie in Scotland. At the core of our model is an age-structured matrix population model, with demographic processes parameterised from published accounts of research in capercaillie. Demographic parameters are modelled using probability distributions, to reflect variation in these parameters in natural populations. There is a close association between the historic range of capercaillie and the distribution of patches of Scots pine woodland. Forest maps of the distribution of pine woodland in Scotland can be utilised to create a patch map for modelling processes of dispersal and recruitment and resulting metapopulation dynamics. Simulations using this model framework can then be used to predict the future abundance and distribution of the species. Sensitivity analysis, conducted on the matrix population model, can identify important demographic processes potentially contributing to growth of the population.

2 Spatial synchrony in red grouse population dynamics

2.1 Abstract

Red grouse (*Lagopus lagopus scoticus*) populations exhibit unstable dynamics that are often characterised by regular periodic fluctuations in abundance. Time-series' of grouse harvesting records collected from 287 management units (moors) across Scotland, England and Wales were analysed to investigate the broad scale patterns of synchrony in these fluctuations. Estimation of the spatial autocorrelation of grouse population dynamics across moors indicates relatively high levels of synchrony between populations on adjacent moors, but that this synchrony declines sharply with increasing inter-moor distance. At distances of greater than 100km, grouse population time-series exhibit only weakly positive cross-correlation coefficients. Twenty-eight geographical, environmental and other candidate variables were examined to construct a general linear model to explain variation in local synchrony. Grouse moor productivity (average size of shooting bag), distance from the Atlantic coast moving in a north-easterly direction, April and June temperatures, and June rainfall significantly increased the explanatory power of this model. An understanding of the processes underlying synchrony in red grouse population dynamics is a prerequisite to anticipating the effects of large-scale environmental change on regional patterns of grouse distribution and abundance.

2.2 Introduction

Population cycles – defined as regular periodic fluctuations in population abundance - have been identified in many species of northern vertebrates including lemmings (*Lemmus lemmus*) and voles (*Microtis* spp), snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) (Krebs et al. 1995, Lindström et al. 2001), and in birds of the grouse family (Tetraonidae) (reviewed by Moss and Watson 2001). Cyclic behaviour is typically attributed to such factors as direct and delayed density dependence, a variety of consumer-resource interactions (predator-prey and host-parasite), and periodic variation in the environment (Kendall et al. 1999, Turchin 2003). Typically such cyclic behaviour is most apparent in populations at high northern latitudes, and becomes weaker in the southern extent of a species range (Sinclair 2003).

Spatial patterns of synchrony in fluctuating abundances have been noted in a number of species. Analysis of the records of fur returns suggested cycles in population abundance in lynx are synchronous across Canada (Elton and Nicholson 1942, Smith and Davis 1981). Moran (1953) concluded that spatially correlated environmental effects, such as climate and weather, could generate these patterns of synchrony, if these populations have the same intrinsic (density-dependent) structure (the Moran effect). Other studies have also demonstrated that synchrony in population cycles can be caused by dispersal of individuals between populations and that synchrony declines with decreasing rates of dispersal or increasing distance between populations (Lindström et al. 1996, Ranta et al. 1999).

Many populations of red grouse (*Lagopus lagopus scoticus*) in the UK exhibit unstable dynamics, often characterised by regular periodic fluctuations in population abundance (Potts et al. 1984, Watson et al. 1984, Williams 1985, Haydon et al. 2002). The red grouse is considered to be a distinct British subspecies of the willow grouse (*Lagopus lagopus*). Red grouse are common in areas of moorland habitat in the British uplands where they have been actively managed for the purpose of sport shooting since the late 19th century (Hudson 1992). The primary aim of grouse management is to maximise numbers available for shooting in autumn. Professional gamekeepers are employed to control parasites and avian and mammalian predators, and to burn heather (*Calluna* *vulgaris*) in order to produce an optimal environment for red grouse (Hudson & Newborn 1995). Whilst the intensity of management varies between sporting estates, it can produce high densities of grouse in excess of 200 grouse km^{-2} and correspondingly high harvesting bags.

Red grouse population dynamics have been the subject of extensive study since the late 1950s. Time-series analysis of harvesting records from 68 red grouse populations in England suggested that red grouse fluctuate in ‘phase forgetting quasi-cycles’ with a variable period (Potts et al. 1984). More recent analysis of over 300 time series from 289 grouse populations in Scotland, England and Wales identified 63% of grouse populations as cyclic, with cycle frequencies of 8-15 years (Haydon et al. 2002). Of the remaining populations, 22% demonstrated no cyclic behaviour, while in 15% of populations the time-series could not be consistently classified, or exhibited dynamics that could not be defined as cyclic but were distinct from white noise.

There are currently two main hypotheses to explain these fluctuations. The *parasite hypothesis* (Hudson et al. 1992, 1998), suggests that the nematode *Trichostrongylus tenuis* generates these cycles by mediating the reduction of female fecundity and increased mortality when grouse are present at high densities. The *kin selection hypothesis* (Moss and Watson 1985, Moss et al. 1996) proposes that fluctuations are generated by delayed density-dependent changes in aggression and the rate at which young males are recruited into the population. Recent work suggests that an interaction between parasites and behaviour may be the main driver of unstable dynamics (Mougeot et al. 2005b, Redpath et al. 2006). While parasites have a large impact on productivity, autumn density and spring density, these studies suggest that parasites alone could not account for all population declines (Redpath et al. 2006). However, parasitic infection has been shown to result in reduced male aggressiveness during the autumn territorial contests and could thereby influence recruitment (Mougeot et al. 2005a). Additional evidence has suggested testosterone increases the rate of parasitic infection (Seivwright et al. 2005). Increased male aggression due to high population densities may result in inflated levels of testosterone, which could in turn result in increased susceptibility to parasites.

Despite intensive research into grouse population dynamics and the causes of population cycling, little is known about the collective regional dynamics of cycle synchrony between grouse populations at a broader landscape scale. There is some evidence that specific large-scale climate events could trigger outbreaks of nematodes, and that such outbreaks could force regional grouse populations into synchronous cycles – “collective forcing episodes” (Cattadori et al. 2005). In particular, climatic conditions in May and June were identified as significant. It was suggested that dry, warm weather in May, at the time of hatching, may reduce chick mortality, while cold rainy periods may reduce foraging opportunities and thus increase chick mortality. Further, dry and warm conditions in May also act to impede the development of parasite eggs and reduce the survival of the infectious stage parasite. Cold, wet conditions in July reduce parasite development further. This study was, however, limited in that it only examined bag records from a small subset of moors in England, and in that it approached the analysis in terms of specific collective forcing episodes, rather than long-term patterns of synchrony.

In this paper we provide a description of patterns of synchrony in grouse populations across the UK averaging over entire time-series. We ask the following questions:

1) Do red grouse populations fluctuate synchronously?

2) How does cyclic synchrony between pairs of moors change with the distance between them?

3) Can any potential factors driving synchrony in red grouse abundance be identified?

2.3 Methods

2.3.1 Data treatment

Harvesting records indexed as the number of grouse shot per year were utilised to provide an indirect measure of grouse abundance. A common concern with the use of indirect measures of abundance is that these may fail to reflect real population abundance. However, in a previous analysis of the current dataset, Cattadori et al. (2003) demonstrated that the relationship between log-harvest and log-population density was linear with a slope close to unity, and therefore suggested this measure can be used as a suitable alternative to count data. Time-series data from 20 regions across England, Wales and Scotland, encompassing 287 moors, including 214 in Scotland (Figure 2.1), were compiled by the Game and Wildlife Conservation Trust. The records were of variable length, dating from 1832-1995. Time-series with less than 32 years of data were excluded from analysis, while time-series with contiguous gaps of 4 or more years were either split into series of at least 32 years in length (if possible) or excluded from further analysis (if not). After splitting and excluding relevant records, analysis was conducted on 304 time-series.

Long-term trends in bag data were removed for each time-series by subtracting annual bag records from a cubic smoothing spline fitted using R (www.r-project.org). The spline was fitted using a number of knots equal to the number of decades in the time series (rounded), +1. Alternate detrending methods did not significantly alter the results presented here.

De-trended time-series were first incremented by the smallest value in the time series +1, then normalised through the use of a Box-Cox transformation (Sokal and Rohlf 1995). Data were then standardised by subtracting the mean for the time-series from the detrended value for each year, and dividing the difference by its standard deviation.

Analyses were conducted in MatLab Version 7.0.1 (The MathWorks Inc.), and SPSS Version 12.0.1 (SPSS Inc.).

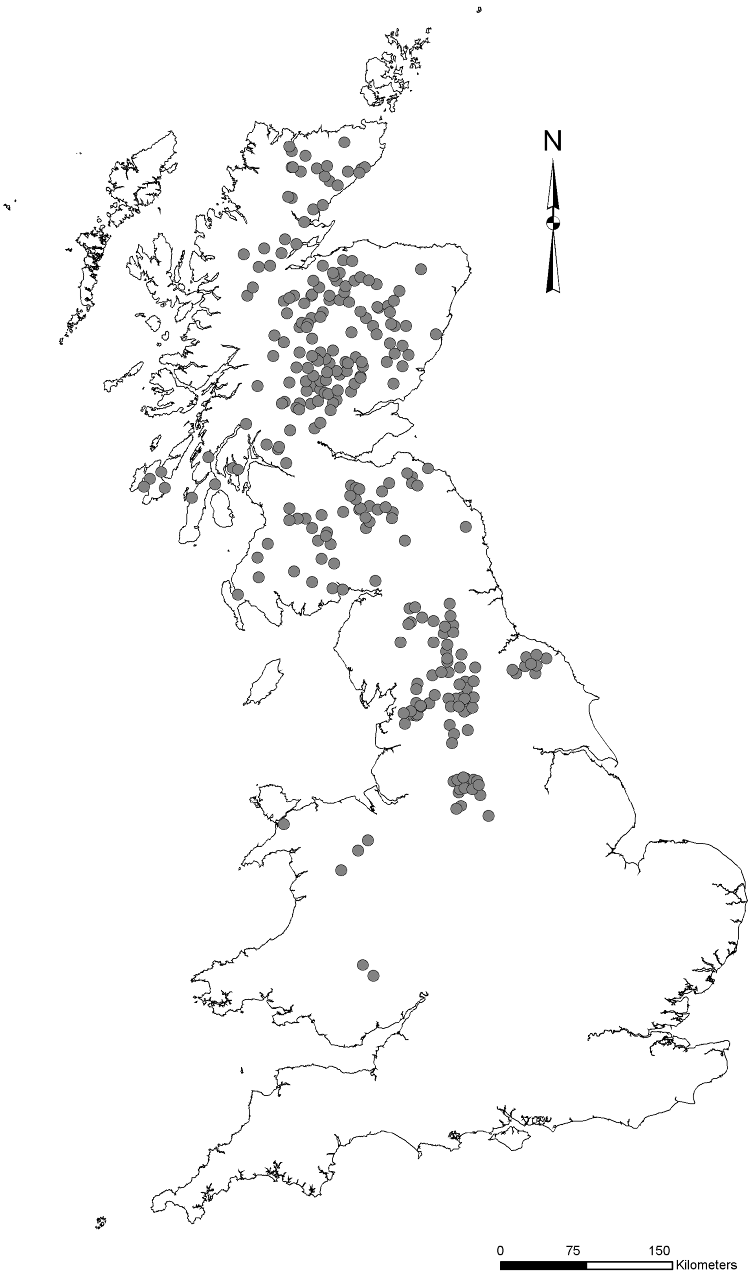

Figure 2.1. Location of the 304 grouse moors used in this analysis.

2.3.2 Analysis of synchrony

A matrix of pairwise Pearson cross-correlation coefficients was then estimated using the detrended, normalised and standardised time-series with each time-series compared to each other time-series, where both time-series share at least 30 years of concurrent data. Owing to statistical non-independence of pairwise cross-correlations, the mean cross-correlation coefficient was estimated using a bootstrap procedure (Manly 1997, Klemola et al. 2006). Pairwise cross-correlation coefficients were sampled with replacement to generate 100,000 matrices of sampled coefficients. Calculation of the mean for each of these matrices produced a normally shaped frequency histogram. This histogram was then used to estimate the mean and 95% CI of the mean of the original matrix of pairwise cross-correlation coefficients.

This matrix of cross-correlation coefficients was analysed with respect to a matrix of inter-moor Euclidian distances to investigate any relationship between the pairwise inter-moor correlation of grouse abundances and inter-moor distance. Due to the nature of the data (pairwise comparisions of this sort are not independent), an estimate of the significance of this relationship might be biased. The significance of this relationship was therefore determined using a Mantel test (Manly 1997).

For each moor, we defined neighbourliness (D_i), to represent a measure of the local density of moor locations, and the extent to which a given moor is located within a cluster of other nearby moors (d_{ij} represents the distance between moors i and j in metres).

$$D_i = \sum_{j=1}^{304} \frac{1}{d_{ij}}$$

For example, a moor in Wales is expected to have a low value for neighbourliness, given its isolated location and lack of other nearby moorland patches. Conversely, a moor located in Perthshire in Scotland is expected to have a high value for neighbourliness, given its central location and the increased density of surrounding moors.

A mean cross-correlation coefficient was calculated for each moor, weighted in favour of nearby moors, but normalised by each moor's neighbourliness, to offer a representation of the degree to which each moor time-series is generally in synchrony with time-series from other nearby moors (local synchrony).

$$\bar{r}_i = \frac{1}{D_i} \cdot \sum_{j=1}^{304} \frac{r_{ij}}{d_{ij}}$$

The relationship between local synchrony and neighbourliness was then assessed for all moors. This relationship was also investigated using a regional scale analysis. To determine whether regions (as defined by Hudson 1992) with a high density of moors exhibit high levels of intra-regional synchrony, a regional average value of neighbourliness and local synchrony was calculated for each region.

Calculated measures of local grouse synchrony were used to create a kriging map to describe patterns in the distribution of synchronous dynamics across the country. The kriging map was generated with the Geostatistical Analyst toolbar in ArcGIS (ESRI). A spherical semivariogram model was used, and predictions required the use of at least 7 neighbours. No vegetation information was included in the kriging process.

2.3.3 General Linear Model

A general linear model was constructed to identify variables that explained variation in local synchrony ($\bar{r}_i$). Twenty-eight geographical, environmental and other candidate explanatory variables were selected based on the known biology of the system. The variables were evaluated for inclusion in the GLM using forward stepwise regression. Variables in the model were average size of the grouse bag, average density of grouse (calculated from grouse bag records and area of moor in 1989), amplitude of cycles of grouse abundance (coefficient of variance for the time series) and non-standardised area of grouse moor in 1989. Values for these variables were taken from the Game and Wildlife Conservation Trust data set. The cyclic behaviour of the grouse population (whether autocorrelation analysis suggested the population was cyclic or non-cyclic) was also included (from Haydon et al. 2002).

Altitude, latitude and longitude were incorporated into this model to attempt to determine the significance of moor location. In addition, principal components analysis was conducted on latitude and longitude to give some additional indication as to the significance of moor location. In particular, this analysis was conducted to determine the significance of distance, and therefore the intensity of impacts of weather and climatic conditions from the Atlantic coastline. Additionally, local weather variables were obtained from 49 UK meteorological office weather stations, averaged from 1960 to 1990. Station data were interpolated to produce a grid of the United Kingdom at a resolution of 1 km from which the average number of days with >100mm of rainfall, average yearly rainfall and average rainfall for the growing season (April-August) were estimated for each moor. Additional data for the average number of days of snow cover, average yearly temperature, and average temperature from the growing season (April-August) were also available. These data were also included in the model. The model was refined by eliminating those variables that did not have a significant impact on explained variation.

2.4 Results

The length of pairwise comparisons (number of years where data is present for both time-series) is depicted in Figure 2.2a. Examination of the generated matrix of cross-correlation coefficients suggests a weak but significant positive correlation between grouse population cycles (Figure 2.2b, mean = 0.119, 95% confidence intervals of the mean 0.117, 0.121).

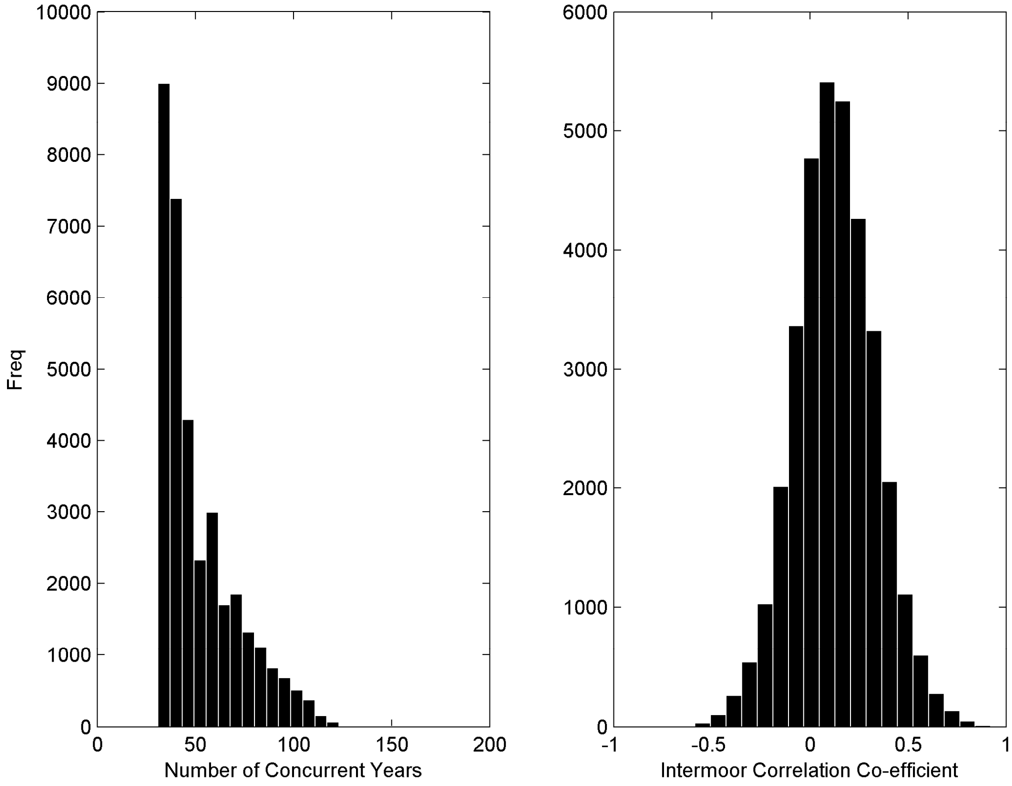

Figure 2.2. Characteristics of the grouse bag data: a) Histogram of number of concurrent years for pairwise comparisons; b) Histogram of intermoor cross-correlation coefficients.

There was a significant relationship between synchrony and inter-moor distance (Figure 2.3). Mantel tests on the relationship between pairwise intermoor distance and pairwise cross-correlation coefficients confirm that this was a statistically significant relationship (correlation coefficient between synchrony and inter-moor distance = -0.28, p<0.001). The data indicate relatively high levels of synchrony between populations on neighbouring moors, but that this declines sharply with increasing intermoor distance. At distances of greater than 100km, grouse populations exhibit only very weakly positive cross-correlation coefficients. The mean of these cross-correlation coefficients (at distances > 100km) is still, however, significantly different from zero, as estimated by a bootstrap procedure (mean = 0.084, 95% confidence intervals of the mean 0.081, 0.086).

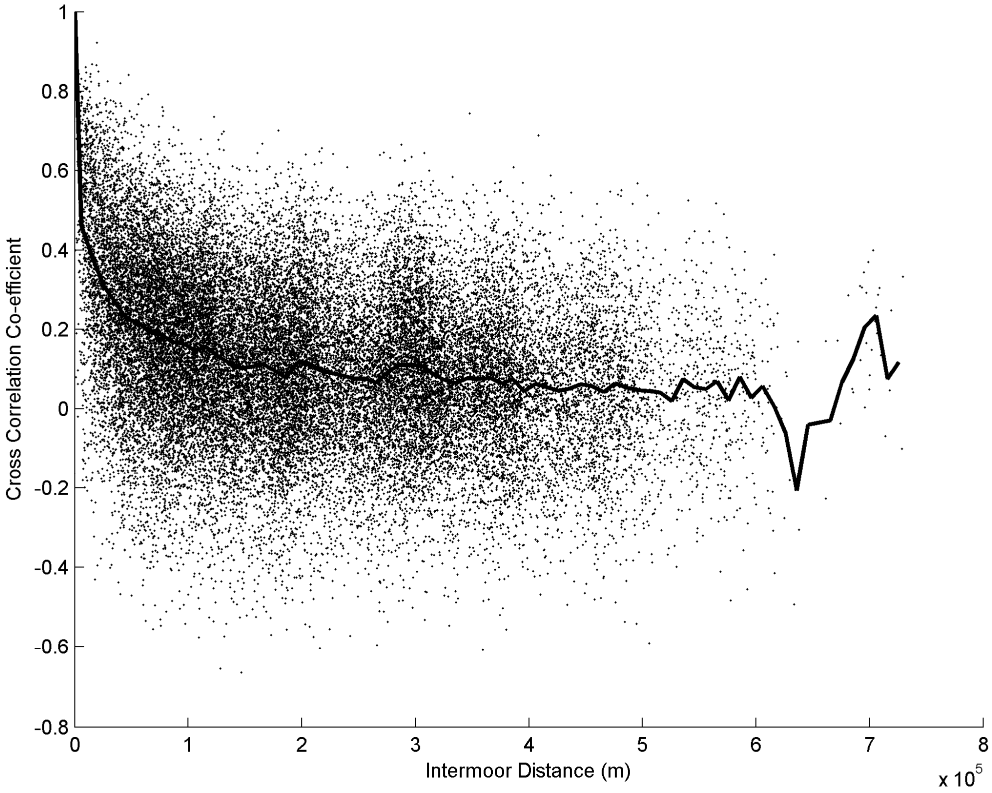

Figure 2.3. Pairwise comparisons of intermoor distance and cross-correlation coefficient. Data is included for 304 grouse time-series (34591 Points). A moving average calculated at every 103 m has been fitted to the data.

There was a statistically significant relationship between local synchrony (mean weighted cross-correlation coefficient) and neighbourliness (r^2 = 0.043, df = 303, p<0.001, Figure 2.4a). This relationship was supported by a trend to a positive relationship between intra-regional local synchrony and neighbourliness but this was not statistically significant (r^2 = 0.160, df = 19, p = 0.08, Figure 2.4b).

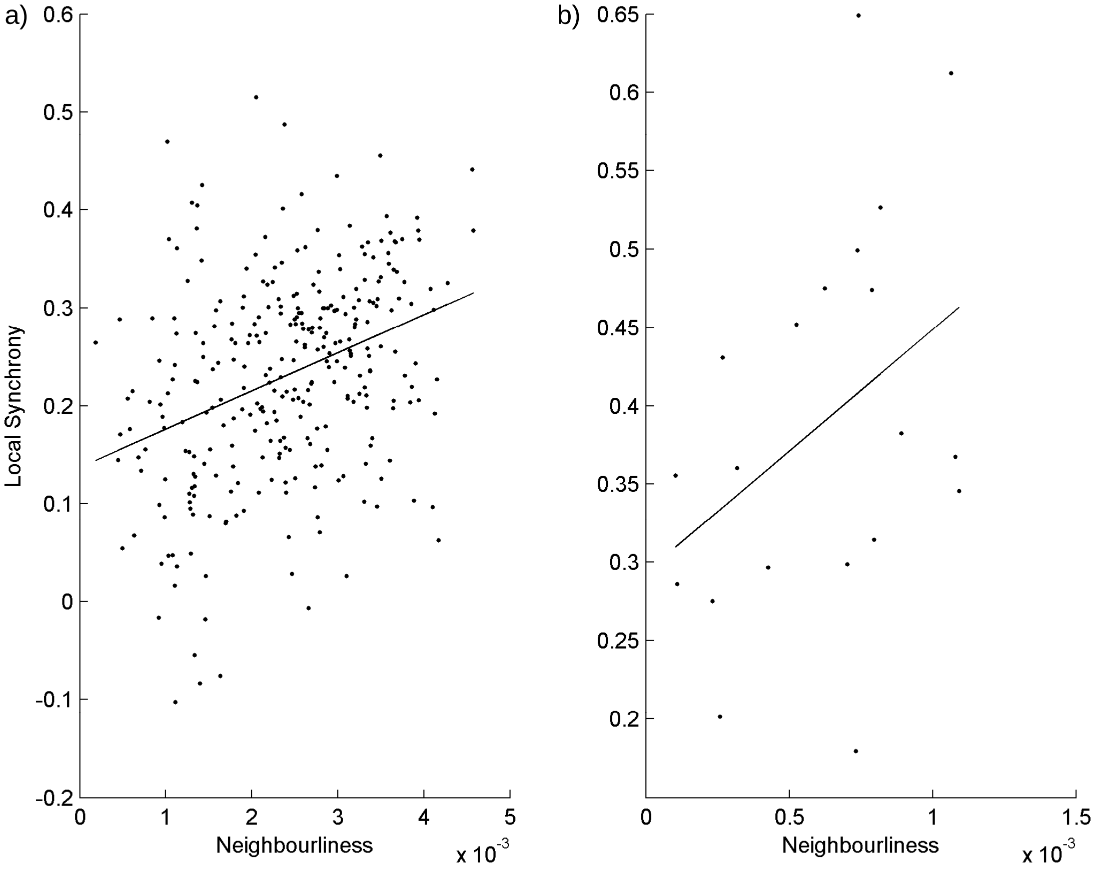

Figure 2.4. Positive relationship between local synchrony and moor neighbourliness: a) By moor (r2 = 0.043, p < 0.001); b) By region (r2 = 0.16, p = 0.08). 304 time-series across 20 regions were analysed.

