MULTI-SPECIES STATE-SPACE MODELLING OF THE HEN HARRIER (CIRCUS CYANEUS) AND RED GROUSE (LAGOPUS LAGOPUS SCOTICUS) IN SCOTLAND

Leslie Frances New

A Thesis Submitted for the Degree of PhD at the University of St. Andrews

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Leslie Frances New

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ST ANDREWS
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Abstract

State-space modelling is a powerful tool to study ecological systems. The direct inclusion of uncertainty, unification of models and data, and ability to model unobserved, hidden states increases our knowledge about the environment and provides new ecological insights. I extend the state-space framework to create multi-species models, showing that the ability to model ecosystem interactions is limited only by data availability.

State-space models are fit using both Bayesian and Frequentist methods, making them independent of a statistical school of thought. Bayesian approaches can have the advantage in their ability to account for missing data and fit hierarchical structures and models with many parameters to limited data; often the case in ecological studies. I have taken a Bayesian model fitting approach in this thesis.

The predator-prey interactions between the hen harrier (Circus cyaneus) and red grouse (Lagopus lagopus scoticus) are used to demonstrate state-space modelling’s capabilities. The harrier data are believed to be known without error, while missing data make the cyclic dynamics of the grouse harder to model. The grouse-harrier interactions are modelled in a multi-species state-space model, rather than including one species as a covariate in the other’s model. Finally, models are included for the harriers’ alternate prey.

The single- and multi-species state-space models for the predator-prey interactions provide insight into the species’ management. The models investigate aspects of the species’ behaviour, from the mechanisms behind grouse cycles to what motivates harrier immigration. The inferences drawn from these models are applicable to management, suggesting actions to halt grouse cycles or mitigate the grouse-harrier conflict. Overall, the multi-species models suggest that two popular ideas for grouse-harrier management, diversionary feeding and habitat manipulation to reduce alternate prey densities, will not have the desired effect, and in the case of reducing prey densities, may even increase the harriers’ impact on grouse chicks.
Declarations

I, Leslie Frances New, hereby certify that this thesis, which is approximately 50000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in September 2005 and as a candidate for the degree of Doctor of Philosophy in Statistics in September 2005; the higher study for which this is a record was carried out in the University of St Andrews between 2005 and 2009.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in Statistics in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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<td>202</td>
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Chapter 1

Introduction

1.1 Statistical modelling

The advent of personal computers has led to many advancements in science, mathematics and statistics in particular. Prior to the availability of mechanical processing power, the intractability of certain types of calculations made it impossible to find their solutions. However, as access to computers has grown, so has people’s ability to solve increasingly complex statistical problems. With growing capabilities has come increasingly complex questions, which has led to the rapid development of new methods and approaches to model fitting.

Although computers make it possible to apply complicated methodologies, such as Markov chain Monte Carlo (MCMC), it was not until the availability of general-purpose software that these methods began to enter mainstream research (Gilks et al., 1996). While general-purpose software can trade computational efficiency for accessibility, these computer programs have led to a wider application of statistics, since the ability to code the model fitting algorithms is no longer required. For example, the methods used to fit state-space models, such as the Kalman filter, sequential importance sampling (SIS) and MCMC, are all computer-intensive and can be difficult to code. Yet, the concepts behind state-space modelling, the synthesis of the model and the data and the direct inclusion of process, observation and model uncertainty (Buckland et al., 2007), are valuable in many scientific applications. However, while the
methods can require considerable experience to be used effectively (Harwood & Stokes, 2003), the availability of general-purpose software, such as WinBUGS (Spiegelhalter et al., 2007) for MCMC, can make the fitting method, and thus state-space modelling, accessible to more researchers.

While WinBUGS is general-purpose in terms of the types of models it can run, the software is specific to model fitting using MCMC in a Bayesian framework. Bayesian statistics, in particular, has benefited from the widespread use of computers. Although the theory was developed in the 18th century (Bayes, 1763), the complexity of the integration needed to calculate the normalising constant limited statisticians to fairly simple examples until recently. The ability of computers to find numerical solutions to analytically intractable problems has lead to an increase in the use and applicability of Bayesian methods. This has aided many areas of research, since Bayesian methods can offer an alternative approach to solving many problems, although there is no inherent advantage in the methodology (Gelman et al., 1995).

1.2 Ecological inference

Ecology has profited from computers and the increased availability of statistical software. Ecologists can use readily available software such as MARK (White & Burnham, 1999) and Distance (Thomas et al., 2009) to aid in estimating animal abundance and species’ vital rates. Population modelling has also benefited from the influx of new technology. While the concepts behind modelling population dynamics have been around for more than six decades (e.g., Leslie, 1945), most models were simplistic, and there were no tools for formally fitting them to time series of data. As models begin to capture the mechanistic and detailed nature of population interactions, the fitting methods can become more complex and harder to implement. Therefore, without the availability of software and computational power, it is necessary to maintain relatively simple models in order to be able to obtain population or parameter estimates. However, recent advances can make the over-simplification of species dynamics models a choice, rather than a necessity.
State-space modelling is particularly advantageous to ecologists, since it provides a flexible, inferential framework that can include many different population processes (Buckland et al., 2004b), as well as allowing for the complexity of natural systems (Clark & Bjornstad, 2004). Additionally, model formulation can take place using Leslie and Lefkovitch matrices, which are familiar to ecologists (Thomas et al., 2005). The models thus constructed can be used for both biological inference and the implementation of management plans (Taylor et al., 2000), where they provide an advantage in their ability to help quantify risk (Harwood & Stokes, 2003). Finally, state-space modelling has the ability to account for unobserved, hidden states, and their associated variability (Clark & Bjornstad, 2004). This is important when only a portion of the population is observable, such is the case with most fish species.

The flexibility of state-space models can be seen in the wide range of species, population structures and data types that have been modelled using this approach. The species have varied from salmon (Oncorhynchus kisutch) (Newman, 1998), to red deer (Cervus elaphus) (Trenkel et al., 2000), to lapwings (Vanellus vanellus) (Besbeas et al., 2003) and even humans (Clark & Bjornstad, 2004). Different population structures that have been modelled include metapopulations (e.g., Thomas et al., 2005) and multiple age- (e.g., Millar & Meyer, 2000a) or stage-classes (e.g., Rivot et al., 2004). Additionally, as well as making use of various data structures, such as aerial surveys (e.g., Thomas et al., 2005) or culls (e.g., Trenkel et al., 2000), state-space models have integrated different types of data to be used in one model (e.g., Brooks et al., 2004).

Research into the capabilities of state-space modelling can focus on the ability of the modelling framework to incorporate different population and data structures (e.g., Buckland et al., 2004b) or can use simulations to determine whether the approach can effectively model different situations (e.g., Anderson-Sprechar & Ledolter, 1991; de Valpine, 2003). However, despite the inclusiveness of the modelling framework and the success of the state-space models in effectively modelling data simulated to mimic various real-life ecological situations, many possible models have remained theoretical, rather than being applied to data. In this thesis I will take advantage
of the general-purpose software WinBUGS to address part of this issue, building a state-space model for the multi-species interactions between the hen harrier (*Circus cyaneus*) and red grouse (*Lagopus lagopus scoticus*) on Langholm moor in Scotland.

In addition to posing a number of interesting biological questions, the grouse-harrier interactions provide an excellent case study around which to explore the capabilities and applications of state-space modelling. For the time period hen harriers are known to be present on the moor, their numbers are believed to be known exactly. This gives rise to a state-space model that has no observation error. It also provides a chance to investigate the effects of the harriers’ prey on their survival and movement (Chapter 3). The population dynamics of the red grouse are complicated, since they are a cyclic species. There are two hypotheses, the intrinsic, ‘territorial behaviour’ hypothesis (Moss et al., 1996; Matthiopoulos et al., 1998, 2003, 2005; Mougeot et al., 2003) and the extrinsic, ‘parasite’ hypothesis (Dobson & Hudson, 1992; Hudson, 1992; Hudson et al., 1992b), that compete to be the cause behind the fluctuations. In addition, there is evidence that the two mechanisms interact (Fox & Hudson, 2001; Mougeot et al., 2005c, 2006; Redpath et al., 2006a; Seivwright et al., 2005), giving rise to a ‘combined’ hypothesis. As well as the complexity associated with grouse population dynamics, missing data provides an additional difficulty. While seeking to determine the cause of the red grouse cycles, the models also provide us with an opportunity to explore the ability of state-space models to investigate multiple hypotheses in the face of missing data (Chapter 4).

Once the two single-species models are successfully constructed, it is possible to combine them to create a model for the multi-species interactions of the hen harrier and red grouse. The two species interact through the harriers’ predation on grouse chicks, which is believed to suppress the grouse population (Redpath & Thirgood, 1997). The single-species models for the two birds act on different spatial and temporal scales, so the grouse-harrier model allows us to investigate whether the state-space framework can incorporate detailed multi-species interactions. The successful modelling of these interactions provides a chance to explore the impacts of different management plans designed to mitigate the grouse-harrier conflict (Chapter 5). The grouse-harrier
multi-species model can be further extended to include models for the harriers’ alternate prey, the meadow pipit (*Anthus pratensis*) and field vole (*Microtus agrestis*) (Picozzi, 1978). While the data on both species are limited, as is knowledge of their population dynamics, simple process and observation models can be fit to allow the exploration of state-space modelling under a community framework. This has the potential to increase the understanding of community modelling and the indirect effects that occur among co-existing species (Chapter 6).

### 1.3 Ecology

The population dynamics of the hen harrier and red grouse have a rich and complex ecological background, with regards to both their individual dynamics and their interactions. The red grouses’ value as a game bird has made it a species of research interest since at least the late 19th century (MacDonald, 1883). However, beyond their material value, the cyclic nature of red grouse on many moorlands in the UK (Haydon et al., 2002) fascinates researchers. The grouse are the only known species to have an empirically and theoretically supported intrinsic hypothesis for the cause of their observed cycles. Other species, despite the continued debates around different hypotheses, all require extrinsic mechanisms to drive the oscillations (Turchin, 2003). In an attempt to reconcile the continued evidence for both the intrinsic and extrinsic hypotheses, Moss et al. (1993) suggested that the processes driving the observed fluctuations varied with geographical location. However, time series analysis of grouse shooting records failed to find evidence for a spatial trend behind the cause of the birds’ cycles (Shaw et al., 2004).

The hen harriers’ ability to suppress grouse densities is a result of the cyclic nature of the tetronid’s dynamics. According to predator-prey theory, generalist predators, such as the harrier, can suppress, or even stabilise, the fluctuations of cyclic species. This results from the predator showing a Type III functional response, where it switches prey when the density of one species drops below a given threshold, but switches back whenever density increases (Begon et al., 1996). Harriers show this type of functional response to grouse chick density (Asseburg, 2005) and are therefore capable
of stabilising grouse populations at densities too low for a profit to be made from driven shooting. This creates conflict between hen harriers and gamekeepers (Redpath et al., 2004; Thirgood et al., 2000b), and can lead to the raptors’ persecution on moorland estates (Redpath & Thirgood, 1997; Thirgood et al., 2000a,b).

The harriers’ prey-switching behaviour means that the density of their alternate prey can have indirect effects on the density of red grouse. Harriers’ movement into an area appears to depend on the presence of voles and pipits (Redpath & Thirgood, 1999; Redpath et al., 2002b), so manipulating these densities may impact immigration into an area. However, once nests have been established, harriers show strong site fidelity (Watson, 1977). Therefore, when the density of their alternate prey declines, harriers will switch to an alternate food source, such as grouse chicks, rather than leave the area. This has implications for management, since while it may be possible to limit the number of harriers moving to a moor by manipulating the density of their alternate prey, the nests already present may increase their predation on grouse chicks.

1.4 Thesis overview

The motivations for this thesis began during my undergraduate degree, when I first learned about ecological modelling and the issues raised by the interactions between the hen harriers and red grouse in Scotland. The complex relationships between the ecology, conservation and economics of grouse moors presents a chance to explore the capabilities of statistical modelling while answering questions framed by the needs of both biology and management.

The first objective of this PhD was to achieve the technical aim of building and fitting multi-species models. It was therefore necessary to address certain issues, such as developing a discrete population model for *Trichostrongylus tenuis*, the parasite behind the extrinsic hypothesis for red grouse cycles. I also needed to work around the limitations of our choice of software. The slow run time of the algorithm required the development of models outside of WinBUGS. As a result, the program BlackBox was
used in conjunction with the original software to enable the inclusion of deterministic models in an otherwise stochastic setting. There was also the difficulty of insuring that my models mimicked the biology of the system as closely as possible, allowing harrier consumption to occur on different spatial and temporal scales from the grouse population model.

Once the models had been formulated, I sought to investigate the behaviours of both the single-species and multi-species systems. I wished to examine the hypotheses behind red grouse cycles to attempt to make inferences about their cause and determine the plausibility of the combined hypothesis. For the harrier-only model, I looked at the drivers behind harrier survival and movement. Empirical studies have suggested relationships between the presence of harriers’ main prey and the raptors’ life history processes, which I wished to try and support or confirm with theoretical models. As well as exploring their individual behaviour, the development of a model for the grouse-harrier interactions provided a chance to investigate their predator-prey relationship and the nature of the harriers’ impact on the grouse. Further extensions to the framework incorporated models for the harriers’ alternate prey, enabling me to examine community interactions through the inclusion of the both the direct and indirect effects of the presence of multiple species.