A kriging map was generated to interpolate values of local grouse synchrony across the country (Figure 2.5). This map was developed without any habitat or vegetation information; however, the map provides a visual description of spatial patterns of areas of high and low grouse synchrony.

The addition of five explanatory variables, identified through a process of stepwise linear regression, into a general linear model increased the explained variation in local synchrony from 4.3% (with neighbourliness as the sole explanatory variable) to 35.14% (Table 2.1). Productive moors, and moors located at increasing distances from the Atlantic coastline demonstrated increased local synchrony. Additionally, local synchrony increased with high average April temperatures and high average June rainfall, but decreased with high June temperatures. Other variables tested in this model did not have a significant effect on the explained variation in local synchrony.

Variable	Parameter Estimate	Significance	95% Confidence Intervals	
			Lower	Upper
Moor neighbourliness	23.480	<0.0001	17.287	29.673
Average grouse bag	4.302×10^{-5}	<0.0001	3.700×10^{-5}	4.890×10^{-5}
North-easterly position	0.0301	<0.0001	0.0231	0.0371
Average April temperature	0.0942	<0.0001	0.0738	0.1146
Average June temperature	-0.039	0.003	-0.0519	-0.0260
Average June rainfall	1.16×10^{-3}	<0.0001	8.38×10^{-4}	1.482×10^{-3}

Table 2.1. Variables explaining patterns of local synchrony in cycles of grouse moor abundance (Type III SS).

An assessment of this model using Akaike’s Information Criterion (AIC) values suggest that this model is the one of the top three models. Variables including the average number of days with >100mm of rainfall, and the average yearly temperature were also included in models with similar AIC values (results not presented here). However, the AIC analysis required the removal of 52 records due to incomplete data for all moors (approximately 1/6th of the dataset), but resulted in only minimal improvements to the calculate r^2 values of the final GLM.

2.5 Discussion

This analysis of more than 300 time-series of red grouse populations across the UK suggests that there is significant, but weak, positive synchrony in population abundance. Hugueny (2006) suggests that both dynamic coupling between populations and correlated noise (the Moran effect) can explain spatial synchrony in population dynamics. Similarly, synchrony in population fluctuations may be generated by processes operating at local scales (such as dispersal or local weather conditions), or at larger scales (such as UK-wide weather systems or the North Atlantic Oscillation). The current study has examined time-series data to attempt to identify which processes are operating to create the patterns of observed synchrony in red grouse populations.

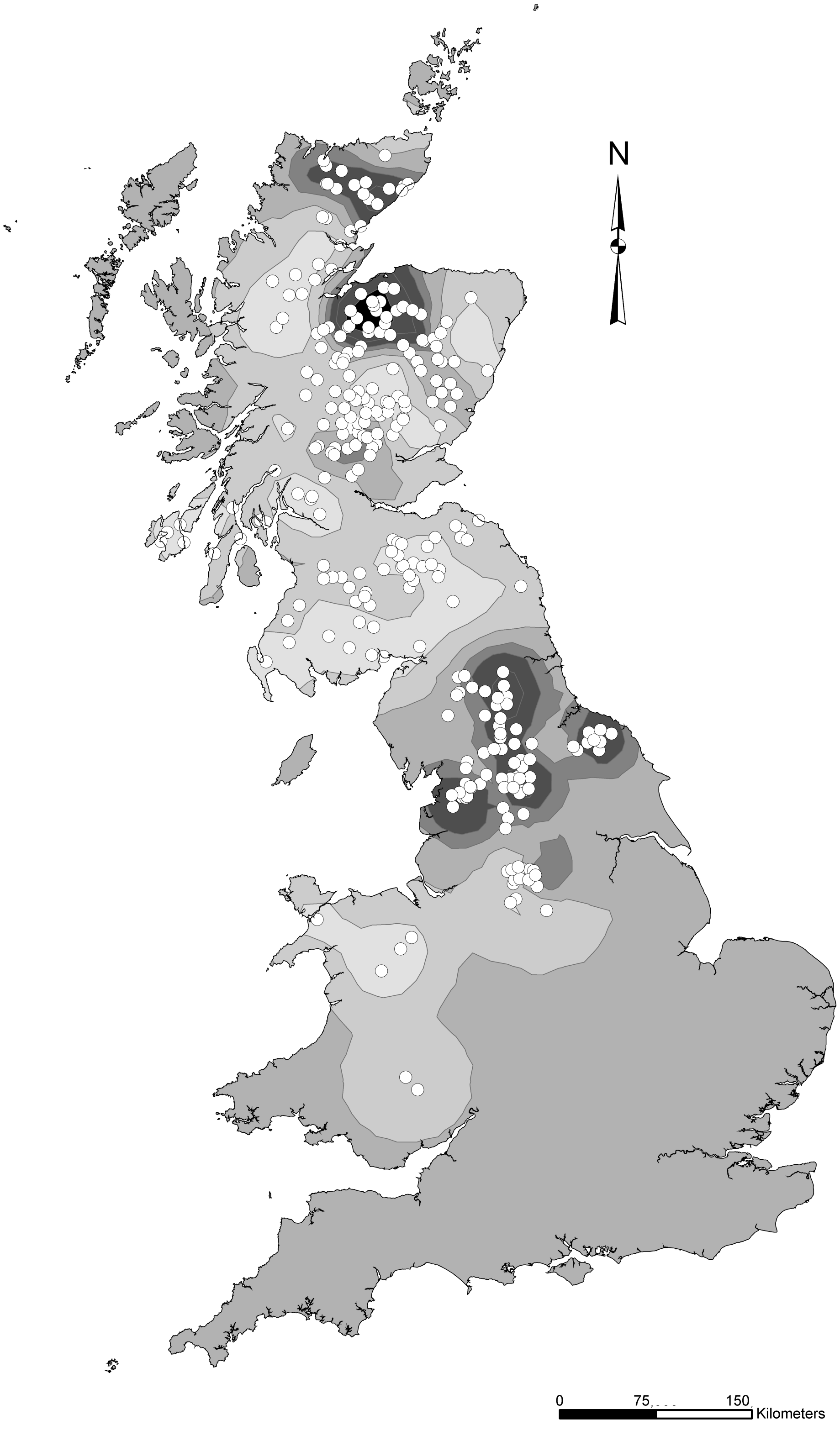

Figure 2.5. Kriging map using interpolated values to predict areas of high (dark) and low (light) local synchrony in cycles of grouse abundance. Areas with a high density of moors (neighbourliness) exhibit high levels of local synchrony.

Evidence of a relationship between pairwise intermoor distance and calculated cross-correlation coefficients indicates that some processes act on a local scale. The data indicate high levels of synchrony between populations on neighbouring moors, which declines sharply with increasing intermoor distance. Analysis of local synchrony and neighbourliness support this finding. Grouse populations on moors in areas of high moor density (high neighbourliness) exhibit increased local synchrony. This is best illustrated in Figure 2.5, where predicted areas of high local synchrony tend to occur in areas of high moor density, while areas of low predicted local synchrony occur in areas where moors are more broadly distributed.

One potential mechanism to explain these patterns is dispersal. Dispersal is often locally restricted and likely to be density dependent to some extent. Populations whose synchrony is maintained by dispersal are expected to exhibit a strong decay in synchrony with increasing distance between populations (Hugueny 2006). Transmission of parasites between populations could also be a process generating patterns of synchrony in grouse populations. As with dispersal, parasitic transmission between populations would be expected to be locally restricted. With increasing intermoor distance, the level of synchrony between populations will decrease as the influence of these factors decreases. Alternatively, spatial patterns of synchrony could be caused by climatic heterogeneity within closely located areas (Lindström et al. 1996), or by a decline with increasing intermoor distance in the similarity of the deterministic skeletons of the underlying dynamics (such as variation in the order and strength of density dependence) of populations (Hugueny 2006).

The average grouse bag provides a measure of the productivity of a grouse moor, as well as a measure of moor area (larger moors tend to be more productive). Productive grouse moors (i.e. those moors with a high average grouse bag) tend to participate in increased local synchrony. This could be attributed to coupling processes such as dispersal of individuals between moors. Increasing grouse numbers on a productive moor could result in individuals dispersing to other less productive moors. Consequently, neighbouring moors may exhibit synchronous increases in grouse numbers. On a cautious note, moorland management may have a significant effect on average grouse bags. As neighbouring moors are likely to be under similar management regimes, moor management practices could have a significant impact on patterns of synchrony. However, little information is available regarding the intensity of management, particularly for moors prior to 1950.

Previous studies have suggested a relationship between cyclic periodicity and latitude (Hudson 1992, Haydon et al. 2002). A relationship between local synchrony and latitude was not detected. However, analysis revealed a significant inverse relationship between weighted synchrony and distance from the Atlantic Ocean. This might suggest that climatic conditions generated by proximity to oceanic climate oscillations may influence changes in grouse abundance on the West coast of the British Isles, reducing the likelihood of synchronous dynamics, but this influence recedes as moors are located further to the north east. Such a mechanism is likely to operate at larger scales.

Weather variables may be operating at both local and regional scales and may generate increased local synchrony, as populations experiencing similar conditions are likely to respond in a similar manner. Late April generally coincides with the onset of egg laying in red grouse and the main period of chick mortality occurs in the first ten days after hatching (Thirgood et al. 2000). Heather does not provide sufficient protein for young grouse chicks and thus invertebrates are a prominent component of their diet at this time (Hudson et al. 1985). A reduced abundance of invertebrates can be caused by poor rainfall, as young invertebrate stages are unable to survive the dry conditions. April is also a key month for the growth of heather, and the development of new shoots may be impeded in dry weather.

The significance of weather conditions in June may be related to the abundance of parasites. Parasites such as ticks, which are a vector for the louping ill virus that can cause declines in grouse abundance (Hudson et al. 1992), require humidity to survive, particularly when they are questing for hosts in the vegetation. Parasite transmission is facilitated by the development of peat and moist sphagnum (Shaw et al. 2004). Thus increased June rainfall and decreased June temperature (resulting in damp vegetation and improved conditions for parasite survival) may result in areas experiencing similar effects of parasites on changes in population abundance.

In a previous study, Cattadori *et al.* (2005) investigated cyclic dynamics in English grouse moor populations, identifying particular years where there was significant evidence of synchrony. The study related temporal variation in climatic variables during May and July to years in which synchrony changed markedly. Years in which synchrony increased significantly were characterised by reduced rainfall and temperature in May, and with high rainfall and temperature in July. The current study examined spatial variation in synchrony and attempted to account for this using spatial variation in climatic variables that have been averaged across years. Of the local weather variables incorporated into the model, high average temperatures in April, high average rainfall in June and low average temperature in June are significantly associated with higher levels of synchrony. However, Cattadori *et al.* (2005) provide a similar explanation regarding the significance of these variables, relating them to conditions for the transmission of parasites. It is likely that climatic conditions in the entire period May through July can have a significant impact on parasite development and the intensity of parasitic infection.

Evidence indicates that grouse moors across the UK display significant but weak positive synchrony, yet not all moors are cyclic. Potentially, cyclic moors could be generating all of the synchrony detected, while non-cyclic moors are merely reducing the significance of the effect. However, examination of calculated local synchrony in relation to cyclic behaviour reveals no relationship (results not shown). Non-cyclic moors exhibit similar levels of synchrony to cyclic populations, indicating that lack of regular periodic behaviour is not a pre-requisite to maintaining locally synchronous dynamics.

We have shown that grouse population fluctuations exhibit significant, but weak, positive synchrony, with high levels of synchrony between neighbouring moors. Further understanding of the processes generating synchrony can be gained through more detailed analysis. We hypothesise that a number of processes may contribute to this synchrony, and that these processes could be characterised along two dimensions, from weak to strong processes, and from constant to intermittent processes. Examination of the strength and constancy of coupling events, and knowledge of the biology of the system, may offer insights into the processes driving cyclic dynamics in grouse populations. Further, we are interested in the generation of synchrony between two grouse moor populations, and the role additional nearby moors might play in this process. To this end, additional work is required to develop appropriate measures of grouse moor density or effective grouse population size in order to establish the importance of neighbouring moors and populations on the processes generating regional dynamics.

3 State-dependent dynamics of cycles in red grouse abundance

3.1 Abstract

Fluctuating populations are frequently demonstrated to co-vary in abundance over space, but the dynamics of coupling between populations that gives rise to this synchrony are poorly understood. Synchrony may arise through coupling that is weak and continuous, but in populations that cycle with a characteristic period, synchrony can be maintained through stronger coupling that acts only intermittently. Here, we apply a discrete Markov model that describes the state of a population trajectory to be in one of 4 possible states. The Markov model reveals the nature of the coupling that gives rise to the weakly synchronous cycles of red grouse abundance. Using time-series data from 287 populations across the species range, we show that grouse populations appear mostly uncoupled through time, but that approximately one year in six, 'collective forcing events' occur, where populations in a region are forced into synchrony to a significantly greater degree than would be expected if their dynamics proceeded independently. In the absence of these events, synchrony between populations dissipates within ~3 years. Analysis suggests that it is the smaller populations that tend to make the less probable phase shifts required to synchronize with larger populations, suggesting that smaller populations are more susceptible to the perturbations responsible for phase shifts than larger populations.

3.2 Introduction

Cyclic fluctuations in population abundance have been observed in a number of species, including mammals (Lindström et al. 2001), birds (Moss and Watson 2001) and insects (Esper et al. 2007). These population cycles are commonly linked to factors such as periodic variation in environmental and climatic conditions, consumer-resource interactions, or density dependence in population dynamics (Kendall et al. 1999; Turchin 2003). Examination of the dynamics of a number of different populations has identified patterns of synchrony in these cycles (Cattadori et al. 2005; Elton and Nicholson 1942). Synchrony may be generated by the exchange of individuals between populations, or correlated stochastic influences on population dynamics, typically a shared experience of (and response to) similar climatic conditions (Hugueny 2006; Lindström et al. 1996).

The red grouse (*Lagopus lagopus scoticus*) is a gamebird endemic to the British Isles, and locally restricted to areas of moorland habitat in the British uplands. Populations of red grouse have been shown to exhibit cyclic fluctuations in abundance (Haydon et al. 2002; Potts et al. 1984; Watson et al. 1984; Williams 1985). Studies have also demonstrated that these population fluctuations exhibit weak, but significant, positive synchrony (Kerlin et al. 2007), but there are few studies on the coupling mechanism that gives rise to these patterns. Cattadori *et al.* (2005) suggest that coupling may occur intermittently through the effect of rainfall and temperature on the infection intensity of a parasitic nematode (*Trichostrongylus tenuis*). However, this study considered only a small subset of populations in the northeast of England, and no studies have examined the nature of coupling across the species range.

We examine three hypotheses to explain the observed weak, but significant, positive patterns of synchrony in grouse populations. The first hypothesis supposes that synchrony could be generated by weak coupling, operating constantly through time. The second that synchrony may be a product of intermittent, but strong coupling, which forces otherwise uncoupled populations into a brief state of high synchrony, interspersed with periods of declining synchrony in which dynamics within each population proceed independently of each other. Intermittent coupling events of this sort have been termed *collective* *forcing events* (CFEs) by Cattadori *et al.* (2005). Finally, population dynamics may be uncoupled over the period that data were generated, but current synchrony may remain as a result of 'historic' coupling that arose prior to time of data collection.

If we are able to produce evidence that coupling is strong and intermittent, and we can detect CFEs across the species range, we can extend the analysis to examine the potential causes of these CFEs. We can ask whether a process or processes acting to increase grouse abundance across a number of populations could generate CFEs. Alternatively, CFEs could be produced by processes acting to suppress grouse numbers on moors, resulting in synchronous declines in population abundance.

Finally, if grouse populations do not exhibit constant synchrony, this would imply that some populations make unexpected shifts in cycle phase, resulting in these populations changing their level of synchrony with other moors cycling through states of high and low abundance. Analysis of population cycles allows us to identify those populations making unexpected phase-shifts. For example, larger moors, or moors with a large number of grouse, may tend to cycle independently of the dynamics of populations on smaller moors. However, smaller grouse populations may be asymmetrically influenced by larger neighbours, and could therefore be forced into synchrony with nearby, larger populations.

In this paper we examine the nature of the processes driving synchrony in red grouse populations across the United Kingdom. We address the following questions:

1) Do strong, intermittent coupling events (CFEs) maintain average levels of synchrony in red grouse populations across the species range?

2) If so, are these coupling events concomitant with synchronous population increases or declines?

3) Are the required phase-shifts that give rise to this synchrony more common in small populations than larger populations?

3.3 Methods

3.3.1 Data treatment

Grouse abundance was estimated using harvesting records compiled by the Game and Wildlife Conservation Trust. Time-series data were available for 287 populations across England, Wales and Scotland. Records were of variable length, and dated from between 1832 and 1995. Time-series with less than 32 years of data were excluded from analysis, while time-series with contiguous gaps of 4 or more years were either split into series of at least 32 years in length (if possible), or excluded from further analysis. In this paper, we focus on patterns of synchrony within regional groups of moors. Therefore, moors were split into 20 regional groups for analysis (Figure 3.1) following Hudson (1992). As there are only six moors in region 20 (Wales), this region was excluded from further analysis. Data for the Trossachs (Region 12) was also excluded due to a lack of adequate concurrent population data. After splitting and excluding relevant records, analysis was conducted on 299 time-series across 18 regional groups.

3.3.2 The Markov model

The Markov model used in this paper has previously been described in Haydon *et al.* (2003).

The k^{th} region contains n_k moors. Grouse abundance on the i^{th} moor (i=1 … n_k), in the k^{th} region (k=1 … 18), in the t^{th} year (t=1 to z^k_i) is indicated by $\{X^k_{i,t}\}$. For each time-series we can describe a new time-series as a progression through a sequence of states $\{Y^k_{i,t}\}$ (t = 2… z^k_i -1), as follows:

$Y^k_{i,t} = 1$ if $X^k_{i,t} < X^k_{i,t-1}$ and $X^k_{i,t} \leq X^k_{i,t+1}$ ($X_{i,t}$ is a trough),

$Y^k_{i,t} = 2$ if $X^k_{i,t-1} \leq X^k_{i,t} \leq X^k_{i,t+1}$ ($X^k_{i,t}$ is the intermediate value of two consecutive increasing years),

$Y^k_{i,t} = 3$ if $X^k_{i,t} \geq X^k_{i,t-1}$ and $X^k_{i,t} > X^k_{i,t+1}$ ($X_{i,t}$ is a peak),

$Y^k_{i,t} = 4$ if $X^k_{i,t-1} > X^k_{i,t} > X^k_{i,t+1}$ ($X^k_{i,t}$ is the intermediate value of two consecutive decreasing years).

Those infrequent years where there is no change have been classified as 'increasing' events. Populations will not (by definition) exist in peak or trough states for consecutive years.

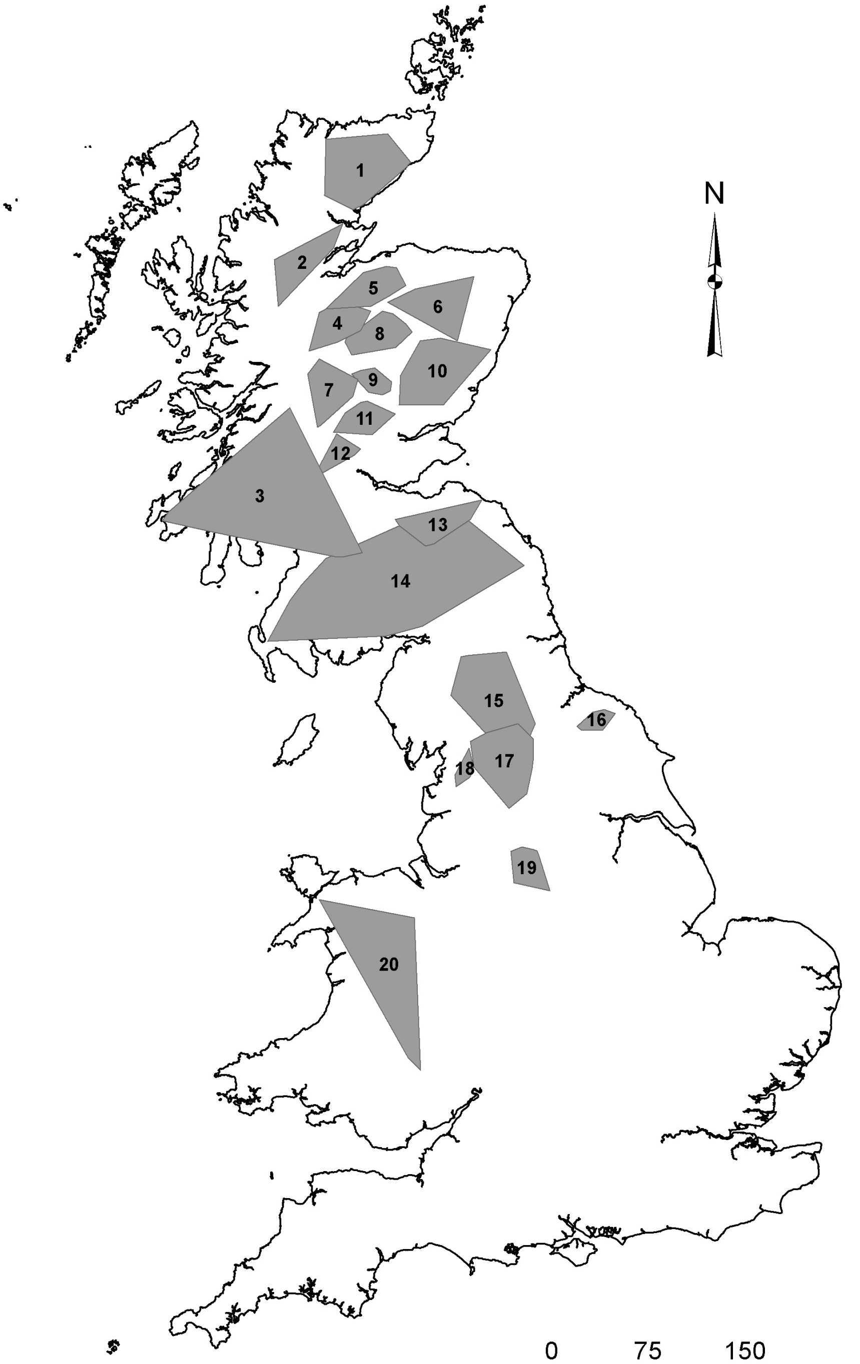

Figure 3.1. Grouse moor regions included in this analysis. Regions have been delineated by creating minimum complex polygons which include all grouse moors within them. Regions 12 and 20 were not included in subsequent analysis due to a scarcity of available data.

For all time-series in the k^{th} regional group, we can construct a 4 x 4 transition matrix T_k with entries $t(a, b)$ indicating the probability of a transition from state *a* to state *b*. Populations will visit these states in some restrictive order, but may spend varying periods of time in the increasing or decreasing states. Because the rows of T_k must sum to one, we can potentially identify four independent parameters in the transition matrix: $t(1,2)$, $t(2,2)$, $t(3,1)$, $t(4,1)$.

$$T_k = \begin{bmatrix} 0 & t(1,2) & 1-t(1,2) & 0 \\ 0 & t(2,2) & 1-t(2,2) & 0 \\ t(3,1) & 0 & 0 & 1-t(3,1) \\ t(4,1) & 0 & 0 & 1-t(4,1) \end{bmatrix}$$

By adding constraints, we can define a number of special scenarios. For instance, it might be that transition probabilities are state independent, i.e. $t(1,2) = t(2,2) = t(3,1) = t(4,1)$. Alternatively, transitions from some states could be state-dependent. We can identify four possible models with only one state-dependent transition probability, six models with two state-dependent transition probabilities, four with three state-dependent transition probabilities and one full model with four state-dependent transition probabilities. We can determine which model most accurately reflects the red grouse system, by estimating the 15 different possible models represented by T_k and calculating and comparing likelihoods in each case (e.g. Haydon et al. 2003, e.g. Menard et al. 1993).

For any given region *k*, we estimate $t_k(a, b)$ as the observed proportion of occasions when the time-series changes to state *b* at time *t*+1, given it was in state *a* at time *t*:

$$\hat{t}_k(a,b) = \frac{\sum_{i=1}^{n_k} \sum_{t=2}^{z_i^k - 2} \delta_{i,t}}{\sum_{i=1}^{n_k} (z_i^k - 2)}$$

where $\delta_{i,t} = 1$ if time series *i* is in state *a* at time *t* and *b* at *t*+1, $\delta_{i,t} = 0$ otherwise.

3.3.3 Model Selection

The estimated log-likelihood of all the data from the k^{th} region $\{Y^k\}$, corresponding to any estimated transition matrix $\hat{T}_k$ is:

$$\mathrm{LL}(\{Y^k\}|\hat{T}_k) = \sum_{i=1}^{n_k} \sum_{t=2}^{z_i^k - 2} \ln \hat{T}_k (Y_{i,t}^k, Y_{i,t+1}^k) .$$

Likelihood ratio tests and analysis of AIC values can then be used to determine the most appropriate model.

The adequacy of the resulting selected model $\hat{T}_k$ as a representation of the dynamics of each time-series $\{Y_i^k\}$ may be assessed by examining the likelihood of each observed time-series:

$$\mathrm{LL}(\{Y_i^k\}|\hat{T}_k) = \sum_{t=2}^{z_i^k - 2} \ln \hat{T}_k (Y_{i,t}^k, Y_{i,t+1}^k) ,$$

within the distribution of likelihoods computed by simulation from a large number of time-series of length z^k_i -2, from the saturated four parameter model. If $\mathrm{LL}(\{Y_i^k\}|\hat{T}_k)$ lies within the 95% confidence intervals (CI) of the likelihoods calculated from these simulated datasets, then $\hat{T}_k$ can be judged a reasonable fit to the dataset.

3.3.4 Comparing properties of the model and the data

We measure synchronisation in the data as follows. Let the elements $s^k(j)_t$ of a row vector s^k_t be the proportion of populations in the k^{th} region, in each state at time t (j = 1…4). We use the Shannon-Weaver diversity index to measure the level of entropy in the system at time t. The entropy (H^k_t) is estimated as:

$$H_t^k = -\sum_{j=1}^{4} s^k(j)_t \ln(s^k(j)_t) .$$

Let H^k_{null} denote possible values of H^k_t under the hypothesis that the n_k time-series are stationary, independent Markov chains, all associated with the transition matrix

$\hat{T}_k$ (a 95% confidence envelope for H^k_t can be estimated by simulation under this independence assumption, the width of this envelope depends only on the number of populations in the regions for which Y_i^k can be calculated). Noting that $s^k_{t+1} = s^k_t\hat{T}_k$ we can approximate the distribution of H^k_{null} by simulation, treating each of the n_k populations as separate and independent. If H^k_t lies outside the 95% CIs for H^k_{null}, the collection of time-series can be regarded as significantly synchronised (and therefore not independent of each other).

A useful measure of the degree of synchronisation is then the quantity Φ^k_t = 1-$H_t^k / \overline{H}^k{}_{null}$ (where $\overline{H}^k{}_{null}$ is the expected value of H^k_{null}) which will be close to zero when the observed time-series are independent, and close to one if the time-series are fully synchronised. Haydon *et al.* (2003) have demonstrated that the synchrony index Φ^k_t falls off exponentially in an initially synchronised but uncoupled set of populations. Similarly, we used the appropriate transition matrix to simulate a number of time-series for each region, with all populations initially in the same state (equal numbers of simulations were done with all moors in each of the four states). The half-life of the synchrony index was estimated by fitting an exponential distribution to the decline in Φ^k_t, and examining the median value of the decay parameter of the fitted distribution. A bootstrapping procedure (4000 iterations) was used to assess variation in our estimate of the half-life.

Given the distribution of states at time t, we can also simulate ‘one-step’ 95% CIs about the expected entropy at time t +1. Comparing the profile of H_t with these one-step conditional CIs indicates over which time-intervals the dynamics of the n time-series are significantly at odds with the assumptions of dynamical independence. We can use this comparison to identify CFEs, that is particular years in which observed synchrony is greater than expected by chance.

We ask whether the occurrence of a CFE in one region is associated with similar occurrences in other regions by estimating the probability a given region will experience a CFE as the proportion of years in each time-series in which a CFE occurs. For each year of the analysis, we calculate a simulated distribution of CFE counts as the sum of a number of independent Bernoulli trials using the calculated probabilities of a CFE event for each region. The probability of observing the actual number of CFEs under the hypothesis that CFEs arise independently in each region can be estimated from this simulated distribution.

3.3.5 Processes creating patterns of synchrony

As a regional group of time-series enter unexpectedly high levels of synchrony (CFEs), we can ask whether this is generated by a number of series moving into growth phases (states 1 or 2) or decline phases (states 3 or 4).

Given the distribution of states at time *t*, and the transition matrix $\hat{T}_k$, we can generate 100,000 simulated state distribution vectors at time *t*+1, based on the number of moors in the k^{th} region. Using these state distribution vectors, we can then establish 95% CIs for the number of moor populations increasing, and decreasing at time *t*+1. Comparison of the observed number of moor populations increasing and decreasing with these 95% CIs, allows identification of those years in which the number of populations increasing or decreasing is greater than we expect.

3.3.6 Which populations are creating synchronous dynamics?

The transition matrix $\hat{T}_k$ provides values for the probability that a moor will move from one state to another. We can use matrix values to calculate standardised log-likelihood values (w^k_i) for the series of observed state changes, $\{Y^k_{i,t}\}$:

$$w_i^k = \frac{\sum_{t=2}^{z_i^k - 1} \ln(\hat{T}_k(Y^k{}_{i,t}, Y^k{}_{i,t+1}))}{z_i^k - 2}.$$

To test our hypothesis, that the population dynamics of small populations are dependent on the fluctuations of larger populations, the relationship between these calculated log-likelihood values and average grouse bag was examined using regression.

3.4 Results

3.4.1 The Markov model

The number of time-series in each group, and the number of years for which abundance data was available for at least 3 moors (time-series length) are given in Table 3.1 (columns 1-3). Additionally, the number of parameters (possible transmission probabilities required to be state dependent) necessary for the Markov model is also provided (Table 3.1, column 4). For two regions (15 and 18) the fully saturated model was required; 8 regions required three of the possible transition probabilities to be state-dependent, while other groups required either 1 or 2 parameters. LL($\{Y^k_i|\hat{T}_k$) was found to be inside the 95% CIs for likelihoods calculated through simulation for all regions, demonstrating that the models were a reasonable fit to the data. The number of parameters required for the transition matrix is significantly higher for more southern regions. Average latitude for regions is a significant predictor of the number of parameters required (ordinal regression model, χ^2 (likelihood ratio) stat = 8.69, df = 1, p=0.003).

3.4.2 Evidence of synchrony in population dynamics

Figure 3.2a describes the distribution of annual synchronisation indices ($\Phi^k{}_t$) in each region. Results suggest that all regions exhibit synchronous dynamics (for example, 13 of the 18 median values of $\Phi^k{}_t$ are greater than 0.2), but there is considerable variation in the degree of synchrony observed, with the synchrony index $\Phi^k{}_t$ often taking values close to 0, indicating populations often approach a state of complete asynchrony.

Simulation of fully synchronised but uncoupled populations using the appropriate transition matrix confirms that the synchrony index Φ_t^k falls off exponentially over time in the absence of coupling, with an average half-life of 0.675 years (Figure 3.2b). In most cases, this index will approach 0 within two-three years of independent dynamics. Thus higher values of Φ_t^k must arise through some form of coupling.

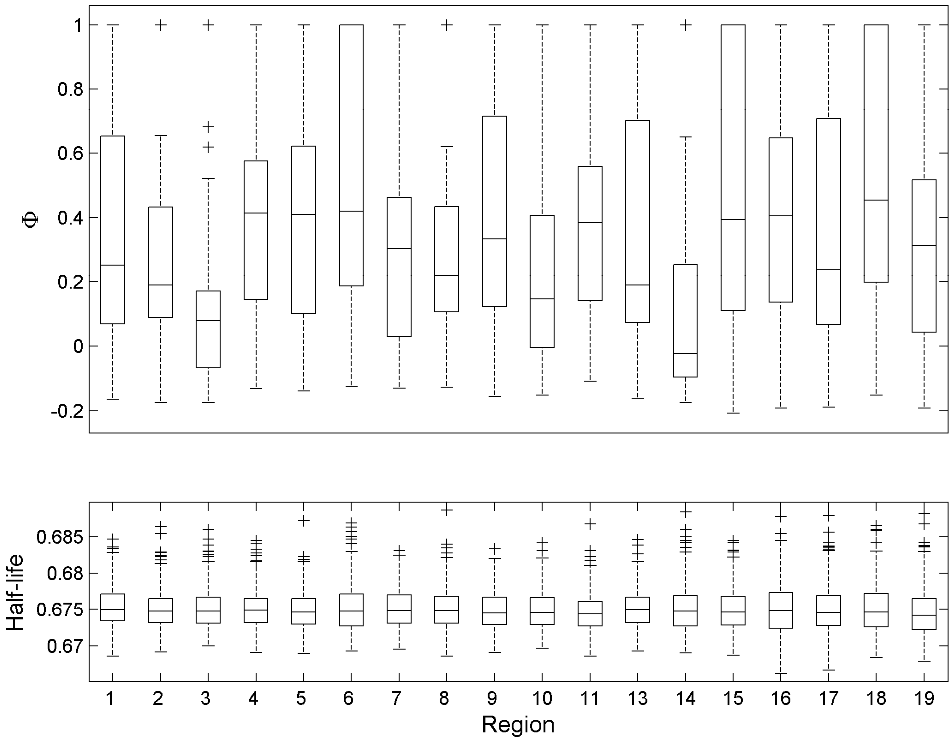

Figure 3.2. Aspects of synchrony in red grouse populations and simulations; a) Boxplot of observed synchrony values (Φkt) for each region, b) half-life of synchrony for 4000 simulations of fully synchronised but uncoupled populations using the appropriate transition matrix for each region.

Figure 3.3 provides sample output for entropy scores over time for two regions (3 and 5). Over all regions, H^k_t values fell outside (below) of the 95% confidence envelope expected from independent dynamics on average 29.12% of years (Table 3.1, column 5 displays results for all regions). The proportion of time that regions were significantly synchronized as judged by this metric varied from 8.22% (region 13) to 54% (region 11). There was no significant trend between region latitude and proportion of time synchronised (F = 0.38, df=16, p = 0.62).

Table 3.1. Summary statistics for grouse moor regions.

Region	No. of moors	Time-series length[1]	Parameters required[2]	Years synchronised[3]	No. of CFEs	Average interval[4]	V[5]	No. of UI events	No. of UD events
1	22	99	3	40	29	2.33	154.86	18	19
2	10	24	1	2	0	-	-	3	4
3	17	114	1	10	8	11.78	121.7	3	6
4	13	79	1	32	13	4.71	119.83	10	16
5	14	117	1	59	36	2.19	157.07	19	20
6	12	92	1	20	10	7.45	107.38	9	9
7	11	71	1	11	5	11	87.58	3	5
8	8	68	2	5	1	-	-	3	1
9	13	76	1	15	9	6.7	81.46	5	4
10	21	105	3	41	25	3.08	178.23	15	18
11	16	87	3	47	23	2.67	125.92	5	20
13	12	73	3	6	2	23.67	83.05	1	1
14	39	117	3	39	20	4.62	117.48	11	18
15	24	102	4	38	22	3.48	213.72	15	20
16	10	74	3	21	10	5.82	144.17	7	9
17	25	116	3	53	33	2.44	134.99	26	14
18	11	72	4	28	11	5.08	141.97	8	12
19	21	64	3	17	10	4.91	79.13	7	10

[1] Number of years for which bag data was available for at least three moors.

[2] Number of independent transition parameters required in the preferred transition probability matrix.

[3] Number of years in which H^k_t lies outside the 95% CIs for H^k_{null}.

[4] Average interval length between CFEs. Calculations assume a CFE occurred immediately prior to, and following, the time-series.

[5] Co-efficent of variation for interval lengths.

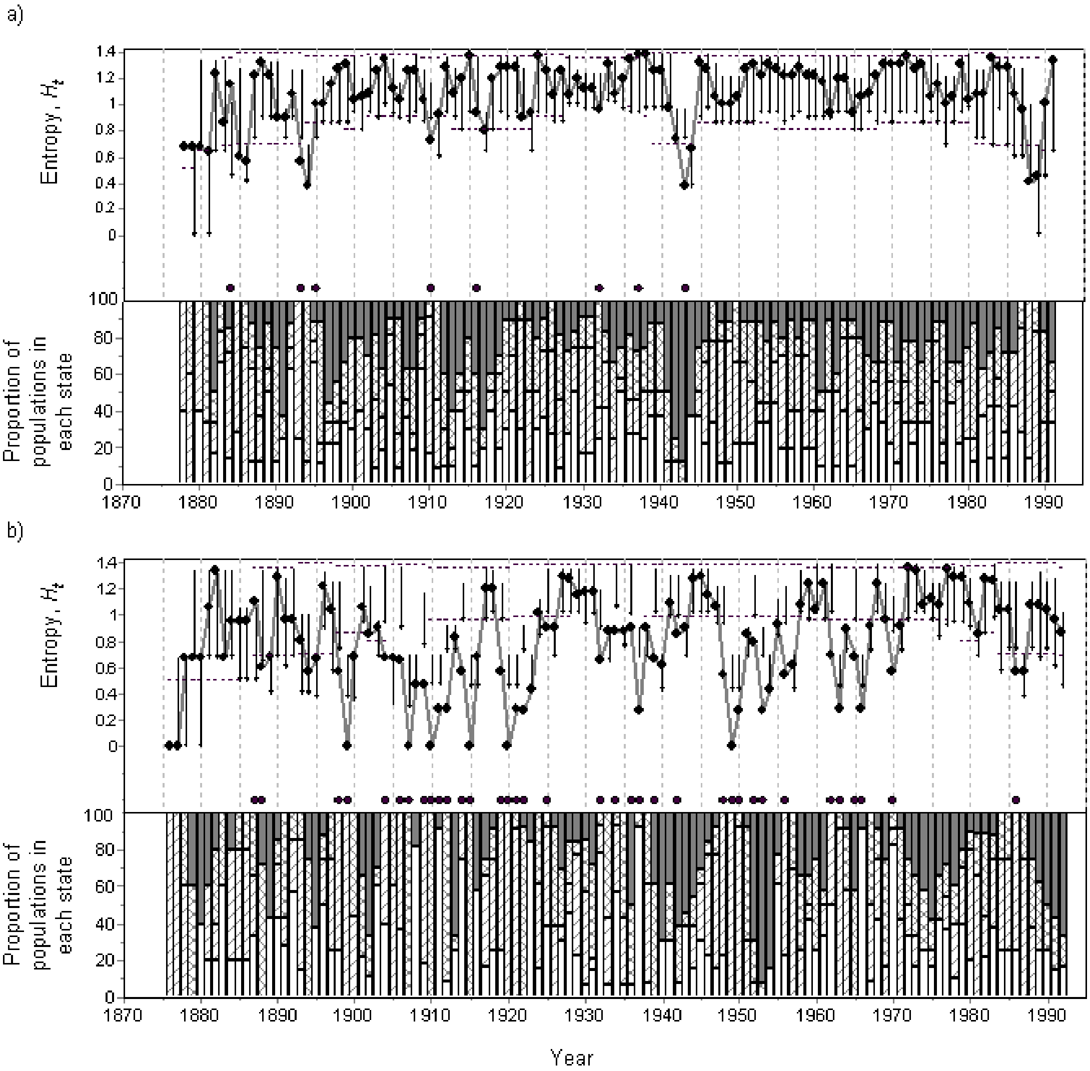

Figure 3.3. Patterns of entropy between populations within 2 sample regions (a) region 3, b) region 5). Observed entropy (H_{kt}) among populations based on the Shannon-Weaver diversity index (grey lines) with 95% confidence envelope predicted by the Markov state transition model (horizontal dashed lines). Vertical black lines indicate one-step 95% CIs on the entropy conditional on the configuration of the system one step previous. Years in which collective forcing episodes forced the populations into unexpected synchrony are shown with black circles at the base of each entropy plot. The proportion of grouse populations observed in one of four states each year is also included. Troughs are shown in diagonal stripes, increases in white, peaks in black and decreases in cross-hatching.

3.4.3 Evidence of collective forcing events

The one-step 95% CIs conditioned on the state distribution within the region at the previous time step indicated the presence of CFEs in all regions except region 2 (Table 3.1, column 6). The average interval between CFEs was 5.75

years, but there was considerable variation in how regularly such events occurred. CFEs were most frequent in region 5 and least frequent in region 2, where we did not observe any CFEs through 24 years of data. Average intervals between CFEs and coefficients of variation for those intervals are included for all regions in Table 3.1, columns 7 & 8. Examination of the patterns of aggregation of CFEs (by way of comparisons to randomly simulated patterns of CFE aggregation) suggests CFEs are not over-dispersed in any region. In contrast, four regions (1, 5, 10 and 15) show evidence of significant under-dispersion (clumping of CFEs).

Similarly, analysis suggests that the occurrence of a CFE in one region is not associated with similar occurrences in other regions. We identify only 11 years (out of 116) in which the observed number of detected CFEs is significantly ($P<0.05$) above that expected assuming independent occurrence across regions, and no years after the appropriate Bonferroni corrected significance threshold is adopted.

There is a significant relationship between the number of CFEs recorded in a region, and the number of years that regions displays synchronous dynamics ($F = 116.81$, $df = 16$, $p<0.001$, Figure 3.4). The slope of this regression is 1.48, suggesting that each CFE is, on average, associated with 1.48 years of synchrony. The intercept of this regression (6.2) suggests that in the absence of any CFE, some weak coupling between populations may result in synchronous dynamics in approximately 6% of years. Following a CFE, synchrony in all regions is typically maintained for no more than 1 year in the absence of further CFEs, reflecting our prior finding that synchrony rapidly declines in the absence of coupling (Figure 3.3). However, we do detect a number of occasions (<5%) in which a single CFE event results in longer periods of synchronous dynamics. For example, such events can be observed in region 11 were a time-series of 87 years shows lower levels of entropy than expected for 47 of these years, but only 23 CFEs were detected.

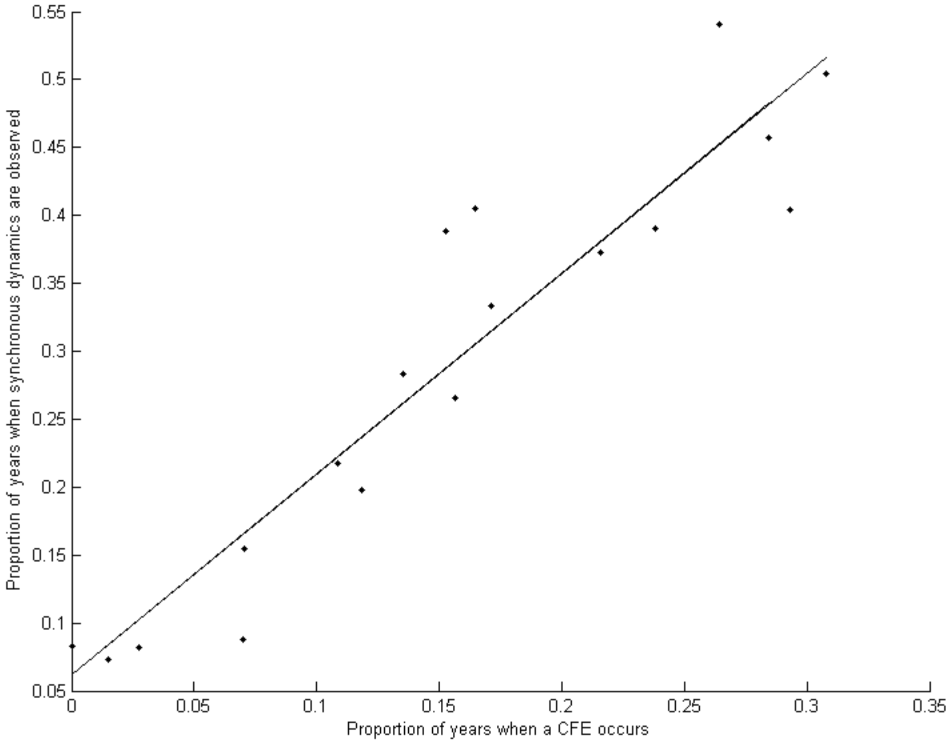

Figure 3.4. CFEs and synchronous dynamics. For each region, there is a significant relationship between the proportion of CFEs in a time-series, and the proportion of years in which H_{kt} lies outside the 95% CIs for H_{knull} (i.e. synchronous dynamics were observed), such that each CFE is associated with 1.48 years of synchrony.

3.4.4 Processes creating patterns of synchrony

In all regions, we can detect years in which more populations than expected increased in population abundance – an unexpected increase (UI) event. Similarly, we can detect years in which more populations than expected exhibited population reductions – an unexpected decrease (UD) event (Table 3.1, columns 9 & 10). Paired t-test analysis suggests no significant difference between the number of UI events and the number of UD events ($t = 1.726$, $df = 34$, $p = 0.102$). As expected, there is a significant correlation between the number of regional CFEs and UI events (correlation coefficient = 0.8966, $p<0.001$), and the number of CFEs and UD events (correlation coefficient = 0.8677, $p<0.001$). There are, however, significantly more UI and UD events than CFEs ($t = 6.317$, $df = 34$, $p <0.001$).

3.4.5 Which populations are making unusual state changes?

Examination of w^k_i for each time-series in region *k* provides comparable measures of the likelihood of the trajectory of state changes observed in a population. A population which consistently selects the state change with the highest probability will feature higher (less negative) values for w^k_i. Regression analysis on the normalised log-likelihood results suggests a significant positive relationship with average grouse bag (F = 11.99, df = 295, $p<0.001$, $r^2 = 0.036$, Figure 3.5).

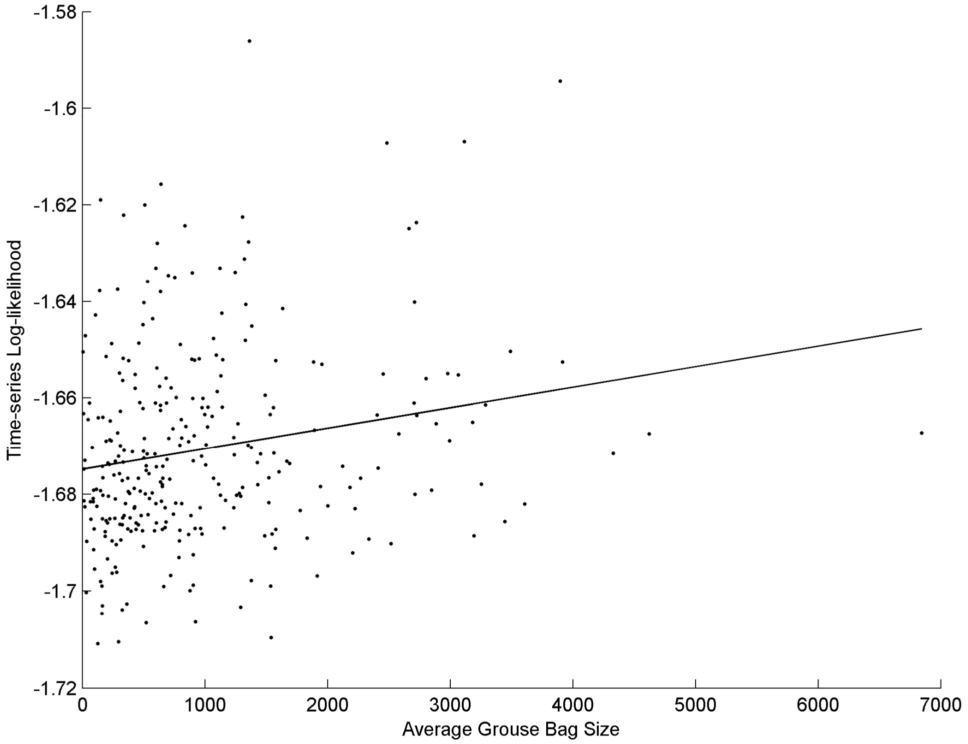

Figure 3.5. Calculated log-likelihood values for observed state changes show a significant increase with increasing grouse bag, suggesting that larger populations are making higher probability state changes.

3.5 Discussion

Synchrony in red grouse population dynamics can be largely explained by the presence of coupling events where populations in a region are collectively forced into a more synchronous state than would be expected if their dynamics proceeded independently of each other. Analysis suggests these coupling events are not generated in a consistent manner - either through synchronous growth or decline in grouse abundance, and, on average, it appears to be smaller populations that ‘break-stride’ and are forced into synchrony with larger populations.

In the formulation of a transition matrix, we would expect regions with a more defined cyclic behaviour to require more Markov model parameters than regions with poorly defined cycles. In well defined cycles, we would expect differences in the probabilities moving from one state to another. For example, given the average length of a cycle is 8.3 years (Haydon et al. 2002), we would expect time-series to feature more periods of increasing or decreasing abundance than peaks or troughs and therefore the probability of moving from a decreasing state into a peak would be lower than the probability of remaining in a state of decrease. Alternatively, poorly defined cycles would be expected to have all probabilities roughly equal, as there would be little difference in expected state change probabilities.

The Markov models illustrate that in all regions, changes in population abundance do not occur independently. Results have shown that in populations fluctuating independently and in the absence of coupling, we expect synchrony to rapidly decline. However, years in which observed levels of entropy fell outside of the 95% confidence envelope estimated assuming independent dynamics provides evidence of coupling between populations. Synchronous dynamics cannot therefore be an artefact of historic coupling events.

Analysis revealed a number of years in which observed entropy fell outside 95% CIs on the entropy conditional on the state configuration of the system one time-step previous (i.e. the population dynamics of a region showed a greater degree of synchrony than expected given the state of the population one year previous). The detection of such years suggests that synchrony in the population dynamics of red grouse appears to be driven by strong coupling acting intermittently (CFEs). This finding supports the previous work of Cattadori *et al.* (2005) based on a much smaller subset of these data. These events act to force populations into a synchronous state, with approximately one such event occurring every six years. In some regions however, CFEs may occur every 3 years, while in region 3 we only detect 2 CFEs over the 73 years of available data, and in region 2 we are unable to detect any CFEs. Analysis implies each CFE event is associated with

1.48 years of synchrony. As suggested by the low half-life of synchrony in these populations, in the absence of further CFEs, synchrony will rapidly decline following a CFE. While we have detected evidence of strong, intermittent coupling, we could not rule out the hypothesis that weak but constant processes may also be contributing.