Finally, given the models and an understanding of the behaviours of the system, this thesis also had the applied goal of answering questions about grouse-harrier management. One way gamekeepers can maintain high grouse densities is to halt the cycles at their peak. This can only be achieved by having some understanding of the cause of the gamebird’s cycles; the results of my grouse-only model can suggest new field experiments to try and achieve this aim. Another way to increase grouse density is to lessen predation by harriers, therefore the grouse-harrier model was used to investigate the feasibility of providing hen harriers with supplementary food to decrease their consumption of grouse chicks. Lastly, the community model could be used to investigate the impact of vole and pipit density on harrier movement into an area, as well as the shift in harrier consumption of grouse chicks due to different alternate prey densities.
1.5 Discussion

Advances in technology and the increasing capabilities of computers have led to many changes in the way research is conducted. These developments make statistics more widely applicable, while new technologies, such as infrared or sonar, make it possible to record data in situations that would have seemed impossible not that many years ago. This has resulted in the development of new methods to deal with the ever more detailed questions that are being asked by researchers around the world. The study of ecology has greatly benefited from these advances, since they allow for the more meticulous modelling of population dynamics, and the collection of the data required for these models.

This thesis aims to take advantage of the advances in technology to further the knowledge and comprehension of the grouse-harrier system and its interactions, not provide a conclusion to the debate surrounding moorland management. Instead, I aimed to further our understanding of the system and the species’ ecology, as well as develop tools capable of aiding management. Additionally, I wished to expand the practical applications associated with state-space modelling, providing real-life examples of how the method can be applied to varying situations and multi-species interactions. While multi-species state-space modelling has the potential to be a powerful tool in the ecologist’s toolbox, the method is data hungry, especially as the number of species in the model increases. In the future, once the data requirements of multi-species state-space modelling are better understood, it will be possible to design new studies to obtain the required information.

To address the goals of this thesis I begin by describing state-space modelling in detail and explain my choice to fit the models in a Bayesian framework using MCMC in Chapter 2. The single-species models for the hen harrier and red grouse are presented in Chapters 3 and 4, respectively, while the grouse-harrier interactions are modelled in Chapter 5. The multi-species state-space model for the grouse-harrier community is introduced in Chapter 6, although it serves primarily as an example of the possibilities of community modelling.
Chapter 2

State-space Modelling

2.1 What is a state-space model?

In the context of population ecology, a ‘state’ refers to a population, or the components that form a population, at a given time $t$. The ‘state-space’ is the mathematical space over which all possible states exist. State-space models serve as a way to integrate population dynamics models and data, embedding them in a statistical framework, providing a general, flexible approach to modelling a wide range of wildlife population processes (Buckland et al., 2007). A state-space model describes two processes, the state process and the observation process, as they evolve in parallel over time (Newman et al., 2006). The state vector, $\mathbf{n}_t$, is an unknown vector of the various states of the population at time $t$. The observation vector, $\mathbf{y}_t$, contains the data available about the states. This vector is measurable, completely observable and a function of the state process (Thomas et al., 2005). The state process incorporates population models, describing the processes that move animal populations from their state at time $t$ to their state at time $t+1$. The observation model utilises the data, matching its components to the structure, or an amalgamation of features, of the state process. Inferences about the state and its parameters are conditional on the observation process (Buckland et al., 2004b). The term ‘state-space model’ is used to refer specifically to first-order Markov models; values for the state in time $t$ depend solely on time $t-1$. This is a special case of the hidden process model, which is not constrained to being dependent solely on time $t-1$, but can have higher-order
dependencies (Newman et al., 2006).

2.2 Why state-space modelling?

State-space modelling allows for a wide specification of models in a flexible, inferential framework. The models can be made to include many varied population processes, such as movement, density-dependence, competition and predator-prey interactions (Buckland et al., 2004b). State-space models can be used for inferences about the past, historical state of the population, the current state of the population up to the present time and the future state of the population (Thomas et al., 2005). The same state-space model used for retrospective and current inferences about the population can be used for forecasting, with only minor alterations to account for the projection into the future. This feature serves to unify biological models, which are used to increase understanding of biological systems, and management models, which focus on implementation of management plans (Taylor et al., 2000).

State-space modelling has the capability to allow for the complexity of natural systems and provides inference on unobservable states that can affect observations as well as the state process (Clark & Bjornstad, 2004). The method unifies models and data, allowing the two to work together directly, as opposed to existing as separate, but complementary, parts of ecological estimation and prediction. Where other methods use ‘best’ estimates, or confidence bounds on population parameters to get estimates of future abundance (Taylor et al., 2000), state-space modelling uses the data to estimate both abundance and population parameters simultaneously, providing better estimates and more direct inclusion of uncertainty.

One of the primary advantages of using state-space models is their ability to account for the three main types of uncertainty: process variation, observation error and model uncertainty (Buckland et al., 2007). In a management context, ignoring uncertainty can lead to inaction and failed management (Taylor et al., 2000). Traditional methods often ignore sources of stochasticity, dealing with process error and some model uncertainty, but largely ignoring observation error (Calder et al., 2003).
This is a problem, since ignoring observation error can lead to incorrect parameter estimates (de Valpine & Hastings, 2002), which would lead to incorrect predictions of future population abundance. Other sources of variability that can be incorporated into state-space models include data not collected at evenly spaced intervals, unknown or indirectly observed state variables and changing observation error with sample methods or effort (Clark & Bjornstad, 2004).

2.3 Uncertainty

Uncertainty plays a major role in the analysis of ecological data. The natural world is inherently variable and scientists only have partial understanding of the workings of ecosystems, single-species dynamics and interspecific interactions (Ralls & Taylor, 2000). If uncertainty is not quantified, or at least acknowledged, then the assumption is being made that an aspect of the analysis, be it the model, observations, or process, are known completely without error.

Traditional models incorporate only one type of error, neglecting to include other aspects of uncertainty. Process error models assume no error in the observations, ignoring sampling variation. Alternatively, observation error models assume the population process takes a deterministic form, thus failing to account for any natural variation in the population of interest. Both process and observation error models ignore the third major source of uncertainty, that associated with the model itself. Ignoring one type of error can result in underestimates of the uncertainty around population size or parameters (Newman et al., 2006). Inclusion of both process and observation error in one model gives a more accurate assessment of the uncertainty around model inferences. It also aids in the differentiation between the two sources of error, rather than incorrectly assigning all the error to one cause (Calder et al., 2003). This may help with problems associated with identifiability and the difficulty in separating environmental and demographic stochasticity, especially when the model residuals are autocorrelated, which is often the case with population models (Jonzan et al., 2002).
In a management context, uncertainty is equated with risk. The more uncertain an outcome, the more risk is involved in taking the course of action that leads to that outcome. Rather than chance a risky decision, managers may make no decision, which is often worse for the species under consideration (Ralls & Taylor, 2000). To fully account for the risk involved in any management decision it is necessary to incorporate all sources of uncertainty. Much of the difficulty with ecological models in the past, and the reasons for the associated high levels of risk, is that traditional, mathematically simple, but biologically unrealistic, deterministic models were fit to the data and stochasticity was only added after the fact (Harwood, 2000).

The inclusion of different types of uncertainty, implementation uncertainty in particular, can have a strong influence, not only on the results, but on their use and people’s perceptions. The precautionary principle serves as an example; it is a major part of EU law that is designed to account for uncertainty, but is surrounded by a great deal of controversy. Much of the conflict is due to a lack of clear definitions and the difficulty in quantifying uncertainty around population estimates and future predictions under different management scenarios (Foster et al., 2000). The ability of the state-space model to incorporate and quantify all types of uncertainty explicitly can therefore help to increase the effectiveness of the law.

### 2.3.1 Process error

Process error, which can also be thought of as process variation, can be divided into two parts; demographic and environmental stochasticity. Demographic stochasticity refers to the inherent variability around a population’s life history processes, such as survival and fecundity. Environmental stochasticity is variation in a population’s life history traits due to some aspect of the surrounding environment. For example, breeding rate may vary from year to year based on weather conditions. While this variability is usually external to the population, it can have a major impact on the species. In the context of a state-space model, process error is incorporated through the state process, which explicitly models process error (Calder et al., 2003).
2.3.2 Observation error

Like process error, observation error consists of two parts; measurement and inference error (Harwood & Stokes, 2003). Measurement error arises from data collection due to the methods and observers involved in the study. Errors due to methods are caused by incorrect application of sampling protocols, while observer error arises from the variability among individuals in their ability to perform an assigned task. Additionally, effort will vary due to individual behaviour and available resources, which also contributes to the variability in the observations. Inference error is often a result of bias in the statistical methods used to obtain information, such as density estimates, from the data. In state-space modelling, the observation error is incorporated by modelling the relationship between the data and the state variable (Calder et al., 2003).

2.3.3 Model uncertainty

Since the exact mechanisms acting on a population are unknown, different models may be used to describe the same system, giving rise to model uncertainty. Model selection needs to be fully incorporated into inference, especially in relation to management, since different models may give different predictions, affecting the choice of management action. Additionally, ignoring uncertainty in model selection results in overconfident estimates of precision. More useful, but less specific, information can be obtained by incorporating model uncertainty into quantifying the precision of the estimator (Buckland et al., 1997). Incorporating model uncertainty into state-space models is done differently from process or observation error. Where process variation is handled through the state process and observation error through the observation process, model uncertainty may be dealt with through the use of information criteria (Sec. 2.7) in model weighting. Other ways to incorporate model uncertainty include the bootstrap (Buckland et al., 1997), or, in a Bayesian context, specifying a prior distribution for the model set (Buckland et al., 2004b; Thomas et al., 2005), treating the model as simply another parameter to be estimated (King et al., 2008; King & Brooks, 2008).
2.3.4 Implementation uncertainty

A fourth type of uncertainty, implementation error, exists only in a management context. It encompasses failures to meet management objectives, primarily due to anthropogenic factors (Harwood & Stokes, 2003), which can include changing laws, policies and political frameworks. All of these add different dimensions of uncertainty that are important to the overall ability of statistical modelling to be effective. Future shifts in laws and policy can be incorporated into analyses by forecasting under different scenarios accounting for these changes. Implementation uncertainty can also be built into the models, taking human error into account, even when no other anthropogenic change is taking place. Past management can provide information regarding previous successes and failures, thus enabling more accurate prediction and a better understanding of what can be realistically achieved.

2.4 State-space framework

Using the state vector $\mathbf{n}_t$ and the observation vector $\mathbf{y}_t$, state-space models can be depicted as a series of three probability density functions (pdfs):

$$
\begin{align*}
g_0(\mathbf{n}_0|\Theta) & - \text{Initial state distribution} \\
g_t(\mathbf{n}_t|\mathbf{n}_{t-1},\Theta) & - \text{State process distribution} \\
f_t(\mathbf{y}_t|\mathbf{n}_t,\Theta) & - \text{Observation process distribution}
\end{align*}
$$

where $\Theta$ is a vector of parameters. The model can be extended so the parameters evolve in time according to a stochastic process or dependencies on other parameters. The parameter vector then takes on the subscript $t$ for the two processes and the initial state distribution, since the parameters now vary with time. This is referred to as a hierarchical state-space model, and is specified by the addition of a fourth pdf (Buckland et al., 2004b; Jonsen et al., 2003),

$$
h_t(\Theta_t) - \text{Parameter process distribution.}
$$
As well as time-based variation in the parameters, hierarchical modelling can also refer to parameter dependencies on different types of layering, such as habitat or individual variation.

In addition to the state and observation process distributions, a prior distribution is needed when working in a Bayesian framework (Buckland et al., 2004b; Newman et al., 2006; Thomas et al., 2005),

\[ g_0(\Theta) - \text{Prior distribution} \]  

in which \( \Theta \) can take the appropriate subscript in the case of hierarchical models. In a Bayesian analysis is is also possible to consider the initial distribution \( g_0(n_0|\Theta) \) as a prior on the initial state vector \( n_0 \).

The first order Markov restriction can be relaxed to include dependence on earlier time periods so that the state process distribution becomes,

\[ g_t(n_t|n_{t-1},...,n_0,\Theta) \]  

resulting in a hidden process model, of which the state-space model is a special case (Newman et al., 2006).

### 2.4.1 State process

The state process models the mechanisms that move the population of interest from their state at time \( t - 1 \) to their state at time \( t \), and can capture demographic and environmental stochasticity (Buckland et al., 2004b). The simplest form the state process can take is a deterministic projection matrix, such as a Leslie or Lefkovitch matrix (Thomas et al., 2005). The standard form of these matrices can handle birth, death and age or growth, respectively (Lefkovitch, 1965; Leslie, 1945, 1948). Conceptualising the state process from the perspective of Leslie or Lefkovitch matrices is advantageous because ecologists are familiar with them. However, these matrices are only an approximation of the changes over time; the expected value of \( n_t \) (\( E[n_t] \))
need not be a linear function of $n_{t-1}$, making the Leslie or Lefkovitch matrix representation a convenience only. The matrices do not, therefore, play a direct role in fitting the model to the data (Thomas et al., 2005; Newman et al., 2006).

The matrices used to conceptualise state-space models differ from the traditional approach to Leslie and Lefkovitch matrices. The state process is modularised, broken into sub-processes characterised by simpler matrices each representing only one process, such as birth or survival (Thomas et al., 2005). It is the product of these sub-matrices that produces the generalised Leslie or Lefkovitch matrix (Buckland et al., 2004b). Modularising the sub-processes creates a more flexible and straightforward approach to model building, allowing complex dynamics to be more easily communicated and manipulated. Additionally, individual sub-processes can be studied in isolation, the order of the sub-processes can be rearranged and alternative hypotheses can be readily generated and tested, all within a single modelling approach (Thomas et al., 2005). However, dividing the state process into sub-processes makes it necessary to discretise the system (Buckland et al., 2004b). This is not a problem in most cases because animal populations often have specific times in which breeding, movement and other life history processes take place.

For example, given a species $N$ with two life history stages, juvenile and adult, we might define three matrices to move the population from time $t-1$ to time $t$; one for recruitment ($R$), one for birth ($B$) and one for survival ($S$), which occur in that order. Starting at the beginning of year $t-1$ with a state vector for $N$ ($n_{t-1}$), consisting of juveniles and adults, we then have,

$$SBRn_{t-1} = \begin{pmatrix} \phi_j & 0 \\ 0 & \phi_a \end{pmatrix} \begin{pmatrix} \lambda \\ 1 \end{pmatrix} \begin{pmatrix} 1 & 1 \\ n_{j,t-1} & n_{a,t-1} \end{pmatrix} = \begin{pmatrix} \phi_j \lambda \\ \phi_a \end{pmatrix} \begin{pmatrix} \phi_j \lambda \\ \phi_a \end{pmatrix} \begin{pmatrix} n_{j,t-1} \\ n_{a,t-1} \end{pmatrix} = E[n_t]$$

where $\lambda$ is the birth rate, $\phi_a$ and $\phi_j$ are adult and juvenile survival, respectively, and the product of the matrices forms a generalised Leslie matrix, where $E[n_t]$ is the expected value of the state vector in year $t$. An important difference between the generalised Leslie matrix produced by the individual biological processes and a
traditional Leslie matrix is that in the matrix produced by the individual processes, only the survivors breed (Buckland et al., 2007).

The matrix format allows for easy manipulation of the model sub-processes and the comparison of different models. Therefore, rather than assuming recruitment is the first process to occur with species \( N \), we may wish to explore the possibility that survival occurs first, followed by recruitment,

\[
\begin{align*}
\text{BRS}_{n_{t-1}} &= \begin{pmatrix}
\lambda \\
1
\end{pmatrix}
\begin{pmatrix}
1 & 1
\end{pmatrix}
\begin{pmatrix}
\phi_j & 0 \\
0 & \phi_a
\end{pmatrix}
\begin{pmatrix}
n_{j,t-1} \\
n_{a,t-1}
\end{pmatrix} = (2.6)
\end{align*}
\]

which produces a generalised Leslie matrix notably different from the matrix resulting from Eqn. 2.5. This easy manipulation of the sub-processes allows for a straightforward comparison of the different possible models and the effects of starting year \( t-1 \) at different time points in a species’ life history.

Breaking Lefkovitch matrices into sub-processes is done no differently than for Leslie matrices. If instead of automatic recruitment into the adult population, juveniles became adults based on the probability, \( \psi \), of obtaining a certain level of growth, otherwise remaining in the juvenile population with a probability of \( 1-\psi \), the matrices become,

\[
\begin{align*}
\text{SBG}_{n_{t-1}} &= \begin{pmatrix}
\phi_j & 0 \\
0 & \phi_a
\end{pmatrix}
\begin{pmatrix}
1 & \lambda \\
0 & 1
\end{pmatrix}
\begin{pmatrix}
1-\psi & 0 \\
\psi & 1
\end{pmatrix}
\begin{pmatrix}
n_{j,t-1} \\
n_{a,t-1}
\end{pmatrix} = (2.7)
\end{align*}
\]

Possibly the main advantage of state-space modelling in comparison to matrix modelling is that whereas both Leslie and Lefkovitch matrices are typically deterministic, state-space modelling can incorporate demographic stochasticity by allowing the result of a biological process to be the realisation of a pdf. For example, survival might be modelled as a binomial distribution where \( n \) is equal to \( n_{j,t-1} \) or \( n_{a,t-1} \) and \( p \) is
equal to $\phi_j$ or $\phi_a$, respectively,
\[
\mathbf{S}n_{t-1} = \begin{pmatrix}
s_{j,t} \sim \text{binomial}(n_{j,t-1}, \phi_j) \\
s_{a,t} \sim \text{binomial}(n_{a,t-1}, \phi_a)
\end{pmatrix}.
\quad (2.8)
\]

Furthermore, environmental stochasticity can be included by allowing parameters to vary at random between years. The parameters could also be modelled as a function of covariates, such as weather or fitness of the parents. If the parameters are known to vary, but the relevant covariates are not available, it is possible to model the parameters as random effects (Buckland et al., 2007). The inclusion of stochasticity in this manner means that process variation is incorporated directly in the state process (Buckland et al., 2007; Millar & Meyer, 2000a; Newman et al., 2006). By assigning a pdf with a known distribution to each stochastic subprocess, the implementation of the evolution of the state process can be thought of as a series of linked pdfs, with the output of the previous pdf providing the input for the next one (Buckland et al., 2004b; Thomas et al., 2005; Newman et al., 2006).

Observations are not required for each of the sub-processes in the model. Instead, many of these individual life processes may lack observations, and thus represent a hidden state. Modelling unobserved, hidden states is achieved through the state process distribution, $g_t(n_t | n_{t-1}, \Theta)$, which, broken down into individual, linked probability distributions, represents each of the sub-processes defined in the matrix representation. Given the process model defined in Eqn. 2.5, there would be three sub-processes, each with a respective pdf; one for recruitment ($G_{r,t}$), one for birth ($G_{b,t}$) and one for survival ($G_{s,t}$). The realisation of the sub-processes is a vector, $u_{k,t}$, for each sub-process $k$ at time $t$, where the vector associated with the final vector forms $n_t$,
\[
\begin{align*}
  u_{r,t} &\sim G_{r,t}(n_{t-1}, \Theta) \\
  u_{b,t} &\sim G_{b,t}(u_{r,t}, \Theta) \\
  n_t &\sim G_{s,t}(u_{b,t}, \Theta)
\end{align*}
\quad (2.9)
\]

where $G$ is a distribution for the appropriate sub-process pdf. While data may only be available from yearly counts representing a sample from $n_{t-1}$, estimates of density associated with each of the sub-processes can also be obtained.
While identifiability can become a problem, there is no theoretical reason for a limitation on the number of sub-processes. Restrictions on the number of sub-processes occur from a practical standpoint. More sub-processes mean a greater complexity of the state pdf and the likelihood. To evaluate the state pdf it is necessary to integrate over all the sub-processes, and a greater number of processes leads to more complex integration (Buckland et al., 2004b). Given a total of \( K \) independent sub-processes moving the population from \( n_{t-1} \) to \( n_t \) the state process could be written as,

\[
g_t(n_t|n_{t-1}, \Theta) = \int_{u_1:K-1,t} \prod_{k=1}^{K} g_{k,t}(u_{k,t}|n_{t-1}, u_{1:k-1,t}, \Theta) du_{1:K-1,t} \quad (2.10)
\]

where \( u_{1:K-1} \) refers to all the subprocesses, \( u \), from the first to one minus the \( K^{th} \). The complexity of the integral makes it difficult, if not impossible, to solve analytically. As a result, necessity has driven the development of different methods to ascertain the value of the integral.

### 2.4.2 Observation process

The observation process relates the observations at time \( t \) to the state, or components of the state, at time \( t \). This gives the probability of the data conditional on the observation model parameters and the actual states. The observation process can be either stochastic or deterministic (Buckland et al., 2004b; Rivot et al., 2004; Thomas et al., 2005) and the probability models linking \( y_t \) to \( n_t \) can be flexible. It is possible to specify a wide variety of sampling and estimation procedures, such as mark-recapture, line-transect surveys, harvest and catch per unit effort data. Also, there is no requirement for the data to be used in the form in which it was collected (Newman et al., 2006). For example, when performing a line-transect survey the direct observations can be turned into estimates of the different components of the state vector (Buckland et al., 2001). The uncertainty associated with the estimation would then provide a measure of the observation error. On the whole, inferences for a state-space model can be summarised as inferences on the states and parameters conditional on the observation process (Buckland et al., 2004b).
2.5 Model fitting

2.5.1 Bayesian versus Frequentist

State-space models can be fit in both a frequentist (e.g., de Valpine & Hastings, 2002) and Bayesian framework (e.g., Calder et al., 2003). In the past, frequentist (‘classical’) approaches have dominated statistics, both in theory and application. However, the development of new computational techniques and increased computer processing power has contributed greatly to the increased interest in Bayesian methods, more because of the increased ease of application as opposed to any inherent advantage or advance in Bayesian theory (Gelman et al., 1995).

The classical paradigm is built upon the idea that the observed data, \( y \), are simply one of multiple possible values of \( y \) that could be obtained if the same data collection methods were done many times (McCarthy, 2007). The probability of observing the data conditional on a model, \( P(y|\theta) \), is used to compare the data to the model. The model is then fit to the data by maximising this likelihood. Model appropriateness is determined through tools such as hypothesis testing and \( p \)-values, which depend on the long run frequencies of the theoretically repeated data, given the model. An advantage to classical statistics is that maximum likelihood methods can be applied in a more ‘automatic’ approach, with a good chance of nearly optimal inference. In contrast, Bayesian methods require more thought about the specific modelling-situation if optimal inference is to be achieved (Efron, 1986).

Where the frequentist approach uses a pdf for the data, given the parameters, Bayesian methods are concerned with a distribution for the parameters, given the data, \( P(\theta|y) \). This is because in a Bayesian framework data are seen as fixed values that can arise from a number of different processes. \( P(\theta|y) \) can be found through the application of Bayes’ Theorem,

\[
P(\theta|y) = \frac{P(y|\theta)P(\theta)}{P(y)} \tag{2.11}
\]

where \( P(y|\theta) \) is the likelihood, \( P(y) \) is the probability of the data, \( P(\theta) \) represents a
joint prior distribution and $P(\theta|y)$ is the posterior distribution from which all inference will be drawn. Alternatively, the posterior can be related to the prior and likelihood according to the proportionality,

$$P(\theta|y) \propto P(y|\theta)P(\theta)$$  \hspace{1cm} (2.12)

where the constant of proportionality, also called the normalising constant, is,

$$P(y) = \int P(\theta)P(y|\theta)d\theta$$  \hspace{1cm} (2.13)

making integration one of the cornerstones of Bayesian statistics (Brooks, 1998).

Fitting the models within a Bayesian framework is less restrictive on the assumptions regarding distributions (Calder et al., 2003) and allows for the inclusion of prior information (Buckland et al., 2004b). Additionally, there are no theoretical impediments to fitting complex models with many parameters and multi-layered probability specifications or models with missing data (Gelman et al., 1995). Bayesian modelling is also more appropriate when there are poorly identifiable model parameters, which can often be the case in ecological modelling when limited data may need to be fit to complex models (Omlin & Riechert, 1999). For these reasons I have decided to use Bayesian techniques to fit my state-space models for the hen harrier (*Circus cyaneus*), the red grouse (*Lagopus lagopus scoticus*) and their interactions.

### 2.5.2 Bayesian state-space model fitting

To begin Bayesian inference for state-space models it is necessary to specify a joint prior distribution, $P(\theta)$, which is now for the initial state, parameters and state vector,

$$P(\theta) = P(n_0, n_{1:T}, \Theta) = g_0(n_0|\Theta) \times g_0(\Theta) \times \prod_{t=1}^{T} g_t(n_t|n_{t-1}, \Theta)$$  \hspace{1cm} (2.14)

where $g(.)$ are the state process pdfs described in Eqn. 2.1.

Next, the data are incorporated through the observation process. The full time-series of observations can be viewed as a sample from a probability distribution. Thus, the
likelihood function, $P(y|\theta)$ is the observation process model and is a function of the states and parameters,

$$P(y|\theta) = P(y_t|n_t, \Theta) = \prod_{t=1}^{T} f_t(y_t|n_t, \Theta)$$ (2.15)

where $f(.)$ is the observation process distribution described in Eqn. 2.1. Finally, the prior distribution is updated on the basis of the data according to Bayes’ Theorem to obtain the posterior $P(\theta|y)$,

$$P(\theta|y) = P(n_0, n_{1:T}, \Theta|y_t) = \frac{g_0(n_0|\Theta) \times g_0(\Theta) \times \prod_{t=1}^{T} [f_t(y_t|n_t, \Theta)g_t(n_t|n_{t-1}, \Theta)]}{P(y_{1:T})}$$ (2.16)

where $n_{1:T}$ and $y_{1:T}$ are the full time series of states and observations, respectively, and $P(y_{1:T})$ is the normalising constant $P(y)$. Eqn. 2.16 gives the posterior distribution from which samples can be taken to provide information about the states and parameters (Newman et al., 2006). The complexity involved in calculating Bayes theorem is in the integration needed to calculate $P(y_{1:T})$,

$$P(y_{1:T}) = \int P(y|\theta)P(\theta)d\theta = \int g_0(n_0|\Theta) \times g_0(\Theta) \times \prod_{t=1}^{T} [f_t(y_t|n_t, \Theta)g_t(n_t|n_{t-1}, \Theta)] d\Theta.$$ (2.17)

The detail of which can be increased by specifying the unobserved, hidden states,

$$P(y_{1:T}) = \int g_0(n_0|\Theta) \times g_0(\Theta) \times \prod_{t=1}^{T} \left[ f_t(y_t|n_t, \Theta) \prod_{k=1}^{K} g_{k,t}(u_{k,t}|n_{t-1}, u_{1:k-1,t}, \Theta) \right] d\Theta.$$ (2.18)

Obtaining an analytic answer to the above integrals can be extremely difficult, if not impossible. This is why numerical or analytic approximation techniques are often used in Bayesian statistics, as a whole (Brooks, 1998). All inferences made in state-space modelling, whether Bayesian or Frequentist, can be seen as the result of integration (Buckland et al., 2004b).
While the integral in Eqn. 2.18 is complex, it forms a normalising constant (Eqn. 2.13), since it is the same for all possible parameter values, $\Theta$, with fixed $y_t$. Therefore, the main computation problem in Bayesian methods becomes finding the value for unknown normalising constants, $P(y_{1:T})$ (Gelman et al., 1995; McCarthy, 2007), so that the posterior summary statistics can be computed.