These results are comparable to the findings of a study into synchrony in grey-sided voles (*Clethrionomys rufocanus*) in Hokkaido, Japan. Synchrony in voles was found to be maintained by similar CFEs, occurring 1 in every 4 to 5 years (Haydon et al. 2003). The detection of CFEs in two such diverse species raises questions as to the ubiquity of CFE driven patterns of synchrony in nature. To date, this methodology has not been used to examine synchrony in other species; such analysis could shed light onto the drivers of synchrony in these species.

While this method has not been applied to many species, parallels can be drawn between this result and aspects of synchrony in other species. Lindström *et al.* (1995) have shown that populations of three other species of Tetraonids in Finland (capercaillie, black grouse and hazel grouse) all exhibit cyclic dynamics, with cycles most frequently displaying a period of six years. These dynamics also display a high degree of temporal synchrony (Ranta et al. 1995b). Modelling work using Leslie matrix-based simulation approach suggests the population dynamics of the three species could be synchronised by introducing a synchronised breeding failure at a given interval (Ranta et al. 1995b). Such an event could be synonymous with the occurrence of CFE events every 1 in 6 years on average; a stochastic event could suppress breeding in a number of populations, providing a strong coupling mechanism to synchronise otherwise uncoupled populations.

Similarly, insect outbreaks may be generated by stochastic events resulting in synchronous increases in abundance. Studies of outbreak data in six species of forest insect suggest favourable weather conditions may result in synchronous insect outbreaks (Peltonen et al. 2002).

Having detected evidence of CFEs, grouse populations appear to indicate no particular patterns in the dynamics leading into these events. There is no apparent bias towards the number of UI events, as opposed to the number UD events (or vice versa). Population abundance appears equally likely to demonstrate greater than expected increases or declines. Synchrony may therefore be an artefact of synchronous increases in abundance through increased breeding success or adult survival, or synchronous decreases, due to increased mortality rates or breeding failure. Synchrony is thus likely to be maintained through the action of more than one type of population perturbation.

In order for grouse populations to become synchronous, some populations must undergo less probable phase-state shifts. We might for example, expect a population to skip an increasing, or decreasing time step, or alternatively pause for multiple years in an increasing or decreasing time step, in order to become synchronised with surrounding populations. If synchrony is maintained as a result of direct coupling of populations through individual dispersal, we might anticipate that the populations making these less probable state changes might be the smaller populations. The results of our analysis support this hypothesis. The log-likelihood (w^k_i) of the sequence of state changes is positively related to the average grouse bag, such that large populations are more likely to have high values of w^k_i and therefore have progressed through a higher probability series of state changes. This finding would support the hypothesis that smaller grouse populations are asymmetrically influenced by larger neighbours, and could therefore be forced into synchrony with nearby, larger populations.

We detect significant variation in our results between regions. For example, the proportion of time that regions were significantly synchronised varied from 8.22% to 54%, while the average interval between CFEs varied from regions in which either 0 or 1 CFE were detected, to regions in which CFEs occurred every 2-3 years. This might represent inter-regional variation in the strength and evenness of population coupling but it could also reflect variation in data quality. The data set used has been collected over a large number of different moors, with different shooting policies, and management practices. There may also be differences in the quality of data recorded on different estates or over time. It is therefore difficult to assess whether the variation in our results across regions is a function of real regional variation in the dynamics of red grouse populations, or a function of variation in data quality between grouse moor estates within these regions.

In summary, we have revealed that ‘collective forcing events’ coerce the population dynamics of red grouse populations in the United Kingdom into a state of synchrony approximately one in every six years. Without such events, synchrony in red grouse dynamics would fall away within a few years. These coupling events appear to be equally likely to be concomitant with synchronous population increases and synchronous population declines, suggesting a number of processes might be involved in the generation of synchrony. Further studies will attempt to identify these processes by examining potential agents of synchrony, both biotic and abiotic. Identification of such processes may have significant implications for the future management of red grouse populations in the United Kingdom.

4 Drivers of synchrony in red grouse population dynamics

4.1 Abstract

Populations of red grouse (*Lagopus lagopus scoticus*) in the British Isles exhibit unstable dynamics characterised by periodic fluctuations in abundance. There is a significant degree of spatial autocorrelation in the occurrence of these fluctuations between different populations, the causes of which remain poorly understood. Here, we use time-series from 287 populations across the species range and attempt to disentangle the causes of this synchrony by examining the importance of abiotic factors mediated through the Moran effect, and dispersal between populations. Examination of a metric describing the degree of similarity between the autoregressive density-dependent structures of population time-series suggests that they are very homologous in structure, and that climate could potentially synchronise red grouse populations. However, if dispersal plays a significant role in driving synchrony, we would expect pairs of moors separated by the same distance to be more synchronous in areas where grouse moors are likely to be highly connected by routes of dispersal, than in less connected areas where fewer moors are present to serve as intermediate 'stepping-stones'. Our analysis indicates a relationship between the level of synchrony between two moors, and the density of grouse in the surrounding landscape, after we account for the effect of distance. Thus while we cannot rule out a role for abiotic factors in the generation of population synchrony, evidence suggests a role for dispersal in population coupling.

4.2 Introduction

Synchrony in a single species system requires some form of coupling between populations. Spatially correlated abiotic factors, such as climate, could act as a density independent coupling mechanism, and generate synchronous fluctuations in abundance. Specifically, Moran (1953) demonstrated that if populations have the same intrinsic linear density-dependent structure (DDS), the correlation between populations would exactly equal the correlation between environmental perturbations experienced by different populations - the so-called Moran effect. Additional studies have also demonstrated that environmental correlation can also synchronise populations even if the dynamics are non-linear (Engen and Sæther 2005; Royama 2005). The Moran effect has been reported across a range of taxa, including great gerbils (*Rhombomys opimus*) (Kausrud et al. 2007), great (*Parus major*) and blue tits (*Cyanistes caeruleus*) (Saether et al. 2007), and species of freshwater fish (Tedesco and Hugueny 2006).

Alternatively, a wide diversity of theoretical studies have demonstrated that synchrony in population cycles can be induced by biotic factors coupling populations, in particular the dispersal of individuals between populations (Bjørnstad 2001; Liebhold et al. 2004; Ranta et al. 1999). Disentangling the synchronizing effects of shared environmental noise and dispersal has proved to be extremely difficult, the results only truly compelling when one of these processes can be completely excluded. For example, Soay sheep occupying different islands in the St. Kilda archipelago display synchrony in abundance that can only be attributed to the Moran effect, as the sheep are unable to disperse between islands (Grenfell et al. 1998).

Individual populations of red grouse (*Lagopus lagopus scoticus*) in the British Isles exhibit unstable dynamics characterised by periodic fluctuations in population abundance (Haydon et al. 2002; Potts et al. 1984; Watson et al. 1984; Williams 1985). Red grouse are common in areas of moorland habitat in the British uplands, where they have been extensively managed for shooting since the late 19th Century (Hudson 1992). Managed populations of grouse are clearly and discretely defined, and therefore present an ideal species for examining cyclic dynamics and synchrony.

The population dynamics of red grouse have been studied intensively for over 50 years and two broad schools of thought about the drivers of cyclic dynamics have developed. It has been suggested that cyclic fluctuations in red grouse dynamics are a result of infections of the nematode *Trichostrongylus tenuis* (Hudson 1992; Hudson et al. 1998). Red grouse population fluctuations may be generated as the nematode mediates a reduction in female fecundity and increased mortality when grouse are present at high densities. An alternative theory proposes that fluctuations are generated by delayed density-dependent changes in aggression and the rate at which young males are recruited into the population (Moss and Watson 1985; Moss et al. 1996). More recent work has offered a synthesis of these two hypotheses, which suggests increased male aggression under conditions of high grouse density result in increased nematode-induced mortality due to elevated testosterone levels (Mougeot et al. 2005; Redpath et al. 2006).

Red grouse populations exhibit weak positive synchrony in these fluctuations in abundance (Kerlin et al. 2007). A significant spatial correlation exists between the synchrony exhibited by a pair of red grouse populations and intermoor distance, although fitting a cubic model to these data suggest this relationship accounts for only 13.5% of overall variation in pair-wise synchrony (Kerlin et al. 2007). High levels of synchrony are observed in the cyclic fluctuations of grouse populations on closely located sporting estates, where the dispersal of individuals between populations provides a potential coupling mechanism. This synchrony declines sharply as inter-population distances approach 100 kilometres. At distances greater than 100 kilometres, populations still exhibit positive synchrony, but the level of synchrony is extremely weak. While decades of research have investigated the causes of cyclic dynamics in red grouse, surprisingly little attention has been given to the causes of synchrony in these dynamics. Here we attempt to disentangle the importance of abiotic factors such as climatic processes, and biotic factors such as dispersal between populations, in the generation of synchrony.

Moran (1953) suggests that if populations have the same DDS, correlated environmental effects could generate spatially correlated patterns of synchrony. Correlated environmental effects could, for example, impact on insect availability (invertebrates are a common component of chick diet in their first two weeks - Hudson et al. 1985) or grouse chick mortality, and produce correlated changes in grouse abundance across a number of populations. Swanson and Johnson

(Swanson and Johnson 1999) suggest that the DDS of populations synchronised by a Moran effect would have to be relatively homogeneous; a similar DDS is a pre-requisite for shared noise to be a potential mechanism. Just as Soay sheep cannot be synchronized by dispersal (and therefore must be synchronized by correlated noise) (Grenfell et al. 1998), so populations with very different DDS cannot be synchronized by correlated noise. Thus, if the DDS of populations are very different, we could effectively exclude abiotic factors in the generation of synchrony, and conclude that synchrony is generated by dispersal. However, if red grouse populations exhibit similar DDS, we cannot exclude these factors and instead seek positive evidence for a role of dispersal in the generation of the spatially correlated patterns of synchrony observed in red grouse.

Synchrony may be generated and maintained by dispersal. As individuals disperse from regions of high density, they synchronise local dynamics by increasing abundance in adjacent populations (Swanson and Johnson 1999). Previous analyses suggest such populations are expected to exhibit a strong decay in synchrony with increasing distance between populations (Bjørnstad and Bolker 2000; Koenig 1999; Swanson and Johnson 1999), though this pattern may also arise from the action of locally correlated environmental noise (Lindström et al. 1996), or a spatially correlated decline in the degree of similarity in the DDS of grouse populations. If synchrony in red grouse is a product of dispersal, for moors the same distance apart, one would expect high synchrony in areas of high grouse density, in which grouse moors are likely to be highly connected by routes of dispersal, and lower synchrony in areas where moors are further apart, between which dispersal is less likely (Figure 4.1).

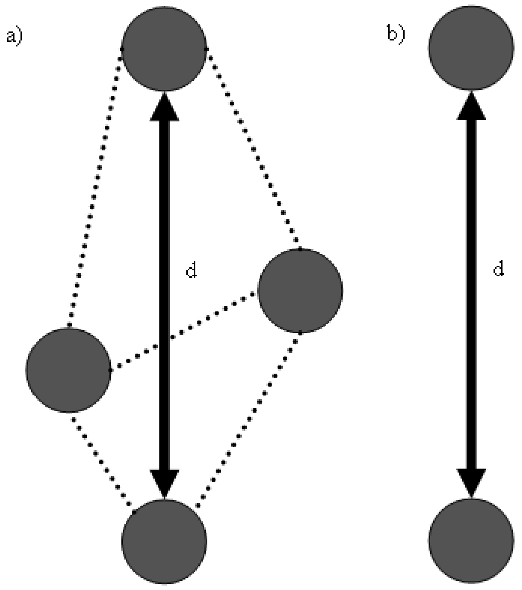

Figure 4.1. Dispersal and synchrony. Consider two pairs of grouse populations (a and b), each separated by a common distance (d). If synchrony was primarily generated by the dispersal of individuals between populations, we would expect that those populations from an area with a greater number of additional grouse moors, and increased connectivity between populations (a) would exhibit a higher level of synchrony than those from an area where moors are isolated (b), due to the increased dispersal between populations (dashed lines).

In this paper, we use a large spatially replicated set of red grouse time-series data and examine the DDS of grouse populations. We then attempt to examine the potential impacts of a Moran effect and dispersal to the generation and maintenance of synchrony in red grouse population dynamics in the United Kingdom.

4.3 Methods

4.3.1 Data treatment and time-series correlations

Time-series data (harvesting records, indexed as the number of grouse shot per year) from 20 regions across England, Wales and Scotland, encompassing 287 moors (Figure 2), were compiled by the Game and Wildlife Conservation Trust. We used these records as an indirect measure of grouse abundance (Cattadori et al. 2003). Records were of variable length, falling within the period 1832-1995. Time-series with less than 32 years of data were excluded from analysis, while those with contiguous gaps of 4 or more years were either split into series of at least 32 years in length (if possible) or excluded from further analysis (if not). Haydon *et al.* (2002) have previously shown that cyclic populations of red grouse exhibit fluctuations with a period of 8-15 years. Therefore time-series of at least 32 years will hypothetically capture at least two population cycles. After splitting and excluding relevant records, analysis was conducted on 304 time-series.

Methods for detrending, normalising and standardising the time-series, and estimation of pairwise cross-correlation coefficients (synchrony), have been discussed previously (Kerlin et al. 2007). In brief, long-term trends in bag data were removed for each time-series by subtracting annual bag records from a cubic smoothing spline. Detrended time-series were normalised through the use of a Box-Cox transformation (Sokal and Rohlf 1995). Data were then standardised by subtracting the mean for the time-series from the detrended value for each year, and dividing the difference by its standard deviation. Finally, a matrix of pairwise Pearson cross-correlation coefficients was estimated using the detrended, normalised and standardised time-series with each time-series compared to every other (where both share at least 30 years of concurrent data). Each cross-correlation coefficient provides a measure of the degree of synchrony between two grouse populations.

4.3.2 The density dependent structure of red grouse population dynamics

For each time-series, multiple regression was used to estimate coefficients for appropriately ordered autoregressive models (Box et al. 1994) of the form:

$$X_t = \sum_{i=1}^{n} a_i X_{t-i} + \varepsilon_t \ ,$$

where *n* defines model order. Royama (1992) does suggest some caution is taken in the use of autoregressive models to describe time-series. Two major problems are identified: overfitting when there is insufficient data, and the biological interpretation of the parameter estimates (Royama 1992). While the biological interpretation of 1st and 2nd order autoregressive parameters can be reasonably deduced (as the relative importance of direct and delayed processes), the interpretation of higher order parameters becomes increasingly difficult. As such, from a biological perspective, AR-3 models are problematic. However, from a statistical perspective, it is difficult to justify the use of AR-2 processes, when AR-3 processes can be shown to provide a significantly better fit. Likelihood ratio tests were used to select between 2nd (AR-2) and 3rd (AR-3) order models as the most appropriate representation of each time-series. The validity of each model was assessed through a visual comparison of the autocorrelation functions of the observed and modelled time-series.

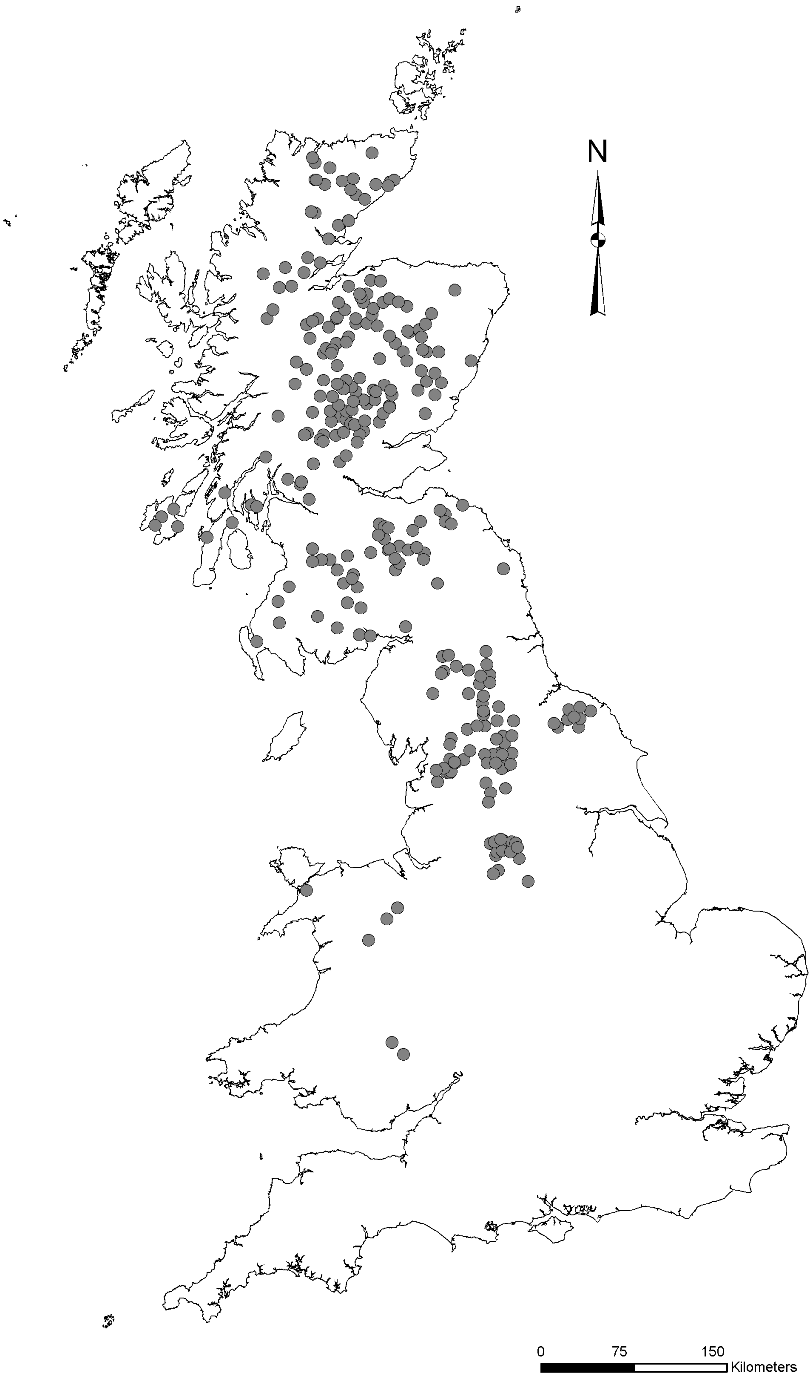

Figure 4.2. Locations of red grouse moors used in this analysis.

Hugueny (2006) has shown that two populations, *x* and *y*, each described by different AR processes will exhibit cross-correlation (r_{xy}) proportional to the correlation of the white noise ($r_{\varepsilon_x \varepsilon_y}$) each process is subject to:

$$r_{xy} = K_{xy} r_{\varepsilon_x \varepsilon_y}$$

The constant of proportionality, K_{xy} is a function of the difference in the autoregressive coefficients. Equations for the calculation of K_{xy} for AR-2 and the derivation of this equation for AR-3 processes are given in Appendix 1.

Examination of K_{xy} for each pair of moors and the relationships between K_{xy}, and intermoor distance and pairwise synchrony are informative regarding the degree to which red grouse population dynamics satisfy the assumptions of the Moran effect. If values of K_{xy} are close to unity, we would expect that the DDS of the respective grouse populations to satisfy the assumptions of the Moran effect. Alternatively, if K_{xy} are close to zero then populations exhibit very different DDS, and cannot be synchronized by correlated noise. A significant decline in K_{xy} with increasing intermoor distance may signify a system in which synchrony is localised to areas where the DDS of populations are similar. Finally, if a Moran effect contributes to synchrony in red grouse, we would expect that as K_{xy} declines, synchrony would also decline (i.e. where populations have similar DDS, correlations in climate result in synchrony, but as the DDS of populations becomes increasingly different, climate can no longer generate synchrony). The significance of these relationships was estimated using Mantel tests (Manly 1997).

4.3.3 Synchrony, dispersal and climate

For each pair of grouse populations, we required a suitable estimate of average density of grouse in the surrounding landscape. To generate such a measure, we used ArcGIS (www.esri.com) to generate line objects connecting the centroids of each pair of moors. We then created a buffer around each of these lines, with a radius of 10km. Warren and Baines (2007), and Hudson (1992) have previously established maximum dispersal distances of male juvenile grouse at 1km, and female juvenile grouse at between 5 and 10km. If dispersal is contributing to the generation of synchrony in red grouse, a 10km buffer is thus likely to capture an appropriate measure of grouse density. For each generated buffer, those grouse moors whose geometric centroid fell within the buffer were recorded, and average annual abundance for each of these moors estimated as average bag count. We summed these averages over all moors whose centroid fell within the buffer and then divided this figure by the total area of the buffer to estimate average overall grouse density in the region between a pair of moors.

We adopted a randomisation technique (to avoid inference problems caused by the pairwise nature of our data) to determine the statistical significance of the relationship between pairwise synchrony and grouse density in the region between each pair. Intermoor distance was included in the model, as Kerlin *et al.* (2007) previously identified a significant spatial correlation between the synchrony exhibited by a pair of red grouse populations and their intermoor distance. As synchrony has been shown to decrease most significantly where intermoor distance <100km, we limited our analysis to those pairs of moors where intermoor distance <100km. A bootstrap randomisation procedure was used to select sets of records, such that each grouse population only appeared in each bootstrapped set of records once. 10,000 iterations were conducted, each producing a randomly generated set of fully discrete pairs of grouse populations. Variation in observed synchrony between these pairs of moors could then be related to local grouse density using a General Linear Model. The distribution of model coefficients across the bootstrap sample allowed determination of the significance of each explanatory variable.

If we satisfy the assumptions regarding the DDS of each population, we can also use this test to examine the nature of the relationship between the synchrony exhibited by pairs of moors, and the degree of correlation in climate. While synchrony in red grouse may be a product of any of a number of climate processes, a previous study (Kerlin et al. 2007) implicated average April temperature, average June temperature, and average June rainfall in the generation of synchronous dynamics in red grouse. These climatic variables were selected as the primary focus of investigation of the importance of abiotic factors. Local weather variables were obtained from 49 UK meteorological office weather stations, averaged from 1960 to 1990. Station data were interpolated to produce a grid of the United Kingdom at a resolution of 1 km from which the focal climate variables were estimated for each moor. For each pair of moors, the absolute difference in each climatic variable was calculated, as an estimate of the differences in climatic experiences between the pair. K_{xy} was also included, as calculated above, to determine whether DDS has an effect on synchrony after accounting for distance. A number of models, incorporating combinations of the explanatory variables (intermoor distance, grouse density, K_{xy}, average April and June temperature, and average June rainfall) were analysed using the bootstrapping procedure described above to determine the explanatory significance of density, K_{xy} and differences in these climate variables.

All analyses were conducted in MatLab Version 7.0.1 (The MathWorks Inc.), and R Version 2.6.2 (www.r-project.org).

4.4 Results

4.4.1 The autoregressive structure of red grouse population dynamics

Likelihood ratio tests revealed that of 304 time-series, an AR-3 model was preferred for 281, whilst an AR-2 model was preferred for only 23 time-series. Values for K_{xy} were calculated for each pairwise combination of moors (where a population described by an AR-2 model was paired with a population described by an AR-3 model, the 3rd order parameter of the AR-2 model was set to 0). 58.13% of K_{xy} values were estimated to be greater than 0.9, while 93.27% of values exceeded 0.7 (Figure 3a). These results suggest that the variability in the deterministic skeletons underlying the dynamics of different populations is generally quite low, and the DDS of red grouse populations was relatively homogeneous.

Grouse populations which share more similar DDS also exhibit more synchronous dynamics (correlation coefficient between K_{xy} and pairwise synchrony = 0.159, $p < 0.001$, Mantel test). This relationship is also found to hold where intermoor distance is less than 100km (correlation coefficient between K_{xy} and pairwise synchrony = 0.155, $p < 0.001$, Figure 3b). A Mantel test to examine the relationship between K_{xy} and intermoor distance suggests there is a significant negative trend (correlation coefficient between K_{xy} and intermoor distance = -0.186, $p<0.001$). However, the pattern of decline is modest in comparison to the reduction in synchrony with increasing intermoor distance (as reported by Kerlin et al. 2007). In particular, while there is a significant negative trend between K_{xy} and intermoor distances less than 100km (correlation coefficient between K_{xy} and intermoor distance = -0.019, p = 0.027, Figure 3c), the corresponding decline in synchrony with intermoor distance follows a much steeper decline (Figure 3d; after Kerlin et al., 2007).

4.4.2 Synchrony, dispersal and climate

A bootstrap randomisation technique was used to examine the significance of grouse density, K_{xy} and climate, in the generation of patterns of synchrony. A number of models were tested, incorporating combinations of the explanatory variables. Intermoor distance was included in the model, to control for the observed decline in synchrony with increasing intermoor distance. Results, including the r^2 value of the model, mean coefficients for each relevant explanatory variable and associated probabilities are reported in Table 5.1.

As expected, intermoor distance had a significant impact on pair-wise synchrony where intermoor distance was less than 150km (for all models examined incorporating distance, $p<0.001$). Grouse density, a measure of the number of grouse in the landscape surrounding a pair of moor, and a qualitative measure of dispersal between the two populations, also exhibited a strong positive relationship with synchrony. Where distance was not included in the model, this relationship was significant (mean coefficient = 4243.7, p=0.03). While the addition of distance to the model reduced the significance of density, p-values associated with estimated density coefficients for all models did provide suggestive evidence of a relationship. This result suggests a degree of co-linearity between intermoor distance and density. Coefficient estimates associated with K_{xy}, April and June temperature, and June rainfall, do not suggest a significant relationship between these variables and synchrony.

If we examine the residual variation explained by each model, we see that intermoor distance accounted for 9.4% of the variation in synchrony. The addition of density to this model including distance provided only minor improvements (1.5%) to the amount of residual variation explained by the model. Inclusion of all explanatory terms produces an r^2 value of only 12.5%, suggesting that the inclusion of density, K_{xy} and the climate variables offer only minimal additional explanatory power to the model, over distance alone.

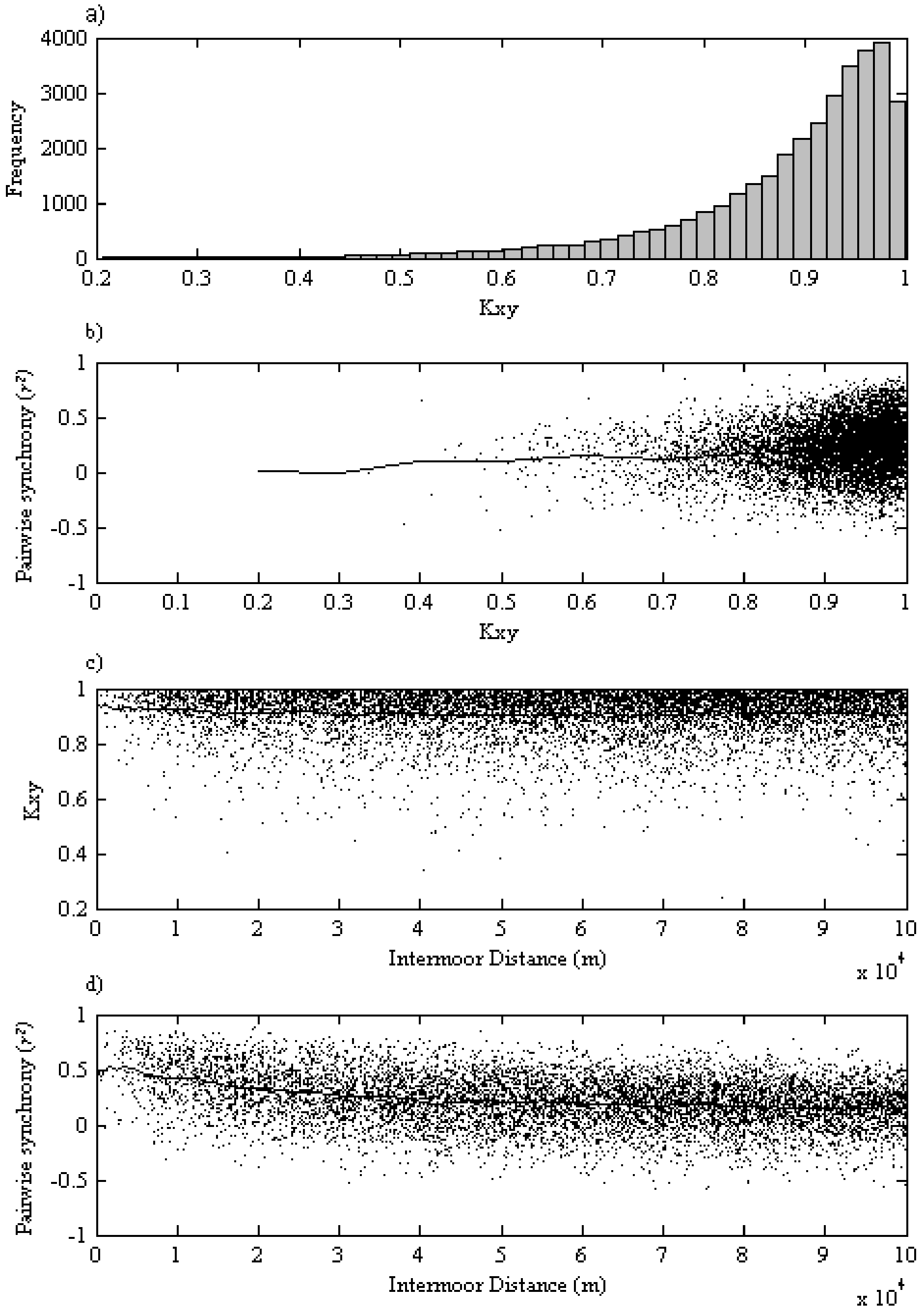

Figure 4.3. K_{xy} as calculated from pairwise comparisons of autoregressive models. The histogram of calculated values of K_{xy} (a) shows that for 93.27% of pairs of moors, K_{xy} is greater than 0.7, suggesting the underlying dynamic structures of these population time-series are relatively similar. We detected a significant increase in synchrony with increased K_{xy} (b – moving average fitted at K_{xy} intervals of 0.1). There is also a significant decline in K_{xy} with increasing intermoor distance to 100km (c – black line indicates moving average, calculated every 2500m), however the corresponding decline in synchrony with intermoor distance follows a much steeper decline (d; after Kerlin et al., 2007).

		Mean coefficient estimates					
Explanatory Variables	Model r^2	Distance	Density	K_{xy}	April Temp	June Temp	June Rainfall
Distance	0.094	-2.64×10^{-6} (p<0.001)	-	-	-	-	-
Density	0.022	-	4243.70 (p=0.03)	-	-	-	-
K_{xy}	0.011	-	-	0.292 (p=0.158)	-	-	-
Distance, Density	0.109	-2.57×10^{-6} (p<0.001)	3285.01 (p=0.102)	-	-	-	-
Distance, Density, K_{xy}	0.119	-2.57×10^{-6} (p<0.001)	3215.19 (p=0.086)	0.252 (p=0.2)	-	-	-
Distance, K_{xy}	0.107	-2.68×10^{-6} (p<0.001)	-	0.276 (p=0.138)	-	-	-
Distance, K_{xy}, Climate	0.110	-2.42×10^{-6} (p<0.001)	-	0.241 (p=0.33)	0.003 (p=0.92)	-0.034 (p=0.636)	-0.001 (p=0.306)
Distance, Density, K_{xy}, Climate	0.125	-2.36×10^{-6} (p<0.001)	3318.14 (p=0.116)	0.212 (p=0.378)	-0.011 (p=0.918)	-0.026 (p=0.712)	-0.001 (p=0.32)

Table 4.1. Randomised regression analysis of variables predicting synchrony in red grouse populations. Each row corresponds to the results of the analysis, as conducted using the listed explanatory variables. Mean r^2 values, and mean coefficient estimates are provided, including p-values as calculated from the distribution of coefficient estimates.

4.5 Discussion

Synchrony in red grouse population dynamics has previously been shown to exhibit a strong negative relationship with increasing intermoor distance (Kerlin et al. 2007). A decline in synchrony as distance between sites increases is typically interpreted as evidence that the cause of synchrony is the dispersal of individuals between populations (Ranta et al. 1995a; Ranta et al. 1995b); however spatial autocorrelations in weather patterns could potentially produce such a pattern (Ranta et al. 1999), as could spatially correlated declines in K_{xy}. In this study, we have attempted to quantify the role of two potential drivers of synchrony, correlated environmental effects (climate) and dispersal.

Moran (1953) previously demonstrated that spatially correlated environmental effects could generate spatially correlated patterns of synchrony. However, the Moran effect only pertains to populations with similar DDS (Hugueny 2006; Moran 1953). We found calculated values of K_{xy} (a metric describing the degree of similarity between the structures of two time-series) to be generally high, suggesting that red grouse populations have similar deterministic skeletons. Such a result suggests that the pre-requisite assumptions of the Moran effect are satisfied, and that therefore we cannot exclude correlated environmental effects as significant drivers of synchrony in red grouse.

K_{xy} is shown to decline with increasing intermoor distance. If abiotic processes such as climate are responsible for synchrony in red grouse, such a decline could explain the strong negative relationship with increasing intermoor distance. As populations are located further apart spatially, the conditions required for a Moran effect are less likely to be present. However, the observed decline in K_{xy} is considerably less marked than the decline reported in synchrony with increasing intermoor distance (Kerlin et al. 2007), thus the magnitude of this effect is by itself insufficient to explain the decline in synchrony between populations. We have also demonstrated a significant relationship between K_{xy} and pairwise synchrony such that as K_{xy} decreases, we observe decreasing synchrony between moors, as predicted by the Moran effect. Such a result would lend support to the hypothesis that abiotic processes may play a significant (but not necessarily exclusive) role in the generation of synchrony.

Previous studies have shown that synchrony can be induced by biotic factors such as the dispersal of individuals between populations (Bjørnstad 2001; Liebhold et al. 2004; Ranta et al. 1999). If dispersal is a key driver of synchrony, we expect that in areas of high grouse density, we would observe increased levels of synchrony between populations, due to the increased probability of individuals moving between populations. In areas of low grouse density, where populations are more isolated, we would not expect synchronous dynamics. Analysis suggests a significant relationship between the density of grouse in the region surrounding a pair of populations and pair-wise synchrony. This result is perhaps surprising, given the low dispersal distances observed in red grouse (Hudson 1992; Warren and Baines 2007); however this may be reflected in the sharp decline in synchrony over intermoor distances less than 100km. With the addition of intermoor distance to the model, the significance of density is reduced, although still suggestive of a trend. Further, intermoor distance and density were not related (mean coefficient = -3.1×10^{-11}, $p=0.32$), indicating density is not merely a surrogate measure of distance. Therefore we can conclude dispersal does play a detectable, if minor, role in generating patterns of synchrony.

Similarly, analysis of K_{xy} and synchrony using Mantel tests provided evidence of a significant decline in synchrony with decreasing K_{xy}. Analysis using the bootstrap randomisation technique does not support this relationship; instead K_{xy} is not considered a significant variable. This is surprising, and may indicate that the use of bootstrapped data may not provide the statistical power required to recognise this relationship. The significance of the three focal climate variables (April temperature, and June temperature and rainfall) on the degree of synchrony in red grouse populations was also explored. Results suggest that differences in the focal climate variables did not appear to be related to the level of synchrony. However, the selection of these three variables is clearly not an exhaustive examination of the potential for climate to synchronise populations. While our results do not suggest these variables have a significant effect on synchrony, there are a number of other variables (e.g. altitude, snow cover etc.) we have not assessed which may be contributing to patterns of synchrony and we cannot exclude the importance of correlated environmental effects in driving synchrony.

If the proportion of residual variation (r^2) explained by each model is considered, we must conclude that, of the variables analysed, intermoor distance is the most important correlate with synchrony. While we have provided evidence suggesting a role for both dispersal and climate as drivers of synchrony in red grouse, their contribution to the proportion of residual variation explained is minimal (2.9% combined, over distance alone). However, it is likely that while grouse density is useful for this analysis (as the effect of density is not confounded with other variables), it may be a poor measure of dispersal between populations, and a more accurate metric could explain more of the residual variation.

We have demonstrated that the DDS of red grouse populations are sufficiently similar to satisfy the pre-requisite conditions for synchrony in population dynamics to be a function of the Moran effect, whereby correlated abiotic processes drive correlations in abundance across populations. We have also established that the density of grouse in the landscape surrounding a pair of grouse moors, is weakly predictive of population synchrony. Our results therefore suggest that both coupling of populations through dispersal, and abiotic correlations in climate, contribute to the generation of synchrony in the population dynamics of red grouse.

5 Impacts of grazing on the population growth rate of meadow pipits: a Bayesian approach

5.1 Abstract

Changes in agricultural management and practices have been implicated in significant declines of upland birds. The meadow pipit (*Anthus pratensis*) is the most common upland passerine in the UK. Previous research has suggested a link between livestock grazing intensity and the breeding density and reproductive performance of meadow pipits. We constructed a Bayesian model of meadow pipit population growth using parameters drawn from the literature and data collected as part of an ongoing grazing field experiment conducted in the uplands of central Scotland. This model was further expanded to examine the effects of four grazing treatments: commercial grazing, reduced grazing, and mixed grazing intensities, and grazing exclusion on meadow pipit population growth. The model suggests that grazing has a significant impact on the demography of meadow pipit populations. Population growth is shown to be higher under commercial or mixed grazing regimes compared to reduced and ungrazed regimes. This result may reflect the importance of grazing as a mechanism to reduce sward height and improve meadow pipit foraging mobility and the accessibility and detectability of prey. These results provide insight into the mechanisms by which grazing practices impact meadow pipit population dynamics, and provide a further note of caution with respect to the significant recent declines in livestock numbers in upland environments.

5.2 Introduction

Grazing management has traditionally been an important driver of land-use change in upland habitats (Bignal and McCracken 1996). Alterations in grazing pressure are implicated in dramatic changes in vegetation structure and declines in the abundance of upland birds (Fuller and Gough 1999; Fuller et al. 2002; Thompson et al. 1995a) , although the mechanisms driving such declines are poorly understood. In particular, livestock numbers in the uplands have been in decline since 1999, with this decline accelerating after reforms to the European Common Agricultural Policy (CAP) resulted in a decoupling of subsidy payments from livestock numbers (Rural Policy Centre2008).

The meadow pipit (*Anthus pratensis*) is the most common upland passerine in the UK and occurs at high density on rough grass and heather moorland (Forrester et al. 2007). The species is an insectivorous, philopatric partial migrant, with individuals migrating from breeding areas in the uplands before winter, and returning to breeding areas in the spring where they establish ground level nests in tussocks of grass, rush or heather (Simms 1992). While some aspects of their population demography are poorly studied, including a number of key demographic parameters, meadow pipits offer a potential indicator species to examine the impacts of grazing management.

The impacts of grazing on biodiversity is the subject of a large-scale field experiment at Glen Finglas in central Scotland, which commenced in 2002. Experimental plots were exposed to one of four grazing regimes, ranging from commercial intensity grazing, to grazing exclusion. The effect of grazing treatment on a variety of biodiversity indicators was assessed. Indicators included vegetation composition, sward height, and corresponding insect (including subterranean), bird and mammal diversity and abundance. Previously published results from this experiment have demonstrated that grazing treatment has a significant impact on the egg size (Evans et al. 2005b), and breeding density (Evans et al. 2006b) of meadow pipits. Additionally, abundance of certain arthropod groups (Dennis et al. 2008) and field voles (Evans et al. 2006a) have been shown to decline with increased grazing intensity.

In this analysis, we apply a Bayesian modelling framework to data from the Glen Finglas experiment to address the following questions:

1) Can we estimate demographic parameters from the Glen Finglas meadow pipit population?

2) Do the various grazing treatments have a significant impact upon the productivity of meadow pipit populations?

5.3 Methods

5.3.1 Data collection

Field studies were conducted at Glen Finglas (56°16’N 4°24’W) in the Loch Lomond and Trossachs National Park in central Scotland. Vegetation consisted of a fine-grain mosaic of mire, rush pasture and grassland communities (for a more detailed description see Dennis et al. 2008). A replicated, randomized block experiment was initiated in 2003, comprising three paired replicate blocks across an altitudinal gradient ranging from 200 to 500 meters above sea level (Figure 5.1, labelled AB, CD and EF). Each replicate contained four plots (plot ~3.3ha) that were randomly allocated to one of four grazing treatments:

1) commercial sheep grazing - nine ewes per plot,

2) reduced sheep grazing - three ewes / plot,

3) mixed grazing - two ewes / plot plus two cows and two suckling calves for four weeks each September, at an equivalent off-take as treatment 2,

4) ungrazed.

Within each plot, meadow pipit breeding territories were mapped using standard ‘Common Birds Census’ techniques restricted to this species (Bibby et al. 2000), with particular attention given to bird breeding behaviour, such as song flight, alarm calls, food carrying and mate guarding. Nests were detected using rope-dragging. Extensive surveys were conducted to ensure all territories within a plot were detected. For the purposes of this study, each plot was assumed to be a single population. The number of breeding territories was used as a surrogate for female breeding abundance. Data were available for the period 2002-2007. As fences were not established until 2003, data from 2002 provide pre-treatment baseline information.

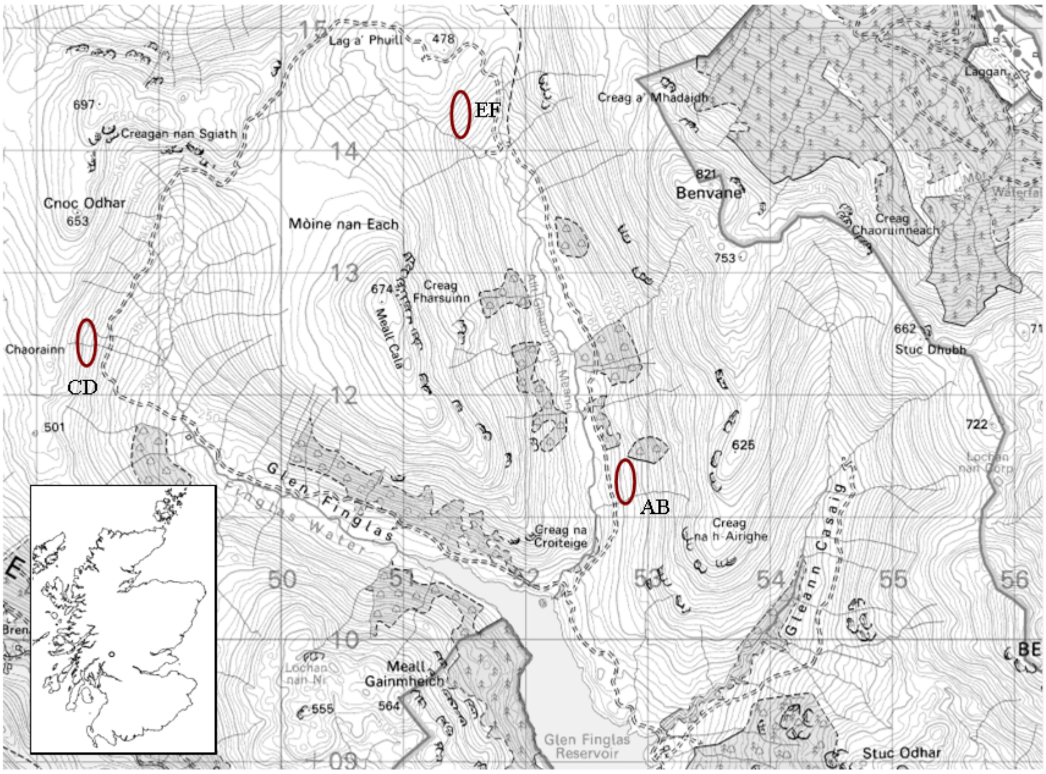

Figure 5.1. Location of Glen Finglas field study site, and three experimental replicates. Grid cells measure 1000m x 1000m.

5.3.2 Model construction

Two models were constructed to describe changes in meadow pipit population abundance. We start with a simple model of population growth:

$$N_{t+1} = N_t \lambda ,$$

where N_t is female breeding abundance at time *t* and λ represents the finite rate of population increase (Gotelli 2001).

We adapted the model to more fully describe the processes affecting changes in the abundance of meadow pipits. Changes in abundance are a product of births and deaths in the population, and emigration into, and immigration out of, the population. Births within the population can be estimated from the number of clutches, number of eggs per clutch, and the probability of an egg producing a successfully fledged juvenile. Emigration is a result of the failure of juveniles and adults to return to the same breeding area each year, and can be estimated by juvenile and adult return rates. Death rates can be estimated as the probability of survival within the population, while immigration depends on surrounding populations. The simple model of population growth can thus be adapted to a more complex form:

$$N_{t+1} = N_t(r_a + efr_j)s + I,$$

where s represents annual survival, r_a adult return rates, r_j new juvenile return rates, e the number of eggs per clutch, and f the probability of an egg producing a successfully fledged juvenile. I represents the number of new individuals immigrating into the population. While meadow pipits typically have two clutches each season, we are in effect modelling only female breeding abundance. As first and second clutch sizes are effectively equal, and assuming the sex ratio of new juveniles is 50:50 we include only one clutch of female juveniles in the final model. For this analysis, we assume no density-dependent factors are limiting population abundance. In particular, we assume the population growth rate is not reduced as abundance approaches a patch carrying capacity (i.e. populations are generally assumed to have a constant, linear growth rate). We also assume the rate of immigration is constant between populations and between years.

5.3.3 Priors

Estimates for a number of demographic parameters were obtained from the scientific literature. The British Trust for Ornithology (www.bto.org) provides a number of demographic parameters for meadow pipits as part of their Birdfacts project (Robinson 2005). Additionally, previous work has been conducted looking explicitly at a number of the demographic parameters in the population of interest (Evans et al. 2005a). From the literature, estimates of survival and fledgling success probabilities, and the number of eggs expected per clutch were identified. The Birdfacts project estimates the annual survival probability of meadow pipits as 0.543, and reports the number of eggs per clutch as 4.28 ± 0.68 (min 2 – max 6). Meanwhile, Evans *et al.* (2005a) reported clutch sizes (first clutch 4.04 ± 0.042, second clutch 4.29 ± 0.146) and the probability of an egg hatching (first clutch 0.616, second clutch 0.466). Distributions to appropriately represent these estimates were constructed to produce prior probability distributions. Where information from two clutches was available, we used simulation to create a distribution of potential parameter values, and then fit an appropriate distribution. In the case of survival and fledgling success probabilities, a beta distribution is assumed, while we model the average eggs/clutch using a gamma distribution.

Difficulties arise with respect to estimation of adult and juvenile return probabilities, and immigration rates. To our knowledge, there have been no studies into these rates and we are unable to parameterise these processes. However, we use expert opinion to inform our prior expectations of these parameter values, and use a Bayesian statistics framework to estimate these parameters. In this instance, we use a beta distribution to model return probabilities, and a truncated normal distribution to model immigration. Expert opinion and anecdotal evidence regarding return probabilities suggests these probabilities should be low, especially for juveniles which are generally expected to return to a completely different breeding site. By fixing the shape parameter a of the beta distribution of juvenile return probabilities to 1, we can produce an exponential type distribution, limited between 0 and 1, which can model this expected outcome.

We use uninformative priors, drawn from appropriate uniform distributions, for the parameters that require estimates: adult and juvenile return probabilities and the immigration rate. Posterior probability distributions for survival and fledgling success probabilities and eggs/clutch are assumed to be equal to the previously constructed prior probability distributions.

5.3.4 Bayesian analysis

Models were fitted using Monte Carlo Markov Chain techniques (MCMC), as implemented within the WinBUGS statistical programming environment (Lunn et al. 2000). Each model was run for 50,000 iterations with 3 chains, after allowing burn-in for 5000. The Gelman-Rubin convergence statistic was calculated within the WinBUGS environment, and this test was used to determine chain convergence.

5.3.5 Impacts of grazing

The impact of grazing was incorporated into the adapted population growth model. Previous research has found no effect of grazing treatment, in the short-term, on fledging success (Evans et al. 2005b). Similarly, estimates of survival and the number of eggs per clutch had been established from a variety of datasets (Evans et al. 2005a; Robinson 2005), ostensibly including birds occupying land under a variety of management regimes. As such, impacts of grazing are likely to be already present in these variables (as increases in parameter variance), and we therefore did not model potential impacts of grazing on these variables. However, grazing may potentially alter the suitability or attractiveness of an area to meadow pipits, resulting in differences in the number of birds returning each spring, or through the immigration of new individuals into the population, thus impacting population abundance and growth. A new categorical variable supplants the immigration rate, allowing for different rates of immigration, dependent on grazing treatment, as follows:

$$N_{t+1} = N_t(r_a + efr_c)s + \begin{bmatrix} g_1 \\ g_2 \\ g_3 \\ g_4 \end{bmatrix},$$

where g_1 represents effects on population change associated with grazing treatment 1 (commercial grazing intensity).

Grazing parameters were given uninformative priors, and models were fitted using WinBUGS as before. Additionally, we fitted models including parameters for year effects, and site effects, as well as interactions. Model comparisons were conducted using Deviance Information Criterion (DIC) after Spiegelhalter (2002). DIC values were used to select the most appropriate models for describing changes in meadow pipit abundance.

5.4 Results

5.4.1 Meadow pipit demographics

All MCMC models were determined to have successfully converged within 10,000 iterations, as calculated values of the Gelman-Rubin convergence statistic were below 1.2 (after Gelman 1996). After analysis of the simple population growth model, an estimated posterior distribution was obtained for λ (Figure 5.2a). The finite rate of population increase was estimated as $\lambda = 1.183$, with 95% credible intervals of 0.589 and 1.778. This distribution describes the range of growth rates observed in the data. Many of the meadow pipit populations exhibited population growth and, as expected, λ is on average greater than 1. However, λ can also take values less than one, which allows this model to describe those populations where abundance has decreased.

DIC comparisons between the simple and complex models indicate a significant preference for the complex model structure ($\Delta DIC = 12.694$). Using the complex model to more fully describe population processes in meadow pipits, we can obtain estimates of adult return probabilities ($r_a = 0.484$, 95% credible intervals 0.129, 0.824), chick return probabilities ($r_c = 0.111$, 95% credible intervals 0, 0.313) and immigration into the population ($I = 2.405$, 95% credible intervals 1.431, 3.26). Posterior probability distributions are displayed in Figure 5.2 (b-d). These estimates reflect the most likely combination of parameters that describe the dynamics of meadow pipit populations. The prior probability distributions used in the Bayesian analysis allowed each of these parameters to potentially take a value of zero, but it appears such a solution has a low likelihood. Further, estimates of adult return rates show considerable uncertainty. This likely reflects an inability within the modelling process to discriminate between the effects of adult returns and new immigration into the populations. Also, estimates of chick return rates are low; this is largely a consequence of the decision, based upon expert opinion, to model this parameter as an exponential type distribution.