Some of the debate around Bayesian methods focuses on the need to specify the priors (Dennis, 1996; Newman et al., 2006). When there is previous knowledge, priors can be used to incorporate the available information (Guo, 2003). Yet, when there are no existing historic facts, priors still need to be chosen. In this case, ‘uninformative’ priors are used in an attempt to minimise the impact of the prior on the posterior. This is an effective way of taking into account, and directly acknowledging, ignorance (Harwood & Stokes, 2003; Buckland et al., 2007). Some feel the choice of prior is arbitrary, negating the usefulness of Bayesian inference methods. Yet, aspects of classical, frequentist statistics, such as alpha levels, can also be chosen arbitrarily. The subjective nature of priors is undeniable (Ellison, 1996; Millar & Meyer, 2000a), making a prior sensitivity analyses necessary to account for any possible posterior dependence on the choice of priors (Clark & Bjornstad, 2004).

### 2.5.3 Fitting methods

Three different methods for model fitting will be reviewed, all of which are applicable to state-space modelling; the Kalman filter (e.g., Besbeas et al., 2002), Markov chain Monte Carlo (MCMC) (e.g., Millar & Meyer, 2000b) and sequential importance sampling (SIS) (e.g., Thomas et al., 2005). Each method has advantages and disadvantages, often depending on the nature of the data or the type of inference that needs to be achieved. Many of the issues with the methods have been addressed using addendums to the basic algorithm in order to make them more efficient or to avoid problems inherent in the basic, unaltered algorithm (Newman et al., 2006).
2.5.4 Kalman filter

Frequentist statistical methods use the Kalman filter (Kalman, 1960) to find an analytic solution to the complex integration. The solution requires a normal dynamic linear model in order to be effective. Assumptions of linearity and normality are not always appropriate and can sacrifice biological realism for mathematical tractability. The extended Kalman filter uses linear approximations of non-linear models to try and shape a non-linear model into a linear framework (Millar & Meyer, 2000a). This method is inappropriate when the approximation is too crude compared to the real relationship, altering the behaviour of the models and making inference unreliable (Rivot et al., 2004; Newman et al., 2006). It may also not be possible to linearise or normalise population dynamics without sacrificing the biological relevance of the models (Newman et al., 2006). However, an advantage to the Kalman filter is that its assumptions of normality allow for the simple updating of estimates (Carlin et al., 1992). It is also possible to apply the Kalman filter through Bayesian techniques (Calder et al., 2003). The relative ease of implementation and fitting is another advantage to the Kalman filter.

2.5.5 Sequential importance sampling

SIS is a Monte Carlo method in which a large number of candidate parameter and state vectors, referred to as ‘particles,’ are chosen from the proposal distribution. The likelihood is evaluated for each particle, and the likelihood weights are calculated and stored, then used to draw samples with vectors chosen in proportion to their weights. This is done at every time step, generating a sample from the posterior distribution for that time point, which becomes the prior for the next time point (Thomas et al., 2005). A problem is that over time, a limited number of particles begin to dominate the particle set, with progressively fewer having weights effectively different from zero. This is known as ‘particle depletion’ and gives an inaccurate representation of the state and parameter posterior densities (Buckland et al., 2007). Modifications, such as kernel smoothing, can be used to combat particle depletion. In kernel smoothing, new samples for the parameters are created at each time step around a distribution
centred on the particles that survived the previous time step. In this case only the parameters are perturbed, not the states. This increases diversity around the particles supported by the data (Newman et al., 2006). Other methods include the auxiliary particle filter (Pitt & Shepard, 1999) and residual sampling (Liu & Chen, 1998), both of which take a different approach to particle depletion than kernel smoothing. Combinations of these modifications can be used and improvements to the methods continue to be an area of research (Newman et al., 2006).

### 2.5.6 Markov chain Monte Carlo

In a Bayesian context, MCMC generates dependent samples from the posterior distribution through use of a Markov chain whose stationary distribution is the required posterior (Buckland et al., 2007). The initial vector of parameters is updated according to draws from a proposal distribution. The chain moves to the updated vector with a probability that depends on the ratio of the proposal and prior distributions, which is evaluated at the projected and current value of the chain (Newman et al., 2006). Monte Carlo methods avoid evaluating the complex integrations needed to obtain the target distribution analytically by drawing independent samples from known distributions in such a way so as to result in realisations from the target distribution. The desired summary statistics are then calculated using these realisations. In MCMC, the algorithms draw samples from a distribution via Monte Carlo integration using a Markov chain so the draw for the current iterate, \( i \), depends solely on the previous iterate, \( i - 1 \) (Gilks et al., 1996). The new sample created is the starting point for the next set of draws. If an appropriate updating strategy is chosen the distribution of the sample vectors will converge on the posterior distribution (Gilks et al., 1996; Harwood & Stokes, 2003). Ideally, the chain will eventually converge to a stationary distribution that is no longer dependent on the starting point assumed for the parameter values or the number of iterations run. The sample averages from the distribution form the expected values for the parameters and states of interest. Convergence on the stationary distribution is usually determined visually or through the use of convergence diagnostics (Gilks et al., 1996). Poor convergence and mixing of the MCMC chains can make inference from MCMC methods unreliable (See Secs.
2.6 MCMC inference

Most applications of MCMC are on Bayesian inference (Gilks et al., 1996), whether or not state-space models are being used. Models fit in a Bayesian framework can yield results comparable to those from traditional approaches (e.g., Omlin & Riechert, 1999), although this is not always the case (Gelman et al., 1995). Bayesian inference from MCMC is achieved by using a collection of the simulated draws from the stationary, or target, distribution to summarise the posterior distribution. By sampling directly from the posterior, the complex integrations seen in Eqns. 2.13 and 2.18 are performed implicitly, providing an efficient way to evaluate the integral (Brooks, 1998).

Since the stationary distribution forms the required posterior, summaries of the quantities of interest, such as the quantiles, median and variance can be obtained directly from the distribution (Gilks et al., 1996). Additionally, unobserved states and covariates can be estimated by conditioning on the observed data and estimated values for the parameters (King et al., 2008). It is important that inferences from MCMC are being made on the correct posterior distribution (Gelman et al., 1995), so checks are necessary to be sure that the stationary distribution has been reached.

There are a number of different algorithms available for MCMC model fitting. One family of simulation methods is the Metropolis-Hastings (MH) algorithm, where the Gibbs sampler and Metropolis algorithm are special, more specific, cases that are also commonly used (Gelman et al., 1995; Brooks, 1998). Both methods generate samples for Bayesian posterior distributions, but each has its advantages and disadvantages. For example, the efficiency of the Gibbs sampler is offset by the fact that it is not always possible to sample from the given posterior conditional distributions the algorithm requires. Algorithms should be chosen based on their appropriateness for the task at hand, as opposed to any other reason (Brooks, 1998).
For the MH algorithm, the state in the chain at iteration \( i + 1, X_{i+1} \), is chosen by sampling a candidate point, \( Y \), from a proposal distribution, \( q(.|X_i) \). The candidate point is then accepted with a probability \( \alpha(X_i, Y) \),

\[
\alpha(X, Y) = \min \left( 1, \frac{\pi(Y)q(Y, X)}{\pi(X)q(X, Y)} \right),
\]

(2.19)

where \( \pi(.) \) is the stationary distribution. If the candidate point is accepted, then \( X_{i+1} = Y \), otherwise \( X_{i+1} = X_i \). The Gibbs sampler is a special case where the acceptance probability simplifies to unity, since the proposal distribution is the posterior conditional distribution for the parameter of interest. In the case the the Metropolis algorithm, where \( q(X, Y) = q(Y, X) \) the acceptance probability takes the form (Brooks, 1998),

\[
\alpha = \min \left( 1, \frac{\pi(Y)}{\pi(X)} \right).
\]

(2.20)

Returning to the MH algorithm, the proposal distribution, \( q(.) \) can take any form, and the stationary distribution of the chain will still be the target distribution. The following arguments will be used to show this point. The MH algorithm has a transition kernel \((K(.))\),

\[
K(X_{i+1}|X_i) = q(X_{i+1}|X_i)\alpha(X_i, X_{i+1}) + I(X_{i+1} = X_i)[1 - \int q(Y|X_i)\alpha(X_i, Y)dY],
\]

(2.21)

\[
I(X_{i+1} = X_i)[1 - \int q(Y|X_i)\alpha(X_i, Y)dY],
\]

(2.22)

where first term in Eqn. 2.21 refers to the acceptance of candidate \( Y \) and the second term comes from the candidates rejection. \( I(.) \) is an indicator function, which equals one when the candidate is rejected, but is otherwise zero (Gilks et al., 1996). The stationary distribution, \( \pi(.) \), enters the transition kernel only through \( \alpha \) (Eqn. 2.19), where is is found as a ratio, so the distribution need only be known up to a constant of proportionality for the purposes of implementation of the MCMC algorithm (Brooks, 1998).

From Eqn. 2.19 it is possible to write,

\[
\pi(X_i)q(X_{i+1}|X_i)\alpha(X_i, X_{i+1}) = \pi(X_{i+1})q(X_i|X_{i+1})\alpha(X_{i+1}, X_i).
\]

(2.23)
Given Eqns. 2.23 and 2.21, the following detailed balanced equation can be obtained,

\[ \pi(X_i)K(X_{i+1}|X_i) = \pi(X_{i+1})K(X_i|X_i + 1), \quad (2.24) \]

which is then integrated on both sides with respect to \( X \) to give,

\[ \int \pi(X_i)K(X_{i+1})dX_i = \pi(X_{i+1}). \quad (2.25) \]

Working on the assumption that \( X_i \) is from the stationary distribution, the left-hand side of Eqn. 2.25 gives the marginal distribution of \( X_{i+1} \). Therefore, if \( X_i \) is from the stationary distribution, then \( X_{i+1} \) will also be from \( \pi(\cdot) \). This does not prove that the MH algorithm will reach the stationary distribution from its initial point \( X_0 \), only that once \( \pi(\cdot) \) is reached, all samples will be from the stationary distribution.

The distribution of \( X_i \) will converge to a stationary distribution if three properties are meet: the chain needs to be irreducible, aperiodic and positive recurrent. Irreducible means that from all starting points, the Markov chain should be able to reach any area of the parameter space with some positive probability. Being aperiodic means the chain is stopped from regular oscillations between different states. Positive recurrance can be defined using Eqn. 2.25, whereby if the initial sample of \( X_0 \) is chosen from \( \pi(\cdot) \), all following samples will also be from the stationary distribution. If irreducibility can be demonstrated, then \( X \) will be positively recurrent (Gilks et al., 1996).

While Markov chain simulation is complicated, it remains the easiest way to obtain reliable results for many problems, including hierarchical modelling (Gelman et al., 1995). Although the algorithms themselves are straightforward, they can be difficult to code on one’s own due to the relationships between the distributions being used. While the existence of freeware such as the BUGS project (Spiegelhalter et al., 2007) reduces this difficulty (Millar & Meyer, 2000a), MCMC may still not be the most efficient or practical choice for model fitting due to its computational expense (O’Neill, 2002).
2.6.1 Why MCMC?

One advantage of using MCMC methods is the high level of modelling complexity that the methods can support (O’Neill, 2002). The population dynamics of the red grouse show cyclic patterns and are therefore unlikely to meet the assumptions of linearity required for the Kalman Filter. While linear approximations could have been used (e.g., Besbeas et al., 2003), it seemed ill-advised to use an approximation when other methods are available that would allow the non-linear nature of the data to be fit more directly (Millar & Meyer, 2000a).

For SIS, the drawbacks with regards to particle depletion were considered to be severe, especially given the complexity of the models I would be fitting. Additionally, the lack of readily available software to help fit SIS models was a difficulty. It was therefore decided to work with methods that could be more quickly applied, from a coding perspective.

While MCMC has practical limitations, especially with regards to long run times for the chains, the disadvantages were deemed to be outweighed by the advantages presented by the flexibility of the approach and availability of software to expedite the model fitting. Therefore, I have fit all the models presented in this thesis in the free software package WinBUGS 1.4.2 (Spiegelhalter et al., 2007) using BlackBox Component Builder 1.5, which allowed me to code and implement my own functions in WinBUGS, where necessary.

2.6.2 Mixing

‘Mixing’ refers to the ability of the Markov chain to move around the parameter space. At each iteration, when updating the Markov chain a candidate draw is taken from a proposal distribution. If the candidate draw is accepted, the chain updates to the new value for the next iteration. However, if the candidate is rejected, the chain does not move, and the value of the draw at the next iteration remains unchanged. If the chain does not move for several iterations, the chain is deemed to be mixing
slowly. Slow mixing chains will need to be run for more iterations in order to reach convergence (Gilks et al., 1996). For mixing to be considered ‘good,’ the chain should mix rapidly for the entire length of the chain (See Fig. 2.1).

![Figure 2.1: Examples of mixing for chains of 1100 iterations. The upper plot shows slow mixing, while the lower plot displays good mixing (Fernandez, 2005).](image)

The speed at which a chain mixes will depend, in part, on the proposal distribution, which will determine the size of the steps between the current draw and the candidate draw. If the steps are small there will be a high rate of acceptance of the candidate draws, but it will take longer for the chain to move about the parameter space, so mixing will be slow. When large steps are taken, the acceptance rate of candidate draws will be low, resulting in a chain that frequently fails to move and thus poor mixing. Ideally, a balance between these two extremes is needed (Gilks et al., 1996). Mixing can be easily assessed from visual inspection of time-series plots, since the pattern of small or large steps is readily apparent. Various methods can be employed to try and improve mixing (see Brooks, 1998, for discussion).
2.6.3 Burn-in and autocorrelation

In order to make reliable inferences a large number of samples are needed, a proportion of which will be ignored as a ‘burn-in’ period to ensure the algorithm is no longer dependent on its starting points, and may be working in equilibrium space (Harwood & Stokes, 2003; Millar & Meyer, 2000a). Even if a Markov chain has quickly reached an equilibrium space, a burn-in period is still required, as these early samples will still be characteristic of the starting points as opposed to the target distribution. The inclusion of a burn-in period is important, since the inferences from the chain depends on the assumption that the distribution of the draws is a close approximation of the target distribution (Gelman et al., 1995; Brooks, 1998).

Autocorrelation between MCMC draws is another issue of which to be aware. Since the individual draws are correlated, inference is artificially precise, as opposed to cases where the draws are independent. In and of itself, this is not a problem, because when the chains have reached the stationary distribution it is possible to ignore the order of the draws since the draws are identically distributed. However, the autocorrelation can lead to slow movement of the chains. Autocorrelation can be accounted for through a process called thinning, in which only every $k^{th}$ draw is kept, and the others are discarded. However, thinning’s main purpose is to allow for storage of the values of the individual draws to avoid computer memory problems (Gelman et al., 1995; Gilks et al., 1996; Brooks, 1998).

The need for a burn-in and the practice of thinning means that a large number of iterations will have to be performed. The exact number will depend on how long the process takes to first reach equilibrium space and to then converge on a posterior distribution. If the chain is too short and thinning is taking place, the inefficiency of the effective number of simulations, compared to the actual number of draws, will be reflected in the posterior intervals around the quantities of interest (Gelman et al., 1995).
2.6.4 Convergence

To simulate the posterior density, $P(n_0, n_{1:T}, \Theta | y_t)$, from a Markov chain it is necessary to run the simulation for long enough to allow the distribution of the most current draws to approximate the stationary distribution. When the iterations from the Markov chain draw close to the stationary distribution, the chain is considered to have converged (Gelman et al., 1995). According to the theory behind the use of MCMC, convergence is guaranteed (El Adlouni et al., 2006), although from a practical standpoint it may not be reached. Convergence cannot be determined through the inspection of a single Markov chain, since while a single chain may appear to have converged, in reality it could have got stuck in one area of the parameter space. Therefore, to assess convergence, multiple chains with different starting points should be run in parallel (Gelman et al., 1995). However, there is some debate as to whether multiple long chains, or one very long chain is better for inference and efficiency (Brooks, 1998).

Determining when convergence has taken place can be done through visual inspection of the time-series plots containing the multiple chains (Gilks et al., 1996). If, after the burn-in period, which may be different for each chain, all the chains are seen to be covering the same area, the chains are considered to have converged. To ensure that the chains are not simply getting stuck in the same area of the parameter space, starting points should be chosen that are overdispersed, so that the chains are starting in very different areas of the parameter space (Gelman & Rubin, 1992). However, visual assessment of the time series plots can be considered unreliable, especially when modelling many different quantities of interest (Gelman et al., 1995; Gilks et al., 1996), since it depends on an individual’s perceptions and cannot be replicated.

As well as visually assessing convergence, it is also possible to use various convergence diagnostics. These diagnostics are still an active area of research, since no one diagnostic will work in every application (Brooks, 1998; El Adlouni et al., 2006). I considered one of the more common diagnostics, the Brooks-Gelman-Rubin statistic (Gelman & Rubin, 1992; Brooks & Gelman, 1998a,b), which looks at the ratio of
the within-chain over between-chain variability to determine convergence. The ratio should be as close to one as possible, and no greater than 1.2, otherwise the chains have failed to converge (Gelman et al., 1995; Gilks et al., 1996).

If convergence is not reached within the set number of iterations, more will need to be run. However, if after a sufficiently long time period convergence is still not reached, it may be necessary to increase the efficiency of the simulations. One way this can be achieved is by choosing more realistic starting points for the MCMC chain (Gilks et al., 1996). Other methods to improve convergence include changing the proposal distribution and reparameterising the model. Once the chains are determined to have converged, inferences about the posterior distribution can be made by treating the iterates from the portion of the Markov chain after the burn-in as samples from the stationary distribution. Inferences from chains that have failed to converge may misrepresent the stationary distribution (Gelman et al., 1995).

2.6.5 Prior sensitivity analysis

Specific to Bayesian methods, the relationship between the prior and posterior distributions is an important part of inference. We would expect the posterior variance to be less than the prior variance, since the posterior distribution incorporates the data. Additionally, we would also hope that the posterior distribution, given sufficient data, will be almost independent of the prior, since the compromise between the prior and the data should be controlled by the data at large sample sizes (Gelman et al., 1995). However, there remains a role for informative priors where strong prior information is available.

While, in theory, the prior contains all reasonable values of the parameter or state of interest, this is not strictly necessary, since if enough information is available, the influence of the data will far outweigh the prior (Gelman et al., 1995), provided that prior choice is even somewhat reasonable. Therefore, while the nature of priors is subjective (Ellison, 1996; Millar & Meyer, 2000a), the choice of prior should have little effect on posterior inference if enough data are available (e.g., Omlin & Riechert,
Thus, it is necessary to investigate the sensitivity of the posterior to prior choice.

Since all inference is made from the posterior, reporting the entire distribution via graphical displays is useful (Gelman et al., 1995). This concept extends to prior sensitivity analysis, where the posterior and prior distributions can be compared to try and judge the influence of the prior. When the posterior probability density is superimposed on the prior probability density for a single parameter on the same plot it is possible to visually assess whether the posterior distribution is being unduly affected by the choice of prior. When the data provide little or no information on the parameter, the posterior distribution will closely match the prior. Another way to assess the dependency on the prior is to calculate the percentage overlap of the two distributions. An overlap of 35% or more has been suggested as an ad hoc guideline for when the parameter of interest is only weakly identifiable. However, while the threshold appears to be consistent in its behaviour, it is only appropriate to use with uniform distributions; otherwise it is difficult to calibrate (Gimenez et al., 2008).

When the signal in the data is not strong, the data do not overwhelm the effect of the prior on the posterior distribution. As a result, even when the posterior appears to have been updated from the prior by the data, there may still be some dependency on the choice of prior itself. To assess this aspect of prior sensitivity, multiple possible priors should be investigated. Then, by comparing posterior summaries, such as the mean and variance, it is possible to determine whether the prior continues to influence the posterior (Gelman et al., 1995). The choice of prior can therefore affect the inference drawn from the analysis, which is acceptable when justifiably informative priors are being used.

The choice of prior remains difficult, especially in cases of high prior sensitivity. It is often best to choose ‘sensible’ priors - priors that are general enough to allow for information from the data to update to a posterior distribution, but still specific to the model being considered. It is possible that prior sensitivity is only apparent when priors are ‘too’ informative, thus overwhelming the data. In this case, a so-called ‘mildly’ informative prior is a better choice, in order to allow inference to be data
driven. Much effort has been placed in trying to identify ‘weakly’ or ‘non’-informative priors that will allow inference to be affected only by data (Gelman et al., 1995). The choice of ‘noninformative’ priors according to formal rules can lead to problems, making such a default solution to the choice of priors unattractive (Kass & Wasserman, 1996). In reality, even noninformative priors give some level of information, even if it is only to acknowledge the lack of information.

2.7 Information criteria

Model selection is usually achieved through information criteria, such as Akaike’s Information Criterion (AIC) or Bayesian equivalents such as the Bayesian Information Criterion (BIC) or Deviance Information Criterion (DIC). All of the information criteria are composed of a model likelihood and a penalty, which pertains to effective degrees of freedom. The value and use of the penalties are derived from asymptotic, theoretical arguments. The choice of information criterion will depend, in part on the aim of the study, especially when dealing with hierarchical models. In general, whichever information criterion is used, the ‘best’ model is deemed to be the one with the lowest information criterion value (Buckland et al., 1997). The AIC, BIC and DIC are arguably the most common information criteria to be used in the biological literature. The reason for this may be the easy implementation of these criteria in freely available software such as MARK (White & Burnham, 1999), Distance (Thomas et al., 2009) and WinBUGS (Spiegelhalter et al., 2007).

2.7.1 AIC

AIC and its variants, such as the QAIC and AICc, are likely to be the information criteria most familiar to ecologists. AIC estimates the difference between the distribution that generated the data and the ‘true’ model it approximates. A function of the likelihoods of different, related, models are compared, penalising for increased numbers of parameters \(k\) where the penalty is equal to \(-2k\). Therefore, while increased numbers of parameters will also increase the likelihood, the penalty works to ensure
that simpler models can remain plausible candidates for the ‘best’ model, as defined by the AIC (McCarthy, 2007). The corrected form of the criterion, AICc, deals with small sample sizes, since AIC is biased towards high-dimensional models when sample size is small relative to the order of the models under consideration. The ‘improved’ AIC, AICi, is meant to provide a criterion for a state-space framework, but can be used only with linear models (Bengtsson & Cavanaugh, 2006).

While the model with the lowest AIC is the closest to ‘truth,’ the distance to the ‘true’ model is still unknown. Furthermore, the differences between the ‘best’ model and another model may be small. The difference in the AIC scores between the model with the lowest AIC (the ‘best’ model) and any other model in the model set is referred to as the δAIC. Models with a δAIC of two or less are considered to have strong support from the data, while models with δAIC values between three and seven are seen to have much less support. Any model with a δAIC greater than ten is considered to have essentially no support from the data (Burnham & Anderson, 2002). When δAIC values are small, the model with the lowest value may still be used, but its outputs and predictions may be compared with those of the models with similar AIC scores. Alternatively, model averaging can be used to make predictions across the supported model set. As well as model selection, the AIC can also be used for model weighting, to help account for model uncertainty (Buckland et al., 1997).

2.7.2 BIC

Like AIC, the Bayesian Information Criterion (BIC) compares the likelihoods of different models, penalising for increased model complexity and assuming the best model is the one with the lowest BIC value. However, where AIC only penalises by \(-2k\), BIC uses the natural log of the sample size, \(n\), instead of the constant \(-2\), giving \(-\log(n)k\) (Schwarz, 1978), which results in a higher penalty for increased model complexity than either AIC or DIC when the sample size is greater than about eight. The BIC is also related to another model selection tool, Bayes factors, which can be approximated using the BIC (Kass & Wasserman, 1995; Volinsky & Raftery, 2000), although Bayes factors can also be related to AIC (Smith & Spiegelhalter, 1980). The BIC is most
appropriate in situations where one of the models being considered can reasonably be assumed to be the truth. An issue with BIC is that the criterion is difficult to implement for hierarchical models (Spiegelhalter et al., 2002).

2.7.3 DIC

The Deviance Information Criterion (DIC) uses the deviance of the posterior distributions in a Bayesian analysis for model selection. The DIC compares the posterior mean deviance of different models, penalising for model complexity according to the effective number of parameters, $p_D$,

$$DIC = D(\theta) + p_D,$$

(2.26)

where,

$$D(\theta) = -2 \log[P(y|\theta)] + 2 \log[(r(y))],$$

(2.27)

in which $r(y)$ is a standardising term that is solely a function of the data.

The effective number of parameters in a model can be estimated using the difference between the posterior mean of the deviance and the deviance of the posterior means,

$$p_D = \bar{D}(\theta) - D(\bar{\theta}).$$

(2.28)

This allows for a measure of model fit when the number of parameters is not clearly defined, such as in hierarchical modelling. This provides an advantage over AIC and BIC, which require a defined focus to determine the effective number of parameters, basically giving all models a non-hierarchical structure (Spiegelhalter et al., 2002). However, DIC is not applicable when there are missing data, since the effective dimensionality can then be negative. While there are possible ‘corrections’ that can be made, they do not have a theoretical basis, needing to be implemented on a case-by-case basis (Celeux et al., 2006).

Like the AIC and BIC, a lower DIC value indicates a model closer to ‘truth,’ thus the model with the lowest DIC is the ‘best’ model. When comparing different models, the
\( \Delta \text{DIC} \) is used in the same manner as the \( \Delta \text{AIC} \), following the same rules of thumb (Spiegelhalter et al., 2002).

### 2.8 Multi-species state-space models

The theoretical framework for state-space modelling already incorporates the ability to model multiple species. However, this aspect of the method has yet to be implemented (Buckland et al., 2007). Other species that may play a role in the process model, through behaviours such as competition or predation, are usually incorporated in the model as covariates. The inclusion of additional species in a static form results in a great deal of information on multi-species interactions being lost. The use of point estimates means that any uncertainty around the alternative species will be ignored, resulting in a failure to fully explore all the possible levels at which the species may be interacting. Additionally, information on multi-species interactions is lost because it is not possible to see the reciprocal effect of the species of primary interest on the species included as a covariate. Two separate models could be run to examine the behaviour of both species, but this still does not account for the uncertainty around the density estimates for the additional species, nor does it allow for a ‘real time’ response of one species to another.

The simultaneous inclusion of uncertainty around density estimates is important when estimating parameter values. The same holds true in multi-species modelling for the density estimates of species not under direct observation at the time. These estimates are usually included in the model as covariates, with no acknowledgment of the variability around these estimates, or how the additional species may react to the presence of the main species of interest. The importance of including multi-species interactions can be seen in the differences between single-species functional response (SSFR) and multi-species functional response (MSFR) models (Asseburg et al., 2006). The full interactions of the species under consideration cannot be captured by studying the predator and only a single prey. SSFR and MSFR models can give different functional forms of what should be the same interaction because of the importance of
the inclusion of multiple species simultaneously. This allows for more explicit inclusion and accounting of behaviours such as prey switching (Asseburg, 2005; Asseburg et al., 2006). Given the importance of accounting for multiple species at this level of interaction, it is just as important to include more detailed multi-species interactions at the population dynamics level.