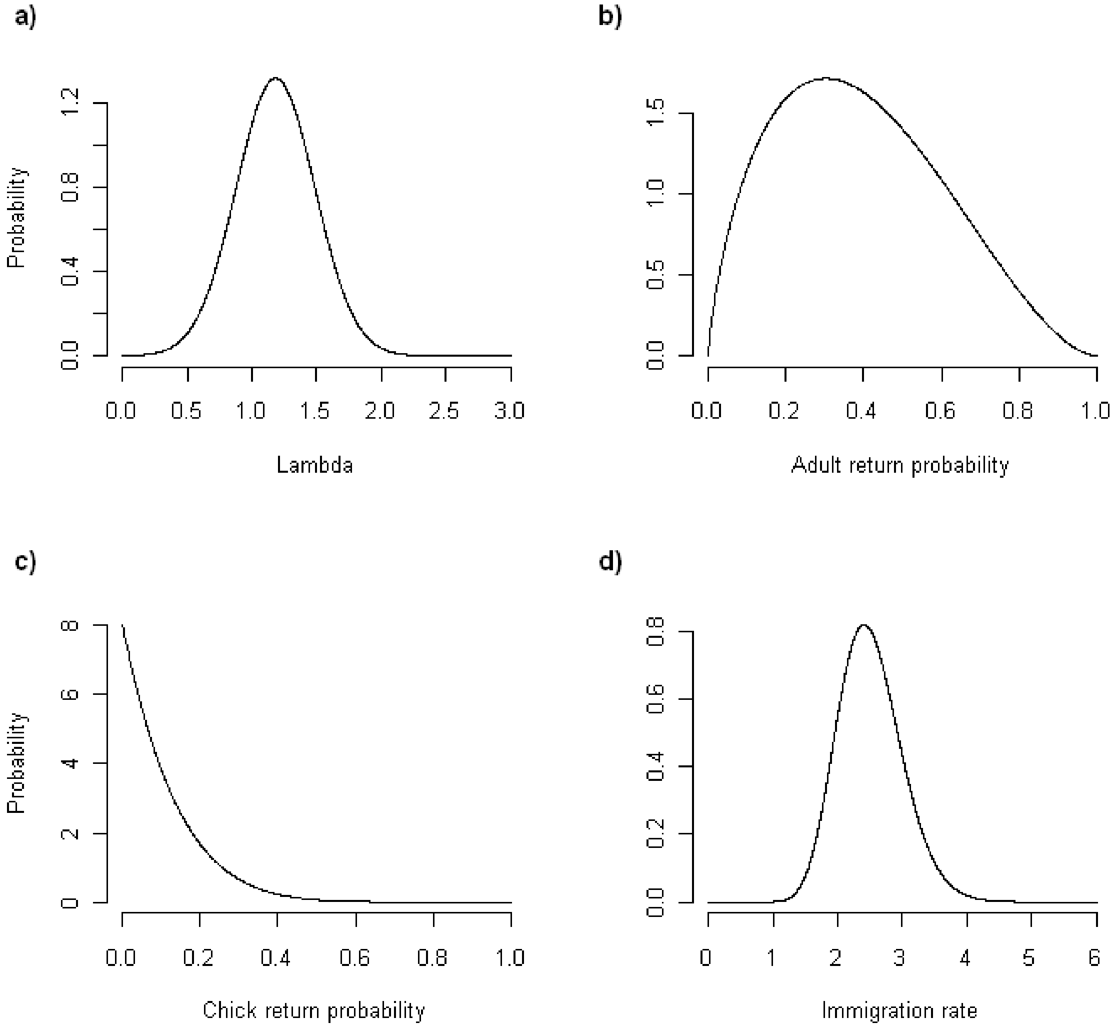

Figure 5.2. Posterior probability density functions for a) lambda, b) adult return probabilities, c) juvenile return probabilities and d) immigration rate.

5.4.2 Impacts of grazing

When differences in grazing treatment are incorporated into the model, variation in the different posterior density distributions is apparent (Figure 5.3). Median immigration rates for the commercial and mixed grazing treatments (3.225 and 3.337 respectively) are greater than for the reduced and ungrazed treatments (2.582 and 2.762 respectively). Thus it appears meadow pipit population growth (particularly with respect to immigration) is greatest in areas of commercial intensity grazing and mixed (sheep and cattle) grazing, and lowest under reduced sheep grazing regimes and ungrazed management strategies.

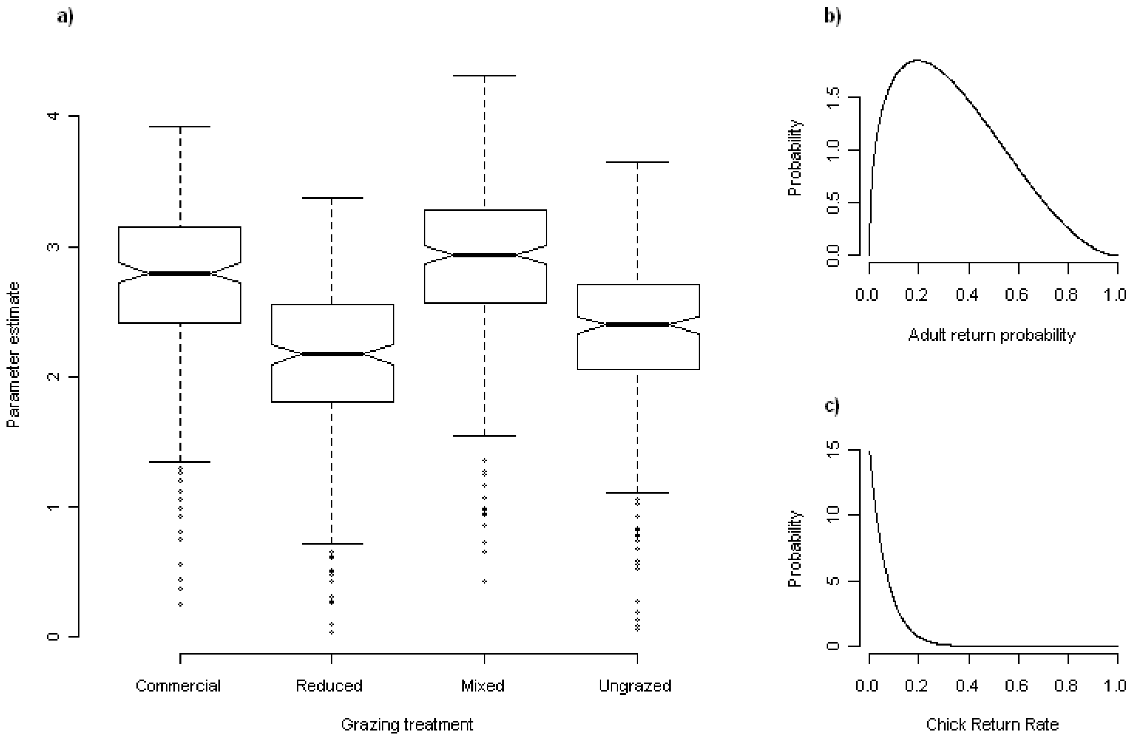

Figure 5.3. Posterior probability distributions (PPDs) for grazing parameters. Differences are detected between the median parameter values for the commercial and mixed grazing treatments compared to the reduced and ungrazed treatments, though the PPDs do appear to overlap (a). (b) and (c) are the recalculated posterior probability density functions for adult and chick return probabilities. Adult return probabilities show a marked difference, with a decrease in average return probabilities.

To determine the significance of these parameter differences, DIC values were calculated and compared. The base model, which contains no information pertaining to grazing management, site or year, has a calculated DIC value of 433.009. Other calculated DIC values are presented in Table 5.1. Preferred models have lower DIC values. However, differences of less than 2 were not considered significant, while differences greater than 5 were considered strong evidence of significant differences in the models under comparison. DIC values suggest that the inclusion of a grazing management parameter confers significant improvements to the explanatory power of the model compared to one that does not consider grazing impacts (ΔDIC = 12.231). Grazing management appears therefore to contribute to significant differences in meadow pipit population growth.

Model	DIC
Base model	433.009
Base model + grazing	420.778
Base model + site	419.031
Base model + year	423.992
Base model + grazing + site	419.219
Base model + grazing * site	428.932
Base model + grazing * site * year	493.981

Table 5.1. Bayesian Model comparisons. The base meadow pipit population growth model ($N_{t+1} = N_t(r_a + efr_j)s + I$**) is compared with models incorporating differences in grazing treatment, site and year.**

Models incorporating site and year effects were also examined (Table 5.1). In addition to grazing treatment, the inclusion of site significantly improves model fit. Results show that site EF exhibits greater population growth than site AB, with site CD showing the lowest population growth (Figure 5.4a). Analyses suggest year effects are less important (Figure 5.4b). While the site model appears to be a better fit to the data than the grazing model, the difference in DIC is only 1.747. Thus the site model can not be considered significantly better than the grazing model, and vice versa. Stepwise examination of the range of potential models (constructed using various combinations of grazing treatment, site and year) reveals that the three best models for describing changes in pipit abundance are the grazing model, the site model, and the model including both of these factors with no interaction.

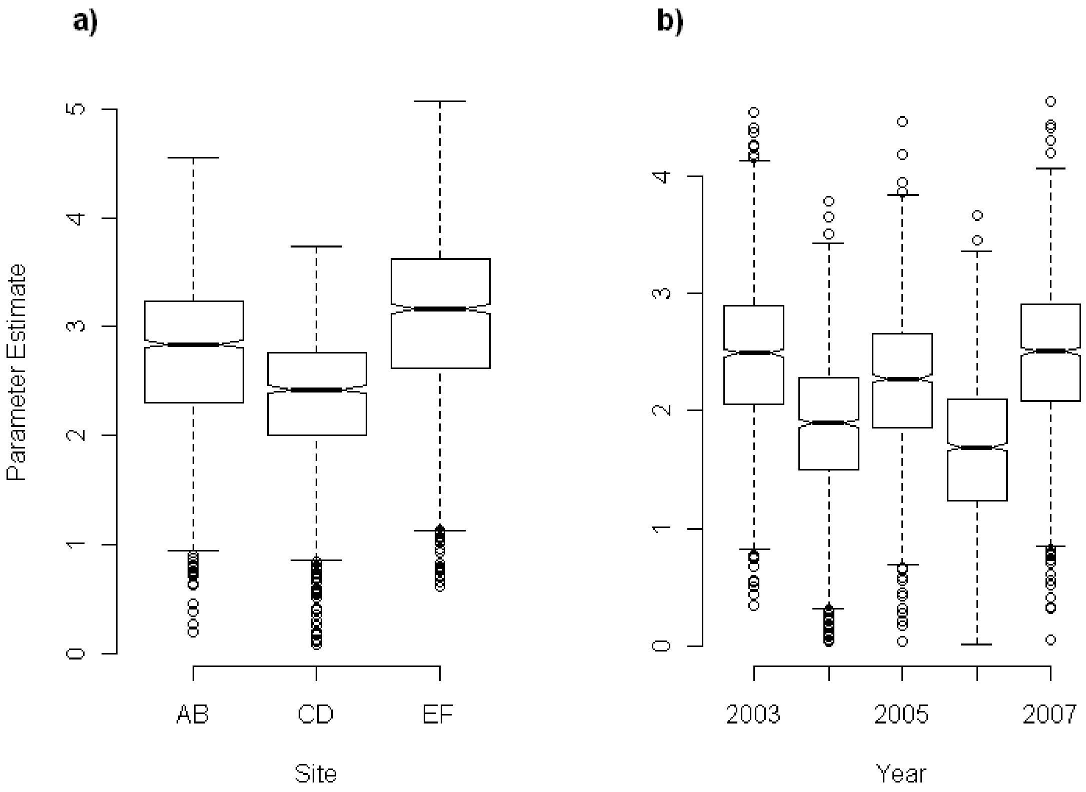

Figure 5.4. Posterior probability distributions for a) site and b) year. Site EF shows a higher median parameter value than sites AB and CD, although the PPDs show marked overlap. Differences in parameter values for year are also apparent, however, DIC analysis suggests year is not a significant parameter.

5.5 Discussion

This study utilized a Bayesian approach to create models of meadow pipit population dynamics. A Bayesian modelling framework was preferred to a standard frequentist approach, as it allowed the estimation of a number of key demographic parameters (which had not been previously reported in the scientific literature), and provided a means to explicitly assess the uncertainty in parameter estimates. The generated models further allowed us to evaluate the effect of grazing management regimes on the dynamics of meadow pipit populations, which was found to significantly affect population growth.

Estimates of the finite rate of population increase (λ) suggest meadow pipit populations in Glen Finglas are, on average, increasing in abundance, although some populations do show decreases in abundance during particular years. Additionally, adult return probabilities, chick return probabilities and immigration rates indicate that these meadow pipit populations maintain a healthy exchange of individuals between locations, supporting established expert opinion that suggests high levels of emigration out of populations and into other areas. Admittedly, our results are not based on direct experimentation. Instead, we have used Bayesian methods to estimate probability density functions for these parameters using maximum likelihood, given the data currently available. These estimates are also reliant upon the accuracy of the estimates obtained for the survival and fledgling success probabilities, and the number of eggs expected per clutch from Robinson (2005) and Evans *et al.* (2005a). The method does however illustrate the power of Bayesian analysis in allowing not just the estimation of these parameters, but also in quantifying the uncertainty in our results.

The model revealed differences in parameter estimates for different grazing regime treatments. DIC values suggest the inclusion of these management differences into the model significantly improve its predictive power, and therefore imply a significant effect of grazing on meadow pipit demographics. In particular, there was a marked difference in median parameter values for the commercial and mixed grazing treatments, versus the reduced grazing and ungrazed treatments. This pattern is not consistent with previous work from the Glen Finglas project (Evans et al. 2005b; Evans et al. 2006b), which concluded that commercial grazing intensities were not favourable to meadow pipit populations. However, our study was based on a larger data set, including several additional years of data. In addition, the use of a Bayesian methodology allowed exploration of the mechanics of meadow pipit population growth, and as such, may reveal differences these previous studies did not detect. While the result was not consistent with previous work from Scotland, a similar grazing experiment in Norway produced similar results; the density of avifauna was higher at high sheep density compared with low sheep density or ungrazed treatments by the fourth year of the treatment (Loe et al. 2007).

Meadow pipits are generalist insectivores and feed on a wide range of invertebrates (Cramp 1988; Walton 1979). Ungrazed areas are often avoided by invertebrate feeders (Vickery et al. 2001), as the increased sward height can restrict forager mobility (Devereux et al. 2004) and reduce the accessibility and detectability of food items (Butler and Gillings 2004). Previous studies have shown that adult meadow pipits exhibit similar preferences; pipits predominantly forage on the ground (Simms 1992), and select foraging sites with low vegetation height and density (Douglas et al. 2008). This pattern is reflected in our results. Population growth is highest under the commercial and mixed grazing treatments (where we expect greater access to forage), and lowest in the reduced grazing and ungrazed treatments. Mixed grazing (i.e. the inclusion of cattle) has been shown to significantly increase heterogeneity in the structure of vegetation, as cattle graze more generally, and less selectively than sheep (Dennis et al. 2008). Thus it is likely that commercial and mixed grazing management results in a reduced sward height and density, which may confer benefits to meadow pipits in the form of increased prey accessibility and detectability.

Alternatively, abundance of certain arthropod groups has been shown to decline with increased grazing intensity (Dennis et al. 2008). Thus grassland areas subject to increased grazing intensities may present a trade-off between food abundance and food availability. However, it is also accepted that cattle grazing may result in increased abundance of insects that are attracted to dung (McCracken and Foster 1994). Further, increased grazing, in particular the addition of cattle to a site, might present difficulties in terms of nest viability. The addition of livestock may increase the probability a nest is damaged by trampling (Paine et al. 1996). Ultimately, there are a number of hypotheses that could explain elevated population growth in areas with commercial or mixed grazing intensities. Further work is required to test these varied hypotheses.

The grazing model was modified to examine the effects of site (i.e. location of the specific study area). The inclusion of site produced similar DIC values to the grazing model. This would imply this variable also has a significant contribution to meadow pipit population growth. Site location may be a proxy for a range of potential variables, such as altitude, local climate and vegetation composition. These results indicate that a universal approach to livestock management throughout the uplands is unsuitable and that a site-specific approach which takes account of environmental ‘variables’ is required to maximise biodiversity.

Bayesian analysis techniques provide a powerful tool for modelling demographic processes in meadow pipits. We have used these techniques to infer a number of key demographic parameters that were not previously reported in the literature, and to quantify uncertainty in these parameters. The production of these estimates may assist in the creation of further models of population dynamics, while these techniques could be applied to create parameterised models for other species of interest. Further work could also incorporate other initial model structures, and additional co-variates including various environmental factors. In particular, examination of alternate models which include density dependent population limitation could provide more accurate results, and may also allow estimation of the carrying capacity of upland habitats under alternative grazing management regimes.

We have also used Bayesian techniques to analyse the impact of grazing management regimes on productivity in meadow pipit populations. Commercial and mixed grazing regimes appear to have beneficial impacts, perhaps resulting from reduced vegetation height, which may in turn allow increased access to prey items.

Reform of the Common Agricultural Policy within the European Union has resulted in a dramatic fall in the numbers of sheep and cattle in upland areas in recent years (Rural Policy Centre 2008). While one significant driver of CAP reform was an increased recognition of the need to protect the environment (Brown and Bainbridge 1995), these results (and a number of other studies) suggest grazing may play a significant role in the maintenance of upland grassland ecosystems. As such, the recent reduction in livestock numbers may produce unexpected changes in the abundance of upland wildlife. While reduced grazing intensities are sure to be beneficial to species such as the field vole (Evans et al. 2006a), other species may not respond favourably to a reduction of pastoralism in upland areas. This may have unanticipated consequences for the conservation of these regions.

6 Spatially explicit population viability modelling of capercaillie in Scotland

6.1 Abstract

Population viability analysis (PVA) is one of a number of methods developed to assess the status of species, and quantify extinction risk. We develop a PVA model to examine the status of populations of capercaillie (*Tetrao urogallus*), a species of grouse listed as a priority conservation species in the United Kingdom. An age-structured matrix population model was parameterised using demographic information reported in the scientific literature. Spatial data, detailing the location of patches of ancient woodland in Scotland, was used to define the size and location of potential populations, and to model processes of dispersal between patches. A spatially explicit PVA model was constructed to examine changes in female capercaillie abundance across Scotland, for a period of 30 years. Elasticity analysis conducted on the matrix population model suggests adult survival is the most important demographic determinant of future capercaillie viability. Models do not predict extinctions in Scotland within 30 years; female capercaillie abundance is envisaged to increase from a mean of 1229 to a mean of 3625. Both patch area and the maximum observed abundance in a patch are negatively correlated with population extinction risk. Populations occupying large patches, and well established populations with greater than 9 individuals, are less likely to go extinct. These results illustrate the considerable power of these methods, and may have important implications for future species management and habitat restoration activities.

6.2 Introduction

The earth is currently in the midst of a global extinction crisis (Pimm et al. 1995; Purvis et al. 2000). Current rates of species extinction are 1000-10,000 times higher than the background rate inferred from fossil records; two to five species are lost per hour from tropical forests alone (Singh 2002). The magnitude of this reduction in biodiversity has resulted in the creation of new methods to monitor species of conservation interest and to assess extinction risk.

Population viability analysis (PVA) is one of a number of methods developed to assess the status of species and quantify extinction risk. PVA models can also be used to address a range of additional questions concerning the conservation status and management of a given species (Morris and Doak 2002). Types of models include count-based PVAs, which ignore the age structure of the population, demographic PVAs, which include the effects of demographic differences in age classes in population change, and spatially-explicit PVAs, which also model the exchange of individuals between populations (Morris and Doak 2002). Examples of PVAs range from models developed to assess extinction risk and minimum viable population sizes of Grizzly bears (*Ursus arctos horribilis*) in Yellowstone National Park (Mann and Plummer 1999), to models examining the dynamics and viability of a marsh fritillary butterfly (*Euphydryas aurinia*) metapopulation in Belgium (Schtickzelle et al. 2005). While these methods cannot deal with unanticipated scenarios, they fulfil a crucial role in endangered species management by providing a quantitative framework to: a) test and compare potential options for species management, b) determine the minimum population size require for viable reintroduction programs, and c) examine the impacts of habitat loss or changes to habitat reserves (Morris and Doak 2002).

The Western capercaillie (*Tetrao urogallus*) was historically distributed throughout climax boreal conifer forests across Europe and Asia (Tapper 1992). Large scale deforestation and hunting pressure led to the extinction of the capercaillie in the United Kingdom in approximately 1785. Attempts to reintroduce the species back into the UK, from populations in Sweden, were successful in the 1830's (Watson and Moss 2008). With this reintroduction, and subsequent supplementary releases, the population re-established itself over a large range. Post-war demand for timber resulted in capercaillie becoming increasingly regarded as a pest species of pine plantations, while the species also grew increasingly popular with the game shooting fraternity. By 1990, the combined effects of a loss of habitat to forestry, and increasing adult mortality associated with shooting and collisions with forest fences, had resulted in obvious declines in abundance. In more recent times however, conservation efforts appear to have slowed, or even marginally reversed, these declines. In a survey in 1998-1999, total abundance of capercaillie was estimated at 1073 birds (95% confidence intervals 549–2041) (Wilkinson et al. 2002). By 2002-2003, abundance appeared to have improved significantly, to 1980 individuals (95% confidence intervals 1284–2758) (Eaton et al. 2007). However, despite these increases, capercaillie remains a species of conservation interest, and is currently listed under Annex 1 of the European Directive for the conservation of wild birds (79/409/EEC).

The priority conservation status of capercaillie in the United Kingdom makes the species an ideal candidate for PVA modelling. A number of studies have been published which provide information pertaining to a range of key demographic parameters (Eaton et al. 2007; Moss et al. 2006; Moss et al. 2000; Petty 2000). Additionally, the species has a historic range that is closely associated with the distribution of patches of ancient Scots pine (*Pinus sylvestris*) and blaeberry (*Vaccinium myrtillus*) (Avery and Leslie 1990; Tapper 1992); conifer needles provide a crucial source of food during winter (Watson and Moss 2008). Therefore, forest maps of the distribution of ancient Caledonian pine woodland in Scotland can be utilised to create a patch map for modelling processes of dispersal and recruitment and resulting metapopulation dynamics.

In this paper, we construct a spatially-explicit, individually-based PVA model of capercaillie to assess the future status of this species in Scotland. The model was used to address the following questions:

1) What is the predicted probability of extinction of capercaillie within the next 30 years?

2) What is the expected future distribution of capercaillie throughout Scotland?

3) Which patch characteristics determine the probability of local extinction events?

6.3 Methods

6.3.1 *The matrix population model*

An age-structured matrix population model was created to predict changes in capercaillie population abundance within each patch. We model female abundance as a measure of changes in the total population. This model took the form:

$$\begin{bmatrix} j_t \\ a_t \end{bmatrix} = \begin{bmatrix} 0 & rf\gamma \\ s_j & s_a \end{bmatrix} \begin{bmatrix} j_{t-1} \\ a_{t-1} \end{bmatrix},$$

where j_t and a_t represent juvenile and adult population abundance at time t. Changes in abundance are modelled as a function of juvenile survival (s_j), adult survival (s_a), and adult fecundity, which is comprised of three further variables, describing the probability of a hen reproducing (r), fecundity (i.e. chicks per breeding female - f) and the sex ratio of the offspring (γ). Individual parameters were modelled as probability distributions created by fitting appropriate distributions to data acquired from the literature (Table 6.1). We restricted our analysis to only encompass information pertaining to Scottish studies. Probability distributions were fitted which reflected these reported estimates for each variable. Parameter estimates were sampled from these distributions for each patch in each year; uncertainty in these estimates reflects the stochasticity inherent in demographic processes.

The matrix population model was examined to recover estimates for the dominant eigenvalue, the intrinsic population growth rate (λ). Additionally, elasticity analysis (Heppell et al. 2000, de Kroon et al. 1986) was performed to identify which of the three main components of the matrix (juvenile survival, adult survival and adult fecundity) had the greatest importance on the dominant eigenvalue. Elasticity analysis quantifies the relative importance of life-cycle transitions on the growth rate of a population, and thus which component has the greatest impact on determining future survival of the population (Caswell 1978). It is generally inferred that conservation management should focus on those life-cycle stages with the greatest elasticities (de Kroon et al. 2000).

6.3.2 The population viability analysis model

To model future changes in the abundance of capercaillie we utilised this matrix population model, and constructed a spatially explicitly model to monitor population dynamics at the patch level. 100 iterations of the model were used to provide an estimate of changes in capercaillie abundance across 30 years. 30 years was selected with reference to the 2001 IUCN Red List criteria, which suggest a species with an extinction probability of at least 20% within 20 years should be listed as endangered (www.iucnredlist.org). Additional iterations would improve the precision of our results, however computational time constraints limited the number of iterations we were capable of completing.

Due to the historic association between capercaillie and Scots pine, it was assumed populations of breeding capercaillie were restricted to these woodland patches. Spatial mapping, detailing the location of patches of ancient woodland in Scotland, was available from the Forestry Commission Scotland website (www.forestry.gov.uk/scotland). Scale and accuracy of this data was sufficiently high to form the basis of our dispersal model. This mapping was used to define our patches. Mapped polygons of ancient woodland were enclosed in a 100 meter buffer. Where buffers overlapped, these polygons were merged together. This process generated a more realistic estimate of patch size - a number of small fragmented patches may not support a capercaillie population alone, but if sufficiently closely located, the total area may be sufficient.

Current estimates of capercaillie abundance have been previously reported from a distance sampling survey conducted in 2003-2004 (Eaton et al. 2007). The population estimate reported was 1980 individuals, with 95% CIs of 1284-2758. We used a gamma distribution to reflect the mild asymmetry in this estimate to produce initial estimates of abundance (Table 6.1). These were converted to estimates of female abundance, using a Normal distribution describing the observed sex ratio (Table 6.1). This survey also reported data suggesting the current geographic distribution of the species.