To include the population dynamics of multiple species in one state-space model is conceptually simple. As with single-species models that prevent males from becoming females within a species, multi-species models are constrained so that it is not possible to move between states corresponding to different species; individual species must stay within their own state-process, e.g. a juvenile hawk cannot become an adult rabbit. Building the models is also straightforward; the state-processes can be constructed individually first, as single-species state-space models, and then combined into multi-species models. This can become complicated, as the different species’ models may work on different spatial and/or temporal scales. There is no reason why this should be an impediment to modelling the multi-species interactions; it is simply an aspect of the modelling process that will need to be accounted for when combining the models.

The main conceptual change to the state-space models is with regards to the state vector, \( \mathbf{n}_t \). Where, previously, the state vector was divided into the age or stage classes for an individual species (e.g., Eqn 2.5), the vector now includes the various states for all species in the model. For example, given two competing species, \( i \) and \( h \), each with a juvenile and adult age class, the state vector for time \( t \) would be,

\[
\mathbf{n}_t = \begin{pmatrix}
  n_{i,j,t} \\
  n_{i,a,t} \\
  n_{h,j,t} \\
  n_{h,a,t}
\end{pmatrix}
\]  

(2.29)

The use of matrices to conceptualise multi-species models can become complicated. This is a result of the increased number of states and the realistic possibility that life history processes such as birth or movement may occur at different points in the life cycles of the multiple species included in the model. The construction of the sub-process matrices becomes more difficult, but is not impossible, so the matrices
remain a useful tool for visualising the life history processes of all the species involved in the modelling process (for an example of a complex, multiple stage, age and sex class matrix for a single species see Buckland et al. (2004b)).

The model fitting process for a multi-species state-space model is the same as for a single-species model. The only difference is in the number of states. Additionally, multi-species state-space models can be extended to multi-species hidden process models, so that the states of the species of interest are no longer dependent only on their states in time $t - 1$, but can also have higher order dependencies. Furthermore, there is no theoretical reason to limit the number of species in a multi-species state-space model. Entire ecosystems could be estimated simultaneously to account for their interactions and associated uncertainties all at once. The biggest issue with this type of modelling is lack of data. While state-space models can handle some missing data, a complete lack of data raises different issues. Where there is no information, the results of the state-space model will be uncertain, since there will be nothing to directly limit the estimation of population parameters and densities into the realm of biological plausibility. Prior knowledge can be incorporated to try and limit the models to what is believed to be appropriate, but this is highly subjective. Even if data were available to fit multi-species models of entire ecosystems, limitations need to be implemented for practical purposes. Just as models can be over-parameterised, so too could they be over-complicated through the inclusion of too many species that do not have a true impact on one another. Finally, there will be high costs with regards to computation time and model selection. More complex models will take longer to run, and as more species are included in the model, there will be more debate over the specific mechanisms driving both individual species' population processes and the mechanisms behind the multi-species interactions.

2.9 Discussion

Population studies are complex and state-space models can be used to help analyse the available data. The models can incorporate linear and non-linear interactions, stochasticity, variable environmental factors (Buckland et al., 2004b, 2007), missing
data, uneven time series (Clark & Bjornstad, 2004; Guo, 2003), changes in observation or estimation methods and more (Thomas et al., 2005). Their flexible nature is part of what makes them such a powerful tool for statistical analysis, allowing for biologically realistic modelling of complex population dynamics.

Model fitting can take place in both a frequentist and a Bayesian framework, and different methods can be used to fit the models, depending on the nature of the models themselves and the requirements of the individual doing the model fitting. While I have chosen to fit my state-space models within a Bayesian framework using MCMC, this choice was due to practical constraints, as opposed to any theoretical debates with the different modelling techniques. The complex, non-linear structure of my models, combined with freely available software to fit MCMC in a Bayesian context, is what drove my decision with regards to my choices in model fitting. The disadvantages, such as the long run-times and inability to use information criteria were deemed to be outweighed by the advantages of this particular method.

Single species state-space models can easily be extended to include multiple species, with the primary cost being in increased computation time. However, the models are also constrained by a lack of data, which can be expensive to collect, both in terms of money and the time and effort needed to obtain all the required information. Yet, the benefits of multi-species modelling can outweigh the costs, especially in those studies where understanding the interactions between multiple species is the goal.

At this point, there are relatively few long-term data sets that fit the requirements of multi-species state-space modelling, in terms of the data available. However, the multi-species model presented in this thesis, that of the predator prey interactions between the hen harrier and red grouse, provides an example of what can be achieved even when only part of the necessary information is available. Additionally, the case study highlights the capabilities of multi-species state-space modelling, and what type of data needs to be collected in the future, both for these, and other, species.
Chapter 3

Hen Harriers

3.1 History

Historical records of hen harriers (*Circus cyaneus*) go back as early as the 16th century. The birds’ name comes from a believed tendency to prey on domestic fowl, particularly chickens, although the earliest records of the hen harrier are from a time period prior to the domestication of poultry. Perceived as vermin, harriers have always suffered from persecution, but still managed to maintain their range through Britain until the late 18th century. Changing agricultural practices and an increase in the popularity of grouse (*Lagopus lagopus scoticus*) hunting led to the harriers’ near-extinction. Heavy persecution by gamekeepers in the 19th century resulted in harriers being completely extirpated from the Scottish Highlands, with only a few remaining in the Western Isles and Orkney. It was not until after World War II, with a decline in keepers and grouse shooting, that harriers began to make a recovery. Another shift in agricultural practices, the introduction of large conifer plantations, resulted in an increase in the harriers’ rodent prey, aiding the raptors’ recovery in Britain. Yet, as these plantations mature, the habitat becomes unsuitable for the harriers (Hull, 2001; Marchant et al., 1990). Legal protection was extended to hen harriers and other birds of prey in 1954, which led to a small recovery. However, hen harriers were still heavily persecuted on the grouse moors and have remained an endangered species within the UK. Marked increases in harrier numbers have been reported on grouse moors where active protection of hen harriers has taken place. Unfortunately, there is still reason
to believe illegal persecution takes place on many grouse moors to try and increase the number of grouse available for shooting in the autumn (Etheridge et al., 1997; Redpath & Thirgood, 1997).

### 3.2 Life history

As in most birds of prey, the female hen harrier is larger than the male. There is also distinct colour dimorphism, with the females being brown and the males a blue-grey, making them easy to sex in the field (Scharf & Balfour, 1971). Juvenile harriers, male and female, are brown; males typically get their grey plumage at one year of age (Picozzi, 1984). Part of what makes *Circus sp.* so unique is their facial disk. It is most noticeable as a ring of white dots forming a mask around the birds’ eyes. The disk functions in the same manner as owls’ facial disks, funneling sound towards the birds’ ears to enhance hearing (Simmons, 2000).

Hen harriers are ground nesting birds, settling in areas that provide cover within their chosen habitat (Millon et al., 2003). Nests can be within 500 metres of one another, as harriers are not strongly territorial birds (Redpath & Thirgood, 1997), even in the breeding season (Millon et al., 2003). While there is some intra-species aggression, mostly between males, aggression levels in hen harriers are still very low, even when compared to the smaller, colonial Montagu’s harrier (*Circus pygargus*) (Garcia & Arroyo, 2002). Breeding usually begins in the second or third year of the harriers’ life, although a few will begin to breed in their first year. Harriers display high rates of polygamy, especially in Orkney (Picozzi, 1984).

A pair’s brood and clutch size will vary according to the type of habitat in which the nest is located (Millon et al., 2003). Different habitat characteristics, such as the density of prey species, will affect productivity, while others, such as the availability of cover, do not have an effect on the number of young harriers produced (Redpath & Thirgood, 1997). During incubation, harriers are very sensitive to disturbances (Millon et al., 2003) and will abandon a nest if the disturbance is large enough (Picozzi, 1978). This makes them particularly susceptible to anthropogenic disturbances,
negating the need for gamekeepers or others to directly destroy the nest.

Harrier nest success should be highest on grouse moorland, since that is their preferred habitat (Etheridge et al., 1997). The increased success may be due to the management of the moor, which works to maintain a patchwork of heather (*Calluna vulgaris*) and grasses, increasing prey density (Green & Etheridge, 1999) as well as areas suitable for nesting (Redpath & Thirgood, 1997). However, due to illegal persecution, managed moors have the lowest rate of successful nests (Etheridge et al., 1997; Green & Etheridge, 1999). Predation can also affect the harriers’ nest success. Since harriers are ground nesting birds, their nests are more susceptible to predators such as foxes (*Vulpes vulpes*) and stoats (*Mustela erminea*). However, studies have shown that the legal control of these predators does not have a noticeable effect on hen harrier nest success (Green & Etheridge, 1999).

A successful harrier nest will typically fledge three young (Picozzi, 1978), although climate conditions will also affect fledging success (Redpath et al., 2002a). The juvenile birds disperse in the fall and typically show no natal site loyalty. Harriers have been known to settle at sites over 500 kilometers from where they were born. However, after successfully nesting in an area, harriers show high breeding site fidelity, even using the same nest site year after year (Watson, 1977). This means that within a region, harrier numbers depend on the survival of the harriers already in the area and the numbers that immigrate to the area. The number of young fledged is therefore immaterial with respect to influencing harrier numbers within a region. Instead, the importance of fledging success is with regards to its contribution to the overall hen harrier population in Britain.

Although site-loyal, harriers, males in particular, do not often remain in an area over winter. This may be due, in part, to the fact that many of the small prey species upon which the harriers depend for food, such as the meadow pipit (*Anthus pratensis*), become scarce in the winter; the males then need to work harder to find prey. As a result, after the young have fledged, male harriers will move south to warmer climes, returning to their breeding site in the spring. In contrast, some females will remain in their nesting area over winter. The difference may be due to the females’ larger size,
which allows them to catch prey, such as rabbits and hares (lagomorphs), that are too large for the males to hunt. Some juvenile birds may also wait until the spring to disperse remaining in the natal area over the winter (Marquiss, 1980).

### 3.3 Feeding behaviour

Hen harriers are generalist predators, feeding on a wide variety of different species. However, their main prey items are meadow pipits and field voles (*Microtus agrestis*) (Picozzi, 1978). Another common prey item are red grouse chicks, which are taken by hen harriers on an opportunistic basis. Other species eaten include lagomorphs and other small passerines and rodents. Analysis of pellets in Aberdeenshire, Scotland, has shown that as much as 80% of the harriers’ diet can be small passerines, with only 18% being small mammals (Picozzi, 1984). The prominence of small passerines in the harriers’ diet in Scotland was supported in later studies as well (Redpath et al., 2001a). However, in France it was noted that the common vole (*Microtus arvalis*) made up 53.7% of the harriers’ prey, while passerines and small gamebirds made up only 22.3% (Millon et al., 2003). Harriers can, therefore, change their diets based upon prey availability, although the staple items, small mammals and passerines, will remain the same. As well as differences between areas, prey will vary between the sexes. The larger females will often take the larger prey, such as lagomorphs, while males will focus on smaller prey, such as meadow pipits (Marquiss, 1980; Picozzi, 1984). These prey are most abundant on moorland, grouse moors in particular, but harriers can also be found in other habitats, such as young conifer plantations, due to the large numbers of rodents available.

Harriers’ preference for a given area due to prey availability also exists within a larger area, such as a grouse moor. The raptors do not hunt uniformly over their home ranges, but rather where prey are more likely to be found (Picozzi, 1978). However, areas in which prey availability is poor are not monitored for changes, even though abundance of some prey species, such as voles, can alter dramatically with the seasons (Hudson, 1992). This behaviour may be due to the fact that harriers will switch between prey species; if one species becomes scarce in the area they switch to
another species rather than monitor areas that have not yielded prey in the past. This is supported by the fact that while harriers’ habitat preference may mirror their prey choice, they show no species preference when hunting, striking at any available prey seen during flight (Picozzi, 1978). Hunting behaviour also differs between males and females, with males’ foraging being more influenced by the location of the nest than habitat characteristics or prey densities, whereas females seem to be most affected by grouse chick abundance (Redpath & Thirgood, 1997; Thirgood et al., 2003). There are seasonal shifts as well, since in the spring, during courtship, hunting is done almost exclusively by males to provide for the females. Additionally, later in the year, once the young hatch and can be left alone in the nest for reasonable lengths of time, the females become more active hunters, foraging more widely than the males in search of food for their young (Redpath & Thirgood, 1997). Catch rates can also vary among the different types of habitats. Managed moors have higher catch rates, indicating there is more food available to the harriers in these areas, although the mechanism for this is unknown (Redpath et al., 2002b).

The rate at which the harriers are able to catch their prey is important because it determines the harriers’ food consumption and their impact on their prey species. Consumption rate can be measured using the species’ functional response. There are three basic types of functional responses. A Type I functional response represents a constant increase in consumption with increasing prey density. This is unrealistic for many predators because factors other than prey density often affect consumption. A Type II functional response takes a hyperbolic shape, representing a limit in the predators’ consumption at high prey densities. The limit on consumption is more realistic for many species, since it takes into account the fact that a predator’s ability to catch prey will be limited by factors such as handling time. Predators that specialise in a particular species often show this type of functional response. A Type III functional response takes a sigmoidal shape, representing prey saturation at high densities and prey switching at low densities (Begon et al., 1996). When modelled with a single species functional response (SSFR), this is assumed to be the typical behaviour of generalist predators, which will switch between different prey types depending on densities of the individual prey species (Matthiopoulos et al., 2007).
Traditionally, harriers have been viewed as a generalist predator and would be expected to display a Type III functional response to their prey. Harriers can, in fact, show a Type III SSFR to red grouse, supporting their classification as a generalist predator (Redpath & Thirgood, 1999). However, Matthiopoulos et al. (2008) shows the fallacy associated with fitting a SSFR to the behaviour of a generalist predator, since very different SSFRs can give close fits to data gathered from the same underlying multi-species system. The multiple specifications of the type of functional response occurs because the SSFR does not take into account the predators’ alternate prey. In the case of the hen harrier, the SSFR does not include the densities of voles or pipits, which will affect the consumption of red grouse. As a result, it is therefore beneficial to use a multi-species functional response (MSFR), which incorporates all of the harriers’ prey species when calculating the rate of consumption. Using a MSFR it is possible to observe the expected Type III response to grouse. However, harriers display a Type II functional response to voles and pipits, implying that harriers may be generalists on red grouse, but specialists on voles and pipits (Asseburg, 2005).