Five metapopulation areas were defined from the survey results (capercaillie isolated on islands in Loch Lomond were excluded from this study). To initialise the model, at the start of every iteration, a randomly generated initial estimate of abundance was drawn from the distribution of initial estimates of abundance.

These individuals were distributed between patches in these metapopulation areas, on the basis of patch size (i.e. larger patches were assumed to hold larger populations). The initial population was divided by the total area of the metapopulation areas to produce a figure for birds/ha. This figure was then multiplied by the area of each metapopulation patch to determine the initial population for that patch. The stable age structure of the population was derived from the eigenvectors associated with the dominant eigenvalue of the matrix population model. Individuals were divided between adult and juvenile age-classes on the basis of this stable age structure.

Patch carrying capacity was estimated based on reported densities of capercaillie from a range of studies (as collated by Petty 2000) which reported mean densities of birds per 100ha. Focusing on reported densities (limited to areas of native pinewood) we took 10,000 randomised bootstrap samples (with replacement) of eleven reported mean density estimates. Each sample of estimated densities was fitted with a gamma probability distribution, and the 95th percentile of the function was recorded. The carrying capacity (i.e. maximum density in birds/ha) of the sample was taken as the 95th percentile of the fitted gamma distribution. After 10,000 samples, a distribution of expected maximum densities was constructed (Figure 6.1). Carrying capacity for each patch was randomly determined at the start of each model run by sampling from this distribution, and used to determine the number of available (unoccupied) territories within each patch. Further model simulations were conducted, using the 75th percentile of the fitted gamma distribution as the carrying capacity of the population. Such a change was not observed to have a profound effect on the results presented here, though insufficient iterations were conducted to confirm this.

Each generation of the model initially required a recalculation of the current population of a patch, using the matrix population model. Adults from the updated population were permitted to remain in their current patch, as established adults generally remain resident (Watson and Moss 2008). While irruptions (in which individuals gather in large groups and travel long distances) are reported, they are thought to be rare and we have excluded these events from the model. Juvenile birds were allowed to move between patches, according to predefined dispersal kernels. The juvenile dispersal kernel was based on the results of tracking radio-

Model variable	Distribution	Distribution parameters	Sources
Juvenile survival	Normal	$\mu = 0.5$, $\sigma = 0.08$	Moss *et al.*, 2000
Adult survival	Normal	$\mu = 0.72$, $\sigma = 0.06$	Moss *et al.*, 2000
Fecundity	Normal	$\mu = 0.96$, $\sigma = 0.16$	Moss *et al.*, 2000; Eaton *et al.*, 2007
Probability of reproducing	Uniform	Min = 0.6, Max = 1	Moss *et al.*, 2006
Sex ration of offspring	Normal	$\mu = 0.55$, $\sigma = 0.02$	Moss *et al.*, 2000; Eaton *et al.*, 2007
Initial population size	Gamma	Shape =30.93, Rate =0.02	Eaton *et al.*, 2007
Birds/ha	Derived	See Figure 6.1	Petty, 2000
Dispersal distances	Weibull	Shape = 13.49, Scale = 1.79	Moss *et al.*, 2006; Petty, 2000

Table 6.1. Probability distributions and parameters used to model capercaillie demographic variables. Distributions were fitted using reported estimates from the sources listed.

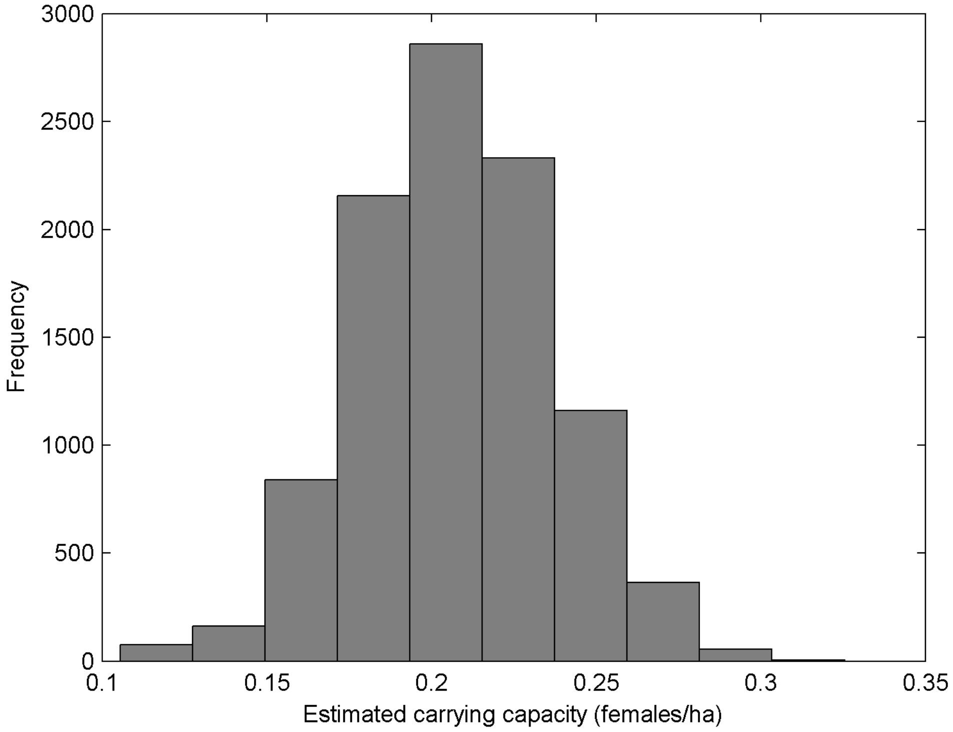

Figure 6.1. Estimated patch carrying capacity. Patch carrying capacity was estimated using a bootstrapped distribution of expected maximum densities, derived from previously reported estimates of capercaillie density (as collated by Petty 2000).

tagged first year hens (Moss et al. 2006). Median dispersal was reportedly 11km, while maximum recorded dispersal was 30km. Using these figures, we generated a Weibull distribution to describe juvenile dispersal distances (Table 6.1). Each dispersing juvenile would require a draw from this distribution. The result of this draw defined maximum dispersal distance. The juvenile would then disperse to the most distant patch with an available territory, within this maximum dispersal distance. If no available territory was found within the maximum dispersal distance, the juvenile was assumed to have died.

For each iteration, the total capercaillie population was recorded for each time-step. We also recorded changes in the occupancy of patches throughout the duration of the model. Model estimates of the total population across thirty years of simulation provided information regarding estimated population growth and the potential extinction risk for capercaillie. We used patch occupancy information to infer the rate of spread of capercaillie through woodland patches in Scotland. The probability of extinction for each patch was determined from the number of extinction events in a patch as a function of the number of years the patch was occupied. Spearman rank correlation tests were used to describe the relationships between characteristics of a patch (patch size and maximum population abundance), and the probability of extinction within a patch.

6.4 Results

6.4.1 The matrix population model

Examination of the matrix population model reveals a mean value of λ = 1.00 (95% CI 0.96, 1.14; Figure 6.2a). Asymmetry in the 95% CIs suggests a tendency for increases in population abundance. Elasticity analysis indicates that population growth rate is most sensitive to adult survival (Figure 6.2b); growth rate is less sensitive to juvenile survival and adult fecundity.

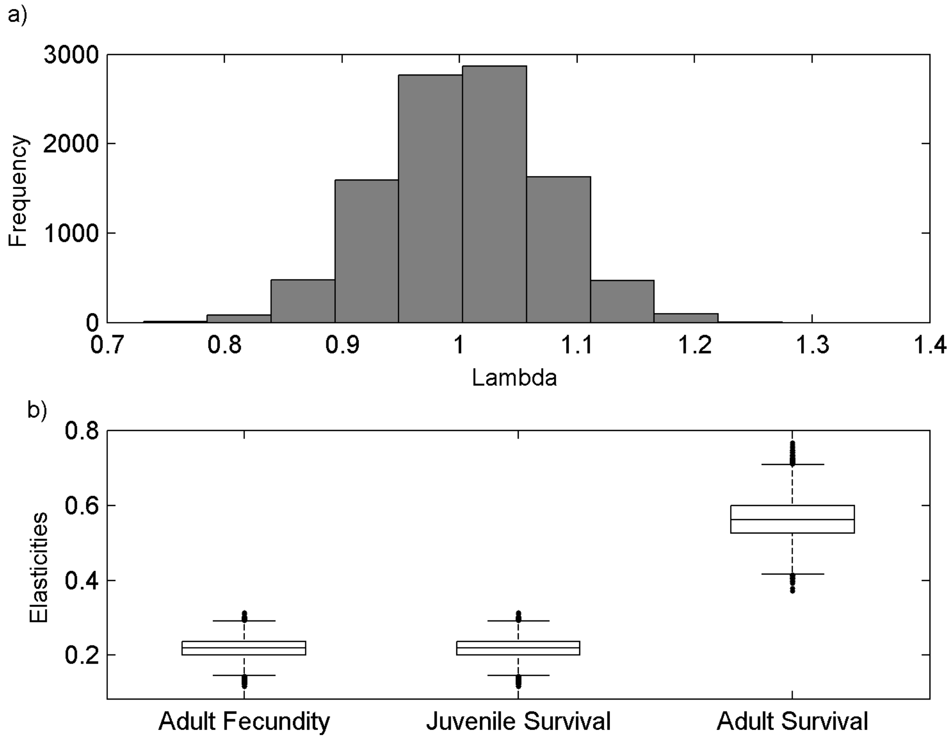

Figure 6.2. Analysis of the matrix population model: a) simulated values of lambda, b) elasticities associated with each of the matrix model components.

6.4.2 The population viability analysis model

Changes in female capercaillie abundance were estimated across the thirty years encompassed by the model (Figure 6.3). Initially, the model suggests populations will remain relatively constant. No significant increases are apparent for the first 15 years (the lower 95% CI does not exceed the average initial starting point until this time). However, over the thirty years the model was evaluated, populations of female capercaillie show substantial evidence of increases in abundance (Figure 6.4). From a mean abundance at year 0 of 1229, abundance of females is estimated to increase to a mean of 3625. Additionally, the model suggests an extinction probability of <0.01. No iterations of the model resulted in a loss of capercaillie from Scotland.

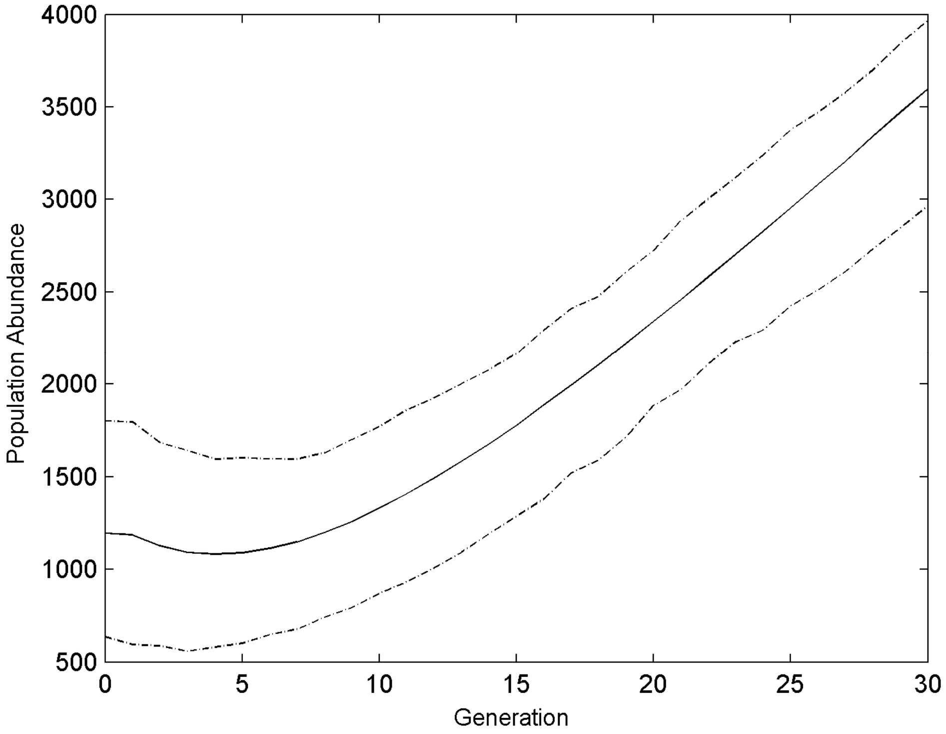

Figure 6.3. Modelled changes in total female capercaillie abundance over 30 generations. Bold line and dashed lines, represent the 2nd and 98th ranked values respectively.

The occupancy rate of each patch was calculated, based on the number of iterations of the simulation for which the patch was occupied after thirty years. These probabilities were used to generate an interpolated map displaying patterns of dispersal of capercaillie (Figure 6.5). Patterns of occupancy suggest capercaillie disperse equally in all directions, but the probability of dispersing individuals successfully colonising new patches rapidly diminishes with increasing dispersal distance. Highest occupancy probabilities (indicated by dark areas in Figure 6.5) are expected to remain clustered around the initial metapopulation areas, with unoccupied patches located between initially occupied patches exhibiting high occupancy. At distances of greater than 30km (maximum juvenile dispersal distances) the probability of occupancy after 30 years diminishes.

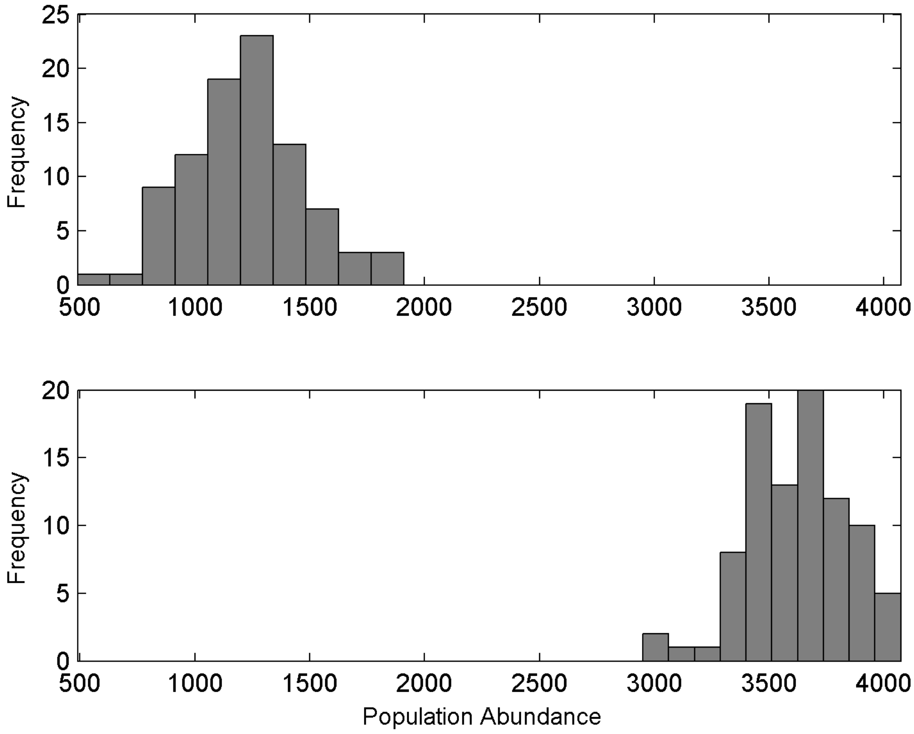

Figure 6.4. Histograms of a) Initial estimates of female population abundance, and b) Final estimates of female population abundance.

Examination of patch occupancy information was used to quantify the frequency of extinction in each patch. There is a significant negative relationship between the probability of extinction and patch area (Spearman's rank correlation coefficient = -0.443, p=0.002; Figure 6.6a.). Populations of capercaillie in small patches are more likely to go extinct than those in large patches. We detect a similar negative relationship between the maximum recorded abundance within a patch, and extinction risk (Spearman's rank correlation coefficient = -0.834, p<0.001; Figure 6.6b).

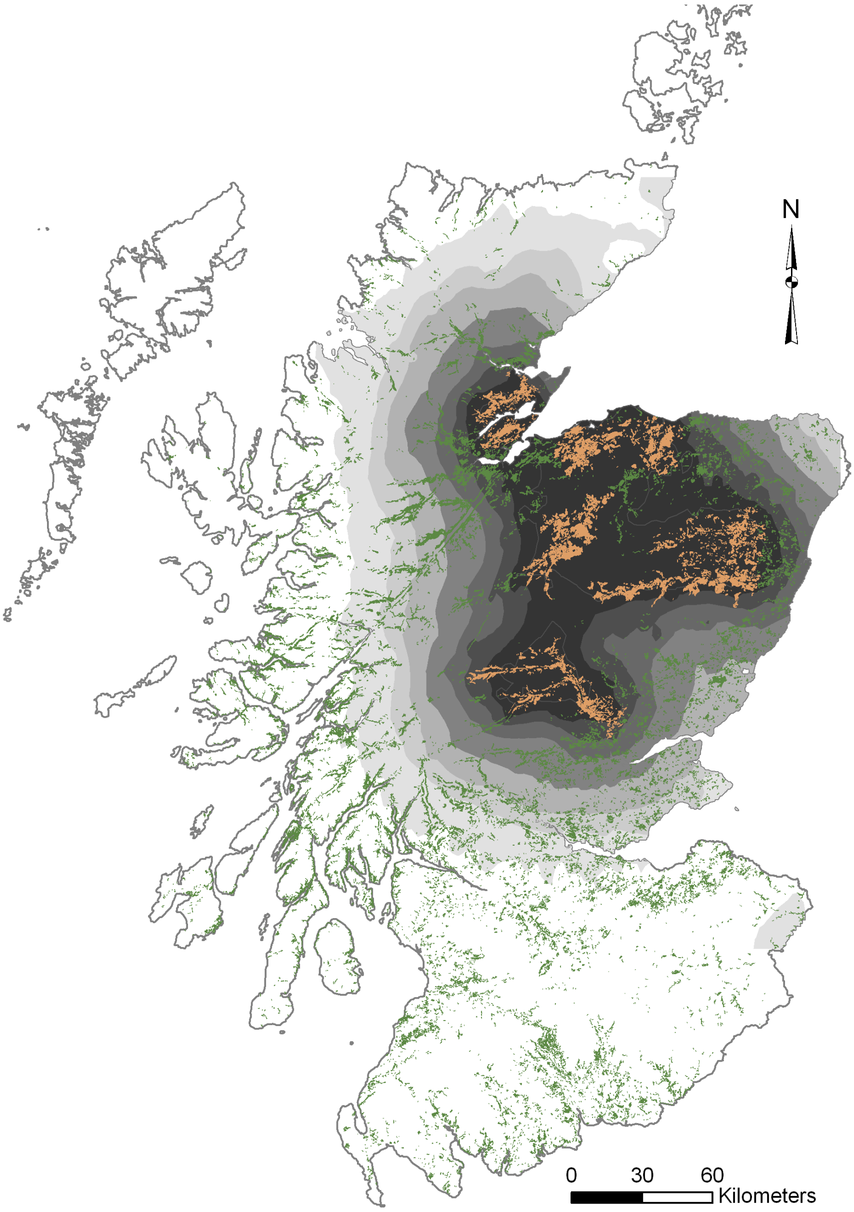

Figure 6.5. Patterns of capercaillie colonisation in Scotland. Orange and green areas represent patches of ancient woodland. Orange patches signify metapopulation areas used in model initialisation. Green patches are unoccupied at year 0. Areas of high (dark) and low (light) patch occupancy probabilities are interpolated from the number of iterations of the simulation a patch was occupied after thirty years.

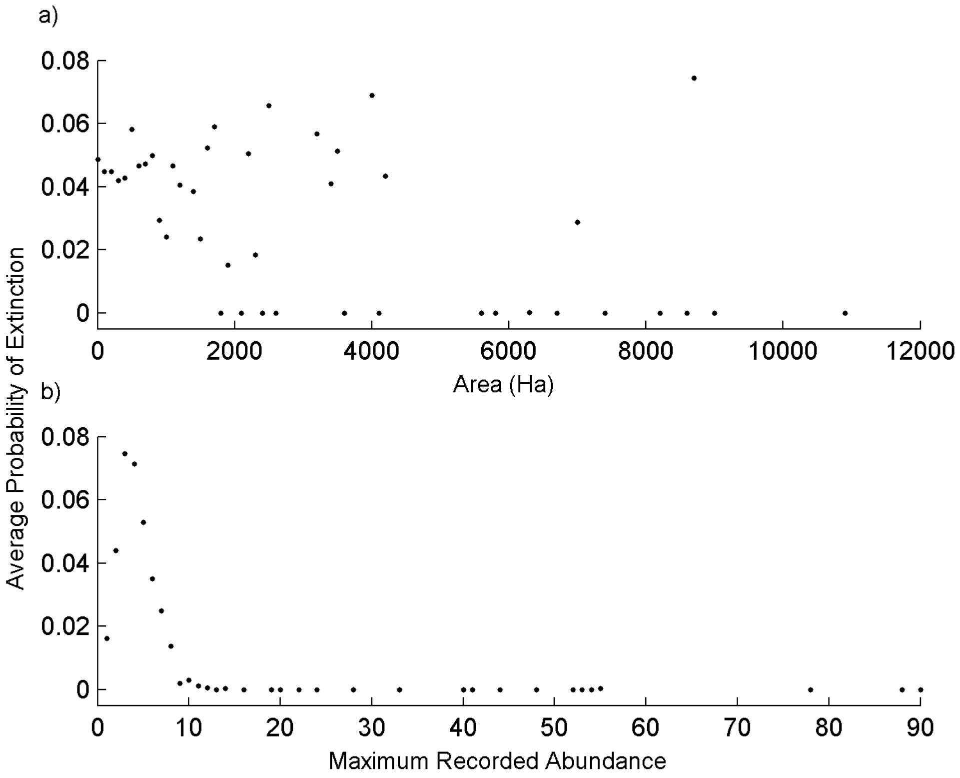

Figure 6.6. Correlates with patch extinction probability. Patch extinction probability is predicted to have a negative relationship with a) Patch area and b) Maximum recorded abundance within a patch. Points show average patch extinction probability calculated over every 100ha (a) and for each integer value of abundance (b).

6.5 Discussion

An age-structured matrix population model was constructed to predict changes in the abundance of capercaillie in Scotland. This model was augmented with spatial data and a juvenile dispersal kernel to describe patterns in the distribution of capercaillie across woodland patches and to estimate the future viability and spatial distribution of the species.

Elasticity analysis of the matrix population model identifies adult survival as a key determinant of population growth in capercaillie. As fecundity rates in Scottish populations of capercaillie have been shown to be low relative to European populations (Moss et al. 2000), it was anticipated that fecundity rates would be most important. However, this result concurs with other findings reported in the literature. A similar PVA study from Switzerland also emphasised the importance of female adult survival in the conservation of local populations (Sachot et al. 2006). In a comparison between birds of the genera Phasianidae (pheasants and partridges) and Tetraonidae (grouse), Trouvilliez *et al.* (1988) concluded that in relatively long-lived species such as capercaillie, adult survival is a key factor in determining population growth rates. Adult survival provides increased opportunities for reproduction, thus increases in survival can be expected to result in increases in abundance, while decreases will reduce the abundance of new juveniles. This result is also supported by studies which linked previous declines in capercaillie to increases in adult mortality after collisions with fences (Catt et al. 1994; Watson and Moss 2008).

Model simulations over 30 years suggest a <1% probability of extinction of capercaillie in Scotland; populations are generally expected to increase. Estimates of lambda (the intrinsic population growth rate) also suggest a similar result (values of lambda between 0.96 and 1.14 suggest capercaillie populations are generally expected to increase rather than decrease). Examining population size 30 years hence suggests an increase in average abundance of almost 300%. An increase of this magnitude would be surprising, but this high rate of growth may be attributed to the assumptions of the model. In particular, carrying capacity was modelled using reported densities of capercaillie from Petty (2000). These densities were assumed to represent a random distribution of capercaillie densities from across Scotland, and carrying capacity was essentially derived from a bootstrapped sample of this distribution. If however, these reported capercaillie densities reflect populations at, or approaching, carrying capacity, we have potentially overestimated carrying capacity and removed significant density-dependent limits to patch population growth. However, there is currently no evidence to suggest this is the case. The model could be greatly enhanced by an evidence-based estimate of the maximum density of capercaillie, rather than an estimate derived from mean densities as recorded by Petty (2000).

Similarly, we have allowed juveniles to disperse to any patch within a distance sampled from a dispersal kernel. While juveniles will ostensibly have four months to find a vacant territory in a patch within this range, we did not model the permeability of the matrix between patches. For example, the model allows capercaillie to disperse across significant bodies of water (Loch Ness), and does not account for human-related barriers to movement. The addition of landscape networks (Theobald 2006), could explicitly model connectivity between patches, including weights which describe the degree of difficulty associated with a particular dispersal route. Limits on the dispersal of juveniles could again force local increases, where density-dependent factors could reduce population growth.

However, the information required to construct relevant landscape networks is not currently available.

Currently, patch quality and carrying capacity are determined from patch size. However, colonisation success and carrying capacity for a particular patch may be heavily dependent on local impacts, including agricultural land-use and roads. The model could be significantly improved by modelling variable patch quality, and calculating carrying capacities based on these differences. It is also important to note that the model assumes the configuration of the environment, and patch quality, will remain stable. While this is an unlikely assumption, it is difficult to include the uncertainty associated with future changes to the environment into the model. Fieberg and Ellner (2001) suggest such difficulties could be addressed by identifying those environmental variables responsible for variation in demographic parameters and including these environmental covariates in the model framework.

While capercaillie were theoretically able to disperse to any patch within 30km (with a mean dispersal distance of 12km) it is surprising that predicted patch occupancy probabilities more than 30km from the initially seeded metapopulation areas were so low. After 30 years of simulation, capercaillie were concentrated around these initial core areas, with limited evidence of consistently successful colonisation of new patches at the periphery of the species range. Consequently, the factors that determine the success of colonisation attempts and the extinction of occupied patches are of interest.

Patch area, and the maximum recorded abundance of a patch appear to be significant predictors of patch occupancy. Small patches are more likely to experience extinction events, though in some simulations, even very large patches recorded high extinction rates. It is apparent that outside of the current core metapopulation areas of the capercaillie, the availability of large areas of woodland decreases. On the periphery of the current core metapopulation area, patches of woodland are relatively small, and new populations may have insufficient numbers to successfully colonise these areas. Patches with a low maximum recorded abundance also appear to have an increased extinction risk. Where abundance is less than 9 females, extinction probabilities are high. Almost 80% of populations with a maximum population size of 3 experience a localised extinction event. It is likely that these smaller populations were not from the core area, but were instead newly colonised patches at the periphery of the species current distribution. Once a population is able to reach a size of 9 or more however, the risk the population will go extinct effectively disappears. Thus these results suggest that once a population is established in a reasonably sized patch, the risk of extinction is low. Connectivity between patches may be crucially important; it appears a newly colonised population is unlikely to successfully establish without a subsequent influx of additional immigrants. This may explain the limited evidence of consistently successful colonisation of new patches at the periphery of the species range. Newly occupied patches may be extremely dependent on the subsequent migration of additional individuals; the ‘rescue effect’ of island biogeography theory (Brown and Kodricbrown 1977). At the periphery of the species range, this rescue effect is less likely and these patches subsequently go extinct.

These results are comparable with a previous study which examined minimum viable populations (MVP) of capercaillie required for successful reintroduction programs (Marshall and Edwards-Jones 1998). While a minimum of 60 individuals with 5000ha of habitat was suggested, the supplementation of 2 unrelated individuals every five years dropped this MVP estimate to 10 individuals, a figure remarkably consistent with our observation that extinction rates approach 0 where the maximum recorded abundance within a patch is greater than 9 (in the presence of dispersal between populations).

Population viability analysis of capercaillie in Scotland predicts populations are unlikely to go extinct in the next 30 years. However, as suggested above, some assumptions of the model may have reduced the role of density-dependent limits to population growth. Further work is required to properly assess the carrying capacity of populations, and to more adequately model the dispersal of juveniles across the landscape. Additionally, further work may be required to adapt the current modelling framework to better suit the mating system of capercaillie. Watson and Moss (2008) suggest that as females disperse into new patches, males will tend to follow across the landscape (with a small lag). As such, the current model does not explicitly account for the lekking behaviours observed in capercaillie and the aggregated distribution of males around leks.

Our work does suggests capercaillie have difficulty establishing new populations. The results presented suggest a number of key issues for future management of the species. The key demographic process contributing to population growth was identified as adult survival. Improving adult survival should be a priority. In particular Catt *et al.* (1994) and Watson and Moss (2008) suggest the removal of unnecessary fences and action to increase the visibility of remaining fences would reduce adult mortality associated with fence collisions. Further, successful colonisation attempts are highly concentrated around existing capercaillie populations. Connectivity between populations is also critical, as a source of additional immigrants is required to establish new populations at the periphery of the species range. Population size and patch area have significant impacts on the viability of populations, and should be considered in future management plans. Undersized populations and populations inhabiting small woodland patches, particularly in areas where numbers of immigrants is low, are likely to become extinct. Ultimately we conclude that these results provide some clear evidence on which to base future management of the species. With appropriate action, established populations of capercaillie in Scotland are likely to persist into the future.

7 General Discussion

This thesis documented the development of a variety of models to examine and explain patterns in the abundance and distribution of three species of upland birds: the red grouse, meadow pipit and capercaillie. We can now discuss the results and outputs of these models in the context of land-use changes in the Scottish uplands.

Cyclic fluctuations in population dynamics have been a focus of much ecological research. The cyclic dynamics of snowshoe hare and lynx in Canada, rodents in Scandinavia and red grouse in the United Kingdom have, in particular, been the focus of a great deal of attention (Elton 1924; Haydon et al. 2002; Kendall et al. 1999; Lindström et al. 2001). Red grouse are considered the paragon of British gamebirds (Tapper 1992). The income generated on moorland estates from red grouse shooting parties plays a crucial role in sustaining the livelihoods of highland communities (Jack 2007). The cyclic dynamics observed in red grouse populations can therefore have dramatic consequences for the viability of these estates; in ‘crash’ years, an absence of grouse will result in the cancellation of shooting parties. Cancelled shooting parties will subsequently result in a loss of income for the broader community. Further, unlike other gamebird species, grouse shoots are entirely dependent on wild birds. Hand reared grouse have high post-release mortality rates (Tapper 1992). The economic importance of good grouse harvests has thus triggered much historical research into grouse population dynamics (Potts et al. 1984, Watson et al. 1984, Williams 1985, Haydon et al. 2002), and the causes of population fluctuations (Hudson 1992; Moss and Watson 1985; Moss et al. 1996). However, while the causes of cycles in red grouse have been the subject of much study, little is known about patterns of cycle synchrony between different grouse populations. In Chapters 2-4, we attempted to address this knowledge gap through a detailed examination of synchrony in red grouse.

Patterns in synchrony in red grouse were examined in Chapter 2. The degree of synchrony in the cyclic dynamics of these populations has historically been poorly studied. Only one study (Cattadori et al. 2005) had examined synchrony in red grouse, yet this study only examined time-series data from a small subset of English moors. Using harvesting records from the entire geographic range, indexed as the number of grouse shot per year, we found statistically significant evidence of synchrony between populations on neighbouring moors. Such a result confirms populations of red grouse, like other species of Tetraonid (capercaillie, hazel grouse and black grouse; refer to Lindström et al.1995; Ranta et al. 1995b), exhibit broad scale synchrony in population dynamics.

Synchrony in red grouse was found to decline rapidly with increasing intermoor distance. At distances greater than 100km, grouse populations exhibit only weakly positive cross-correlation coefficients. However these relationships were extremely noisy. Using a general linear model, we detected significant relationships between the average degree of synchrony observed in a population, and a range of explanatory variables: average intermoor distance, grouse moor productivity, distance from the Atlantic coast, April and June temperature and June rainfall.

Mechanisms underlying the generation of synchrony were investigated in Chapter 3. We applied a discrete Markov model that describes the state of a population trajectory as it cycles between one of 4 possible states: increasing, peak, decreasing and trough. Analysis of this model offers insights into the nature of the coupling that gives rise to the weakly synchronous cycles of red grouse abundance revealed in Chapter 2. We show that grouse populations are generally uncoupled through time. However, we detect significant strong intermittent coupling, which forces populations into a greater degree of synchrony than expected under the assumption of independent dynamics. This result supports the prior work of Cattadori *et al.* (2005), where ‘collective forcing events’ (CFEs) were detected after analysis of a much smaller subset of these data. These CFEs were found to occur approximately 1 in 6 years. In the absence of these events, synchrony would generally dissipate within 3 years. We detect no clear patterns determining whether these CFEs are a function of correlated increases or decreases in abundance. However, evidence suggests that it is the smaller populations that tend to make the less probable phase shifts required to synchronise with larger populations, suggesting that smaller populations are more susceptible to the perturbations responsible for phase shifts than larger populations.

The mechanism by which a CFE could produce patterns of synchrony are easily imagined. For example, a stochastic event could suppress breeding in a number of populations, providing a strong coupling mechanism to synchronise otherwise uncoupled populations. Such a suggestion was postulated by Ranta *et al.* (1995b); modelling work using Leslie matrix-based simulation approach suggested the population dynamics of three species of grouse in Finland could be synchronised by introducing a synchronised breeding failure at a given interval. Studies of the cyclic dynamics of these species have shown populations exhibit cyclic dynamics with a high degree of temporal synchrony, with cycles most frequently displaying a period of six years (Lindström et al.1995; Ranta et al. 1995b).

Finally, in Chapter 4 we examined the causes of coupling between populations. We investigated two potential hypotheses: synchrony is a product of correlations in climate, or synchrony is driven by dispersal acting to couple populations. Moran (1953) demonstrated that if populations have the same intrinsic linear, delayed density-dependent structure (DDS), correlations between populations would exactly equal correlations in the environmental perturbations experienced by the populations. Hugueny (2006) provides a method for quantifying similarities in the DDS of populations. We find that the DDS of red grouse populations is sufficiently similar to allow the Moran effect to synchronise populations. In addition, we investigate importance of dispersal in driving synchrony. A number of theoretical studies have demonstrated that synchrony could be a product by biotic coupling mechanism, in particular the dispersal of individuals between populations (Bjørnstad 2001; Liebhold et al. 2004; Ranta et al. 1999). We use the density of grouse in the landscape surrounding two moors as a proxy measure of the degree of dispersal between two populations. Where density is high, the area between two moors would likely contain an increased density of grouse habitat, and thus facilitate increased immigration between patches.

We detect a weak relationship between the level of synchrony between two moors, and the density of grouse in the surrounding landscape, after we account for the effect of distance. This is consistent with the results of Chapter 4, where our conclusions suggested that smaller populations are more susceptible to the perturbations responsible for phase shifts than larger populations, arguably as they are more dependent on dispersal to increase abundance. Similarly, we examined the relationship between synchrony and climate. While the DDS of populations would allow climate to synchronise populations, we tested three candidate variables implicated by previous analyses (Chapter 2) and failed to detect a significant relationship with any of them. Given the very low percentage of variation explained by a possible dispersal process, it is likely that climate does indeed play a role in generating synchrony between red grouse populations, and a more extensive search of potential covariates would likely reveal significant drivers. The results of Chapter 4 did not provide a mutually exclusive mechanism to explain synchrony in red grouse. While this result is disappointing, it is perhaps not unexpected. Previous studies have demonstrated that synchronous dynamics may be a product of interactions between dispersal and correlated environmental noise (Kendall et al. 2000). Future research could improve this result; in particular, density is not necessarily an ideal measure of dispersal, and better quantification of dispersal potential may increase our power to detect a role for dispersal.

We have thus demonstrated that red grouse co-vary in abundance over space. However, the nature of this coupling is intermittent, with strong CFEs forcing populations into a synchronous state approximately 1 in 6 years. We have also found evidence that this coupling is driven in part by dispersal of individuals between populations, though climate is likely to also play a role. The results of our examination of synchrony in red grouse provide useful insights into the drivers of population change. The results of this work may also inform studies into similar processes at work in other natural populations.

In Chapter 5, changes in the population demography of meadow pipits were examined in response to different grazing treatments. A Bayesian approach was developed to model changes in the abundance of female meadow pipits. The use of a Bayesian framework allowed a priori information to be incorporated into the model, while also permitting the estimation of a number of key parameters for which little information was available. Further, differences in the growth rates of populations with respect to grazing treatment, site and year were investigated. Grazing and site emerged from this analysis as having a significant impact on meadow pipit populations. In particular, results suggest commercial and mixed grazing treatments have beneficial impacts of meadow pipits. By trampling vegetation, livestock may increase prey accessibility and detectability and improve meadow pipit foraging efficiency.

Recent reform to the Common Agricultural Policy (CAP) resulted in the decoupling of subsidy payments from production (Brown and Bainbridge 1995). As many upland farms operate at the margins of financial viability (Mowle and Bell 1988), this has resulted in widespread declines in livestock numbers, as farmers have sought to cut operating costs (Rural Policy Centre 2008). These declines could potentially impact wildlife and ecosystem health. The results of Chapter 5 suggest that some degree of grazing is important for the maintenance of upland species, a result supported by a number of other studies (Dennis et al. 2008; Evans et al. 2006a; Evans et al. 2006b; Loe et al. 2007).

Chapter 6 detailed the development of a spatially explicit population viability analysis model for capercaillie. Key demographic parameters were obtained from the scientific literature, and this permitted the construction of an age-structured matrix population model, which was used to model within patch demographic processes. Spatial data of the location of patches of remnant pine woodland in Scotland provided a mechanism for incorporating the effects of dispersal and a way of examining the importance of the size and location of patches. Outputs from the model suggest that capercaillie are unlikely to go extinct in the next 30 years. Analysis suggests that reducing adult mortality should be a major management objective. Also, the model revealed that once a population is well established in a suitably large patch of woodland, the probability of extinction is substantially reduced.

Changes in forestry practices are particularly relevant to discussions regarding the future of capercaillie in Scotland. A thriving population of capercaillie is thought to indicate a healthy forest ecosystem (Watson and Moss 2008). Capercaillie show a strong preference for mature pine woodland, with an open structure which permits light to penetrate and stimulate a rich shrub and herb understory (Tapper 1992). However much mature pine habitat has been cleared to give way to more profitable stands, often lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*). While capercaillie can exist in such habitat, numbers are significantly suppressed (Watson and Moss 2008). Our analysis was therefore restricted to patches of remnant Caledonian pine woodland, areas of preferred habitat for capercaillie.

The results of Chapter 6 suggest that while capercaillie are unlikely to go extinct in the near future, their distribution will remain relatively restricted to existing core habitat areas. Additionally, larger woodland patches, and larger populations are unlikely to go extinct, suggesting future management should concentrate on the enlargement of patches in current metapopulation areas, and on the reduction of adult mortality associated with fence strikes. This model also has potential to inform the management of other species of conservation interest. In particular, the model provides a wealth of data about the future structure and distribution of the species or population in question, which can be used to analyse a wider range of management questions than addressed here.

Through the course of this thesis, I have developed a number of models to document and predict patterns in the abundance and distribution of upland birds in Scotland. These models provide useful insights into the processes driving population change in these species, and will hopefully guide future research and management decisions in these upland habitats. On a more personal note, this thesis charts my own developing skills in ecological modelling. In Chapter 2, I commenced with relatively simple statistical models, and through Chapters 3 and 4, I advanced to increasingly mechanistic/probabilistic models to describe red grouse dynamics. In Chapter 5 I explored the use of Bayesian statistics to address ecological questions, and relate changes in the abundance of meadow pipits to various grazing intensities. Finally in Chapter 6, I developed a custom made spatially explicit PVA model, used to examine a species of conservation interest in the uplands, which provides useful insights into the future management of capercaillie populations. Thus this thesis provides a chronological record of my advancing knowledge of modelling techniques, and the application of these techniques to examine the spatial and temporal dynamics of upland birds in Scotland.

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Appendix 1

Hugueny (2006) has previously shown that for two populations that are described by AR-2 processes:

$$X_{t+1} = a_1 X_t + a_2 X_{t-1} + \varepsilon_{t+1}$$

$$Y_{t+1} = b_1 Y_t + b_2 Y_{t-1} + \omega_{t+1},$$

K_{xy} is defined as:

$$K_{xy} = \frac{\sqrt{(1-a_2^2 - \frac{a_1^2}{1-a_2} - \frac{a_1^2 a_2}{1-a_2})(1-b_2^2 - \frac{b_1^2}{1-b_2} - \frac{b_1^2 b_2}{1-b_2})}}{1-a_2 b_2 - \frac{(a_1 + b_1 a_2)(b_1 + a_1 b_2)}{1-a_2 b_2}}.$$

We use the same logic to derive an equation for K_{xy} for AR-3 processes. Consider two populations described by AR-3 processes:

$$X_{t+1} = a_1 X_t + a_2 X_{t-1} + a_3 X_{t-2} + \varepsilon_{t+1}$$

$$Y_{t+1} = b_1 Y_t + b_2 Y_{t-1} + b_3 Y_{t-1} + \omega_{t=1}.$$

If the system described is a stationary, multivariate time-series, it should satisfy the Yule-Walker equations:

(1) $$\Gamma(k) = \sum_{i=1}^{3} AR(i)\Gamma(k-i)$$

(2) $$\Gamma(0) = U + \sum_{i=1}^{3} AR(i)\Gamma(i)^T$$

where:

$$U = \begin{bmatrix} Var(\varepsilon_t) & Cov(\varepsilon_t, \omega_t) \\ Cov(\varepsilon_t, \omega_t) & Var(\omega_t) \end{bmatrix},$$

$$\Gamma(i) = \Gamma(-i)^T = \begin{bmatrix} Cov(X_{t+i}, X_t) & Cov(Y_{t+i}, X_t) \\ Cov(X_{t+i}, Y_t) & Cov(Y_{t+1}, Y_t) \end{bmatrix},$$

$$AR(i) = \begin{bmatrix} a_i & 0 \\ 0 & b_i \end{bmatrix}.$$

Equation 2 reduces to:

(3) $$Var(X_t) = a_1 Cov(X_{t+1}, X_t) + a_2 Cov(X_{t+2}, X_t) + a_3 Cov(X_{t+3}, X_t) + Var(\varepsilon_t)$$

(4) $$Var(Y_t) = b_1 Cov(Y_{t+1}, Y_t) + b_2 Cov(Y_{t+2}, Y_t) + b_3 Cov(Y_{t+3}, Y_t) + Var(\omega_t)$$

(5) $$\begin{aligned} &Cov(X_t, Y_t) = a_1 Cov(X_{t+1}, Y_t) + a_2 Cov(X_{t+2}, Y_t) + a_3 Cov(X_{t+3}, Y_t) \\ &+ Cov(\varepsilon_t, \omega_t) \end{aligned}$$

Using Equation 1 we find that:

(6) $$\Gamma(1) = AR(1)\Gamma(2) + AR(2)\Gamma(1) + AR(3)\Gamma(0)$$

(7) $$\Gamma(2) = AR(1)\Gamma(1) + AR(2)\Gamma(0) + AR(3)\Gamma(1)^T$$

(8) $$\Gamma(3) = AR(1)\Gamma(0) + AR(2)\Gamma(1)^T + AR(3)\Gamma(2)^T$$

We use wxMaxima (www.wxmaxima.sourceforge.net) for further substituting and factoring; the use of this program allows for increased accuracy in reporting results. Assuming the two populations are uncoupled with no migration, co-variances in equations 3 and 4 do not contribute to variance. Thus we can show that:

(9)

$$Var(X_t) = Var(\varepsilon_t) \frac{a_1 + a_2 a_3 + (a_2 + a_1 a_3)(a_1 + a_3) - 2a_1 a_2 + 2a_2 a_3 + 2a_1 a_3 (a_1 + a_3)}{j}$$

Where j = $$\begin{aligned} &(1 - a_1^2 - a_2^2 - a_3^2 - 2a_1 a_2 a_3)(a_1 + a_2 a_3 + (a_2 + a_1 a_3)(a_1 + a_3)) \\ &- 2a_1 a_2 + 2a_2 a_3 + 2a_1 a_3 (a_1 + a_3)(1 - a_3^2 - a_2^2 - a_1 a_2 a_3) \end{aligned}$$

and

(10)

$$Var(Y_t) = Var(\omega_t)\frac{b_1 + b_2b_3 + (b_2 + b_1b_3)(b_1 + b_3) - 2b_1b_2 + 2b_2b_3 + 2b_1b_3(b_1 + b_3)}{k}$$

where k = $\begin{gathered}(1 - b_1^2 - b_2^2 - b_3^2 - 2b_1b_2b_3)(b_1 + b_2b_3 + (b_2 + b_1b_3)(b_1 + b_3)) \\ -2b_1b_2 + 2b_2b_3 + 2b_1b_3(b_1 + b_3)(1 - b_3^2 - b_2^2 - b_1b_2b_3)\end{gathered}$.

Now we focus on the computation of the covariance between X and Y. We wish to obtain Cov(X_t, Y_t). Using equations 1, 6, 7 and 8, we can obtain equations describing patterns of covariation:

$$Cov(X_t, Y_t) = a_3Cov(X_t, Y_{t-3}) + a_2Cov(X_t, Y_{t-2}) + a_1Cov(X_t, Y_{t-1})$$

$$Cov(X_t, Y_{t+1}) = a_3Cov(X_t, Y_{t-2}) + a_2Cov(X_t, Y_{t-1}) + a_1Cov(X_t, Y_t)$$

$$Cov(X_t, Y_{t+2}) = a_3Cov(X_t, Y_{t-1}) + a_1Cov(X_t, Y_{t+1}) + a_2Cov(X_t, Y_t)$$

$$Cov(X_t, Y_{t+3}) = a_1Cov(X_t, Y_{t+2}) + a_2Cov(X_t, Y_{t+1}) + a_3Cov(X_t, Y_t)$$

$$Cov(X_t, Y_{t-1}) = b_3Cov(X_t, Y_{t+2}) + b_2Cov(X_t, Y_{t+1}) + b_1Cov(X_t, Y_t)$$

$$Cov(X_t, Y_{t-2}) = b_1Cov(X_t, Y_{t-1}) + b_3Cov(X_t, Y_{t+1}) + b_2Cov(X_t, Y_t)$$

$$Cov(X_t, Y_{t-3}) = b_1Cov(X_t, Y_{t-2}) + b_2Cov(X_t, Y_{t-1}) + b_3Cov(X_t, Y_t)$$

Substitution allows us to solve for Cov(X_t, Y_t):

(11) $Cov(X_t, Y_t) = -\frac{d}{n}$,

where:

$$d = a_3^2b_3^2 - a_1a_3b_1b_3 - 2a_3b_3 - a_1a_2b_3 - a_3b_1b_2 - a_2b_2 + 1,$$

$$\begin{aligned}n = {} & a_3b_3 - a_2a_3^2b_2b_3^2 - 2a_1a_3^2b_1b_3^2 + a_2^2a_3b_1b_3^2 - 3a_3^2b_3^2 - 3a_1a_2a_3b_3^2 + a_2^3b_3^2 + a_1a_3^2b_2^2b_3 \\ & - 3a_3^2b_1b_2b_3 - a_1a_2a_3b_1b_2b_3 - a_2a_3b_2b_3 + 2a_1^2a_3b_2b_3 - a_1a_2^2b_2b_3 + 2a_2a_3b_1^2b_3 + a_1^2a_3b_1^2b_3 \\ & + a_1a_3b_1b_3 + 2a_2^2b_1b_3 + a_1^2a_2b_1b_3 + 3a_3b_3 + 3a_1a_2b_3 + a_1^3b_3 + a_3^2b_2^3 - a_2a_3b_1b_2^2 + 2a_1a_3b_2^2 \\ & - a_2^2b_2^2 + a_1a_3b_1^2b_2 + 3a_3b_1b_2 + a_1a_2b_1b_2 + 2a_2b_2 + a_1^2b_2 + a_3b_1^3 + a_2b_1^2 + a_1b_1 - 1\end{aligned}$$

If $Corr(X_t, Y_t) = \frac{Cov(X_t, Y_t)Corr(\varepsilon_t, \omega_t)}{\sqrt{Var(X_t)Var(Y_t)}}$, we can substitute equations 9, 10 and 11 to arrive at a solution for K_{xy} for AR-3 processes:

$$K_{xy} = \frac{-d}{n_1 * n_2 * n_3},$$

where:

$$d = a_3^2b_3^2 - a_1a_3b_1b_3 - 2a_3b_3 - a_1a_2b_3 - a_3b_1b_2 - a_2b_2 + 1$$

$$n_1 = \sqrt{\frac{1 - a_3^2 - a_1a_3 - a_2}{1 + a_3^4 + a_1a_3^3 + (-a_2^2 + a_2 - a_1^2 - 2)a_3^2 + (a_1a_2^2 - 4a_1a_2 - a_1^3 - a_1)a_3 + a_2^3 - a_2^2 + (-1 - a_1^2) - a_1^2}}$$

$$n_2 = \sqrt{\frac{1 - b_3^2 - b_1b_3 - b_2}{1 + b_3^4 + b_1b_3^3 + (-b_2^2 + b_2 - b_1^2 - 2)b_3^2 + (b_1b_2^2 - 4b_1b_2 - b_1^3 - b_1)b_3 + b_2^3 - b_2^2 + (-1 - b_1^2) - b_1^2}}$$

$$\begin{aligned}n_3 = {} & a_3b_3 - a_2a_3^2b_2b_3^2 - 2a_1a_3^2b_1b_3^2 + a_2^2a_3b_1b_3^2 - 3a_3^2b_3^2 - 3a_1a_2a_3b_3^2 + a_2^3b_3^2 + a_1a_3^2b_2^2b_3 \\ & - 3a_3^2b_1b_2b_3 - a_1a_2a_3b_1b_2b_3 - a_2a_3b_2b_3 + 2a_1^2a_3b_2b_3 - a_1a_2^2b_2b_3 + 2a_2a_3b_1^2b_3 + a_1^2a_3b_1^2b_3 \\ & + a_1a_3b_1b_3 + 2a_2^2b_1b_3 + a_1^2a_2b_1b_3 + 3a_3b_3 + 3a_1a_2\beta_3 + a_1^3b_3 + a_3^2b_2^3 - a_2a_3b_1b_2^2 + 2a_1a_3b_2^2 \quad . \\ & - a_2^2b_2^2 + a_1a_3b_1^2b_2 + 3a_3b_1b_2 + a_1a_2b_1b_2 + 2a_2b_2 + a_1^2b_2 + a_3b_1^3 + a_2b_1^2 + a_1b_1 - 1\end{aligned}$$

This solution can be validated by comparing with the results of Hugueny (2007). If a_3 and b_3 are set to 0, we can recover the original equation for K_{xy} for AR-2 processes.