The harriers’ role as a generalist predator has important implications for their impact on red grouse densities. The raptors feed opportunistically on grouse chicks, switching to other prey when grouse density is too low. However, because the chicks are not the harriers’ primary food source, harrier numbers can remain high at low grouse density. While the number of chicks taken by harriers will decline with reduced densities (Asseburg, 2005), the highest proportion of grouse chicks are taken from the moors where adult density is low (Redpath, 1991). This prevents grouse densities from increasing, possibly forcing the grouse into a predator pit depending on the densities of alternate prey (Matthiopoulos et al., 2007). As a result, grouse moors with breeding hen harriers consistently produce fewer young per female grouse than moors in which harriers are absent (Redpath, 1991). Although hen harriers do not push grouse to extinction, they do repress the population. Unfortunately, these densities are too low to allow for driven shooting on grouse moors, which is an important source of income for many estates (Redpath et al., 2004; Thirgood et al., 2000b). The result is the heavy persecution on harriers by some gamekeepers on grouse moors as they try to maintain grouse numbers high enough for shooting (Amar et al., 2004; Redpath &
3.4 Conservation

Conservation interest in the hen harrier is high, since the species is both threatened and indigenous to the UK. However, the conservation of the hen harrier has been a difficult issue ever since the first UK legislation protecting birds of prey. Hen harrier numbers are believed to remain low due to the raptors’ habitat preference for grouse moors. The gamekeepers that maintain the moors for grouse shooting perceive the hen harrier as a threat to the economic viability of the estate, due to the harriers’ predation of red grouse chicks. As a result, the hen harrier is persecuted illegally in these areas, keeping the overall numbers of harriers from increasing (Etheridge et al., 1997).

Stronger protection for the hen harrier, or increased penalties for those caught persecuting the bird, will not necessarily result in an increased harrier population (Woodroffe et al., 2005b). The grouse moors, the harriers’ preferred habitat, are maintained only through human intervention. As is often the case, it is the desire of private landowners to hunt that maintains wildlife habitat in what would otherwise be an agricultural setting (Leader-Williams & Hutton, 2005). Gamekeepers actively work to maintain habitat that is favourable to the red grouse in order to earn money through grouse shooting (Amar et al., 2004). The maintenance of the moorland is done through controlled burning of strips of heather to ensure that grouse have the different range of habitat they require to flourish; new heather for food, old heather for cover (Thompson et al., 1995; Picozzi, 1968). If the estate can’t generate income through grouse shooting there is no need to maintain the moors. Without the process of rotational burning and grazing the land would follow a natural successional state and begin to shift towards young woodland (Tudor & Mackay, 1995). Alternatively, to continue to generate income, the estate may change their land use practices, planting conifer plantations or introducing sheep grazing (Hudson et al., 1995; Robertson et al., 2001). Either way, habitat that is of value to the hen harrier, and needed for its conservation, is lost. It is therefore necessary to balance the conservation needs of the hen harrier
with the economic needs of the hunting estates.

Besides the hen harrier and red grouse, other species of conservation interest, such as the peregrine falcon (*Falco peregrinus*), curlew (*Numenius arquata*) and lapwing (*Vanellus vanellus*), use the grouse moorland. While these species do not depend on the grouse moors as their only habitat, the moorlands do form an important part of their environment (Brown & Bainbridge, 1995; Tharme et al., 2001). Shifts in habitat management will therefore affect more than just hen harriers and red grouse. For effective conservation of all the species using the managed moors, it is necessary to account for the needs of the hunting estates. Without some assurance of the continued prosperity of the grouse moors when harriers are present, gamekeepers will continue to persecute the raptors, hindering their recovery. However, persecution of the gamekeepers will result in a loss of the very habitat needed to ensure the recovery of the hen harrier, as well as many other species of interest (Joint Raptor Study, 1998; Redpath et al., 2004).

To understand which management actions would best balance the needs of the gamekeepers with those of the harrier, it is necessary to understand how the grouse and harrier interact. Field experiments and theoretical modelling can help build this understanding. Field experiments provide concrete data on the species’ behaviour, but are time consuming. Given the long periods of grouse cycles, there could be a significant time lag between the start of the study and its conclusions. Theoretical models can be constructed in less time and can be used to estimate the species’ response to different management scenarios. However, the theoretical model lacks data, and so would still need to be tested in the field. Field experiments and theoretical models complement each other, each addressing the lack in the other.

### 3.5 The model

The model developed here is primarily meant to investigate UK harrier populations, since my primary interest in modelling hen harrier dynamics is to determine their effect on their prey, red grouse in particular. The model therefore moves from spring
in time \( t - 1 \) to spring in time \( t \), as harrier numbers impact the red grouse through predation on grouse chicks, which hatch in the spring. Determining spring numbers of harriers is not trivial due to the high rate of polygamy in hen harriers, which makes it difficult to accurately use the abundance of one sex as an indicator for the abundance of the other (Hudson, 1992). The matter is further complicated by the fact that the sex ratio can vary from year to year (Picozzi, 1984). The consumption rate is calculated per harrier pair (Asseburg, 2005), so here I model the number of pairs (nests), as opposed to the total number of birds. Males are not a limiting resource due to the presence of polygamy, so females serve as a better indicator of the number of nests present. Using the number of nests as an indication of predation pressure will overestimate predation slightly, since bigamous males do not catch more prey than monogamous males, but are essentially counted twice. Polygamy, while common, is not so rife as to create a large disparity in the measure of predation. Like males, female predation remains unchanged by their breeding status. However, females paired with a bigamous male are likely to catch larger prey to compensate for the lower provisioning rate of the male. As a result, there is no significant difference in fledging success between the two classes of female (Redpath & Thirgood, 1997). In catching larger prey, females paired with bigamous males ensure that the relative consumption of biomass remains the same between the two classes of nests. Since the females are catching larger prey, as opposed to more prey, their consumption of grouse chicks does not increase. Given the low rates of hen harrier predation on adult grouse (Redpath & Thirgood, 1997) it is also unlikely that females in bigamous relationships are increasing adult grouse mortality.

Nest numbers will be determined through female movement and survival. Fecundity will not be taken into account, for while it can be used as a measure of overall success of the species, it does not affect hen harrier density in a given area. This is due to high rates of juvenile dispersal, with almost no natal site fidelity. However, after dispersal, harriers are site faithful (Picozzi, 1978), so movement is important and essentially replaces fecundity in terms of increasing harrier numbers in an area. Given this information, the basic population model is as follows,

\[
H_t = H_{t-1} \phi_{t-1} + \eta_t, \quad (3.1)
\]
where $H_{t-1}$ is the density of female hen harriers on the grouse moor at $t-1$, $\phi_{t-1}$ is the survival rate between time $t-1$ and $t$, and $\eta_t$ is immigration at time $t$.

Survival and movement are themselves determined by other factors. Movement into an area is dependent on the density of the hen harriers’ primary prey species, voles and pipits (Redpath & Thirgood, 1999; Redpath et al., 2002a); I might model this dependency as,

$$\eta_t = \exp(\beta_0 V_t + \beta_1 P_t - \beta_2 H_{t-1} \phi_{t-1}),$$

(3.2)

where $\beta_0$, $\beta_1$ and $\beta_2$ are parameters to be estimated and $V_t$ and $P_t$ are vole and pipit densities, respectively, per km$^2$ in the study site at year $t$. Movement is limited by the density of female harriers already in the area, $H_{t-1} \phi_{t-1}$. In the absence of any voles, pipits or harriers the equation still allows for a single young harrier to settle in an area. This allows for the possibility that, at high overall densities of hen harriers, young birds may be forced to settle in areas lacking voles and pipits, but where secondary prey species are present.

Survival is dependent on prey consumption and is affected differentially by prey of different energetic values. However, only the consumption of pipits plays a direct role in hen harrier survival (Redpath & Thirgood, 1997). Males leave the moors as pipit numbers begin to fall and most females do not stay on the moors over winter (Watson, 1977). Yet, during the winter months voles will often show an increase in numbers, while the decline takes place during the summer (Lambin et al., 2000). This implies that winter survival is not being driven by vole densities. Furthermore, harriers can be found in the absence of voles and grouse and will remain at high densities even after vole populations crash (Redpath et al., 2002a). Survival can therefore be modelled as,

$$\phi_t = \frac{\exp(\alpha_0 + \alpha_1 P_t)}{1 + \exp(\alpha_0 + \alpha_1 P_t)},$$

(3.3)

where $\alpha_0$ and $\alpha_1$ are parameters to be estimated, $P_t$ is the density of pipits in time $t$ and $\alpha_0$ encompasses all other sources of mortality. I assume, with the exception of the effect of pipits, that per capita mortality is constant across years. Ideally, for a model
to be generally applicable to any hen harrier population, illegal persecution should also be taken into account (Etheridge et al., 1997), but data on illegal killing is not available, so it is not possible to include its effects directly. However, the parameter $\alpha_0$ can incorporate the effects of persecution on harrier survival; when illegal killing is occurring, the estimate of $\alpha_0$ should be lower in comparison to areas where the harrier is protected.

### 3.6 The data

I used data collected in Langholm moor in the period 1992-1999. Langholm is divided into six grouse beats. A beat is an area of the moor managed by a specific keeper for grouse shooting. For the grouse counts, twelve 0.5 km$^2$ areas, two on each of the beats, were selected. The areas were widely spaced across the entire moor and were chosen to be representative of vegetation within the beat while being accessible terrain in which to count grouse. The counts provided an absolute measure of grouse density per km$^2$ (Redpath & Thirgood, 1997).

For meadow pipits and other passerines, line transects 1 km in length were used to estimate abundance. A total of 18 one km$^2$ squares were chosen at random, three in each of the six beats on Langholm moor. Each square contained two line transects and the same observer conducted all the counts, recording the number of individuals, by species, within 200 m of the transect. An index of small mammal abundance was estimated through snap trapping at two sites within each of the six beats, chosen to be representative of the beats’ habitat. At each site 50 traps were set over two nights to give a total of 100 ‘trap nights’ per site (Redpath & Thirgood, 1999).

Estimates for meadow pipit density were obtained using the computer program Distance 5.0 (Thomas et al., 2009), which enables the application of distance sampling methods to line transect, and other distance sampling, data. The recorded number of voles was converted to density using a scaling factor of 520 previously estimated to relate voles caught per 100 trap nights to density per km$^2$ (Asseburg, 2005).
The number of harriers attempting to breed was determined by observing the moor for displaying harriers in the early spring. Through observation of the birds it was determined whether a male was bigamous, and, if so, the relative status (primary or secondary) of the female was recorded. All the female nests were monitored closely through the breeding season and regular checks were done to ensure that no late breeders or other females were missed. The managers of the moorland had agreed to refrain from illegal persecution of hen harriers during the eight years of the study, so there was no reason to be concerned with the effect of illegal killing on hen harrier survival in this case (Redpath & Thirgood, 1997).

### 3.7 Model fitting

The hen harrier model was fit in a state-space framework as described in Chapter 2. The fitting of the model varied slightly from what was described earlier, as harrier numbers were believed to be known without error. There is therefore no need for an observation model. Instead, a super-population model was fit to the hen harrier dynamics, using the known number of nests for time \( t \) to estimate nest numbers for time \( t + 1 \). This acknowledges the fact that while a set number of harrier nests were found each year, other numbers were possible under the same conditions due to environmental and demographic stochasticity.

Estimates from the super-population \( (H_t) \) will be found for time \( t \), using the observed number of harrier nests from time \( t - 1 \) \( (H_{Obs,t-1}) \). The true, observed numbers will have a distribution with relation to the estimates from the super-population. Since there cannot be negative nests in a region, a gamma distribution was used to constrain the values to be positive. A continuous distribution was used to model the harrier nests due to the practical constraints imposed by WinBUGS, which was unable to handle a discrete distribution, such as the Poisson, without some difficulty.

The parameters for the gamma distribution were found by assuming a binomial distribution for harrier survival \( (\phi_{t-1}) \) and a Poisson distribution for movement \( (\eta_t) \).
The mean ($\mu_t$) and variance ($\sigma_t^2$) of the gamma distribution were then found by summing the distributions for survival and movement. The parameters of the gamma distribution ($\alpha_{\Gamma,t}, \beta_{\Gamma,t}$) could then be calculated,

\[
\begin{align*}
\sigma_t^2 &= H_{t-1} \phi_{t-1} (1 - \phi_{t-1}) + \eta_t \\
\mu_t &= H_{t-1} \phi_{t-1} + \eta_t \\
\beta_{\Gamma,t} &= \frac{\mu_t}{\sigma_t^2} \\
\alpha_{\Gamma,t} &= \mu_t / \beta_{\Gamma,t} \\
H_{\text{Obs},t} &\sim \Gamma(\alpha_{\Gamma,t}, \beta_{\Gamma,t}),
\end{align*}
\]

where $\mu_t$ is the estimate from the super-population.

### 3.8 Priors

The parameters in the harrier model, $\alpha_0, \alpha_1, \beta_0, \beta_1$ and $\beta_2$, are used to define harrier survival, $\phi_t$ (the $\alpha$ parameters) and harrier movement, $\eta_t$ (the $\beta$ parameters). While I do not explicitly define priors for $\phi_t$ and $\eta_t$, their values are calculated through the use of estimated parameters (Eqns. 3.2 and 3.3), which results in the presence of implicit priors on survival and movement. Therefore, when selecting priors for the $\alpha$ and $\beta$ parameters, it is necessary to check that they combine to form reasonable implicit priors on $\phi_t$ and $\eta_t$, respectively.

Mildly informative priors were chosen for the parameter values to fit with what was known about their behaviour. For survival (Eqn. 3.3), $\alpha_0$ can take both positive and negative values to allow survival estimates to range from zero to one. A slightly restrictive prior was chosen for $\alpha_0$ to allow for an uni-modal implicit prior on $\phi_t$. Therefore, the parameter was given a $N(0,1)$ prior. A prior with a larger variance, such as a $N(0,10)$, gave a bi-model implicit prior on survival with spikes at zero and one. The second parameter, $\alpha_1$, is constrained to be positive, as pipits are known to increase, not decrease survival (Redpath & Thirgood, 1997). Given the estimated densities of pipits (216.5-575.2 km$^{-2}$), a prior needed to be chosen that would not
automatically overwhelm $\alpha_0$, but that would still leave the possibility for larger values of $\alpha_1$. The raw values of pipit densities, instead of standardised values, were used to allow for comparison with the community model in Chapter 6, where a process model was fit to pipit density. While it is possible to calculate the standardised values within WinBUGS, such deterministic calculations can increase the run time of the models, further supporting the use of the raw values. By back transforming from a normal distribution with a small mean and a large variance, a seemingly precise prior of LN(-5.29, 0.833) was chosen to avoid allowing $\alpha_0$ from being overwhelmed.

Not accounting for the pipit densities, the combination of the priors for $\alpha_0$ and $\alpha_1$ give a hill-shaped implicit prior on survival. However, when the different values for $P_t$ are taken into account, the implicit prior for survival skews strongly to the left, spiking at one (Fig. 3.1). Since harriers are known to have a high survival rate (Etheridge et al., 1997) the implicit prior is not completely unreasonable. Additionally, choosing a prior that gives a more reasonable prior on $\phi_{t-1}$ means decreasing the prior’s variance, which would make it too informative on $\alpha_1$, resulting in the failure of the posterior to move away from the prior.

![Figure 3.1: The implicit prior for harrier survival ($\phi_t$), when pipit density ($P_t$) is equal to 216 pipits km$^{-2}$ and the implicit prior for harrier immigration ($\eta_t$), when pipit density ($P_t$) is equal to 216 pipits km$^{-2}$, vole density ($V_t$) is equal to 900 voles km$^{-2}$ and the number of harrier pairs to remain in the area from time $t-1$ ($H_{t-1} \phi_{t-1}$) is equal to ten.](image)
For movement (Eqn. 3.2), parameters $\beta_0$ and $\beta_1$ were constrained to be positive to account for the fact that the presence of voles and pipits is known to cause harriers to move into, not out of, an area. The priors were chosen based on previous estimates from a similar equation for the hen harriers’ aggregative response (Matthiopoulos et al., 2007), which indicated that the values would be low given the possible high densities of both voles and pipits. Therefore a $\Gamma(1,50)$ prior was chosen for both parameters. The last parameter, $\beta_2$, measures the effect of current harrier density on restricting movement into an area. The prior was also constrained to be positive, as the negative effect of the prior presence of harriers on movement is defined in the model itself. It seemed unlikely, given the low territoriality of harriers, that the number of birds moving into an area would be reduced by more than the number of birds already present. However, it is possible, especially in limited habitats, that each bird present would stop more than one new bird from settling in an area. As a result, $\beta_2$ was given a $\Gamma(1,5)$ prior, since while the body of the distribution is less than one, the long tail allows for values as high as three. The combination of the three priors, when taking possible vole, pipit and harrier densities into account, creates a strongly right-skewed implicit prior on movement. The implicit prior essentially allows for a nearly infinite number of harriers to move into any given area. While not biologically realistic, by allowing for the possibility of extremely high numbers of immigrants, the implicit prior avoids limiting $\eta_t$ by being too informative (Fig. 3.1).

<table>
<thead>
<tr>
<th>$\Theta$</th>
<th>Prior</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_0$</td>
<td>N(0,1)</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>LN(-5.29, 0.833)</td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>$\Gamma(1,50)$</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>$\Gamma(1,50)$</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>$\Gamma(1,5)$</td>
</tr>
</tbody>
</table>

Table 3.1: Priors for the hen harrier parameters that form survival $\phi_t$ and movement $\eta_t$.

### 3.9 Results

The model was fit in WinBUGS 1.4.2 (Spiegelhalter et al., 2007) and took 373 seconds to run three chains for 100,000 iterations. A burn-in of 10,000 iterations was used.
Autocorrelation was low, so there was no need to thin the MCMC trials. Convergence was assessed using the Brooks-Gelman-Rubin statistic, as well as visual inspection of the multiple chains with different starting points. Trace plots were used to assess mixing.

Over 60 variations of the model were run to test the sensitivity of the parameter estimates to the choice of priors. The only parameter to show prior sensitivity was $\alpha_1$, the measure of the effect of pipit density on harrier survival. The parameter proved to be sensitive to the choice of variance, resulting in no change from the prior if the variance was too small. However, when a large variance was used $\alpha_1$ proved to be less sensitive to the prior, resulting in an updated posterior. No other parameter showed any type of prior sensitivity (Fig. 3.2). Since none of the priors were uniform, the 35% threshold suggested by Gimenez et al. (2008) is not appropriate in this case. There was some correlation between the values of $\alpha_0$ and $\alpha_1$, with higher values for $\alpha_1$ resulting in slightly lower values for $\alpha_0$.

![Figure 3.2: Prior (black) - posterior (red) plots for the parameters of the hen harrier model.](image)

Additionally, an intercept term ($\beta_I$) was included in Eqn. 3.2 in some of the variations.
of the model that were run to investigate prior sensitivity. The intercept term proved to be almost completely dependent on the prior and did not affect the estimates for the other $\beta$ parameters. The presence of $\beta_I$ in the equation only affected the final immigration term $\eta_t$, since some of the estimates of the intercept term could allow more than one harrier to move into an area in the absence of voles and pipits. It was therefore considered more reasonable to exclude the term from the model.

All the parameters and states showed good mixing and convergence. The prior-posterior plots (Fig. 3.2) show that the prior distributions have been updated with the data to give posteriors that are no longer unduly influenced by the choice of prior, although the parameter $\alpha_1$ remains sensitive to this choice. The posterior means for the survival parameters, $\alpha_0$ and $\alpha_1$, were 0.37 and $2.49 \times 10^{-3}$, respectively, which resulted in posterior means for survival, $\phi_t$, ranging from 71-85%, which includes the previous point estimate of 78% and are well within the 95% Confidence Interval (57%, 90%) (Etheridge et al., 1997). However, the upper limits of the 95% credible intervals on the yearly survival can fall above the previously estimated range (Table 3.2). While Etheridge et al. (1997) estimated a separate, lower survival for hen harriers on grouse moors, this value is likely due to illegal persecution. Given that harriers were protected on Langholm moor during the course of the study, using the survival estimate for moorlands not managed for grouse shooting was more reasonable. However, since the legal control of other predators, such as red fox and carrion crows ($\textit{Corvus corone}$), occurred on Langholm, the possibility remains that the estimate of adult survival provided by Etheridge et al. (1997) could be an underestimate of harrier survival for Langholm, since predator control would not have occurred on moorlands not managed for grouse shooting. Additionally, the wide 95% confidence intervals for harrier survival on unmanaged moorland reported by Etheridge et al. (1997), (57%, 90%), should be highlighted. The width of this interval is due to the sparsity of data, since only 21 females were available for the study.

The parameter values for movement also fell within a range of realistic values. The parameters $\beta_0$ and $\beta_1$ have posterior means of $1.31 \times 10^{-3}$ (95% CI: $6.095 \times 10^{-4}$, $1.902 \times 10^{-3}$)) and $9.4 \times 10^{-4}$ (95% CI: $5.04 \times 10^{-5}$, $2.357 \times 10^{-3}$)), respectively,
Table 3.2: Yearly survival estimates for hen harriers ($\phi_t$, %), with their corresponding 95% credible intervals.

<table>
<thead>
<tr>
<th>Year</th>
<th>$\phi_t$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>78.3 (64.7, 89.7)</td>
</tr>
<tr>
<td>1993</td>
<td>84.6 (70.5, 95.7)</td>
</tr>
<tr>
<td>1994</td>
<td>84.4 (64.8, 89.8)</td>
</tr>
<tr>
<td>1995</td>
<td>78.4 (62.3, 87.4)</td>
</tr>
<tr>
<td>1996</td>
<td>77.3 (63.8, 88.7)</td>
</tr>
<tr>
<td>1997</td>
<td>71.9 (57.8, 84.1)</td>
</tr>
<tr>
<td>1998</td>
<td>70.9 (56.5, 83.4)</td>
</tr>
</tbody>
</table>

as compared to previous estimates of $1.24 \times 10^{-4}$ for the aggregative response to voles and $2.63 \times 10^{-3}$ for the aggregative response to pipits (Matthiopoulos et al., 2007). The last parameter, $\beta_2$ was estimated at 0.031, supporting the evidence of low territoriality among hen harriers.

<table>
<thead>
<tr>
<th>$\Theta$</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_0$</td>
<td>0.3713 (-0.6036, 1.233)</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>$2.49 \times 10^{-3}$ (6.562 \times 10^{-4}, 5.719 \times 10^{-3})</td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>$1.306 \times 10^{-3}$ (6.095 \times 10^{-4}, 1.902 \times 10^{-3})</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>$9.403 \times 10^{-4}$ (5.04 \times 10^{-5}, 2.357 \times 10^{-3})</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>0.03099 (9.776 \times 10^{-4}, 0.099)</td>
</tr>
</tbody>
</table>

Table 3.3: Estimates and 95% credible intervals for the hen harrier parameters.

For the most part, the estimates of the expected number of successful hen harrier nests fit very closely with the true values (Table 3.4), indicating a super-population not too far off of the observed population. The greatest dissimilarities are in 1996, with the super-population value estimated as almost nine nests, while 14 nests were really observed. This seems to be a result of the combination of low nest numbers in the previous year (only eight nests) and low densities of voles and pipits limiting the immigration of harriers into the area.

The estimates for the amount of movement into the population ($\eta_t$), varied significantly from year to year, depending on the available prey densities (Table 3.5). Vole densities appeared to have the greatest effect on harrier movement, although comparisons are more difficult since normalised covariate values were not used. The greatest immigration seems to occur at peak vole densities, even when the corresponding pipit
<table>
<thead>
<tr>
<th>Year</th>
<th>Observed</th>
<th>Estimated</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>5</td>
<td>8.2 (5.6, 11.6)</td>
</tr>
<tr>
<td>1994</td>
<td>11</td>
<td>10.37 (8.1, 13.3)</td>
</tr>
<tr>
<td>1995</td>
<td>8</td>
<td>10.91 (9.4, 12.5)</td>
</tr>
<tr>
<td>1996</td>
<td>14</td>
<td>8.63 (7.5, 9.8)</td>
</tr>
<tr>
<td>1997</td>
<td>20</td>
<td>19.05 (14.3, 25.3)</td>
</tr>
<tr>
<td>1998</td>
<td>17</td>
<td>16.19 (13.6, 18.5)</td>
</tr>
<tr>
<td>1999</td>
<td>13</td>
<td>13.08 (10.7, 15.2)</td>
</tr>
</tbody>
</table>

Table 3.4: The observed numbers and super-population estimates for the hen harrier population with their corresponding 95% credible intervals.

density was low. The harriers that survive, remaining in the area from the previous year ($H_{t-1} \phi_{t-1}$) have very little impact on immigration ($\beta_2$: 0.03099, 95% CI: ($9.776 \times 10^{-4}$, 0.099)).

<table>
<thead>
<tr>
<th>Year</th>
<th>$\eta_t$</th>
<th>Voles</th>
<th>Pipits</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>6.62 (4, 10.1)</td>
<td>1050.4</td>
<td>382.4</td>
</tr>
<tr>
<td>1994</td>
<td>6.14 (3.8, 9.2)</td>
<td>1060.8</td>
<td>575.2</td>
</tr>
<tr>
<td>1995</td>
<td>1.62 (0.79, 2.7)</td>
<td>280</td>
<td>570.1</td>
</tr>
<tr>
<td>1996</td>
<td>2.36 (1.6, 3.3)</td>
<td>535.6</td>
<td>358.8</td>
</tr>
<tr>
<td>1997</td>
<td>8.23 (3.3, 14.9)</td>
<td>1648.4</td>
<td>239.4</td>
</tr>
<tr>
<td>1998</td>
<td>1.80 (0.71, 2.7)</td>
<td>598</td>
<td>219.1</td>
</tr>
<tr>
<td>1999</td>
<td>1.02 (0.39, 1.6)</td>
<td>104</td>
<td>216.5</td>
</tr>
</tbody>
</table>

Table 3.5: Estimates of the number of harriers to move into the area ($\eta_t$), with the corresponding 95% credible intervals and prey densities (km$^{-2}$).

### 3.10 Discussion

The harrier model is a relatively straightforward application of state-space modelling, providing estimates for the birds’ life history processes. The super-population model, which provides hypothetically possible alternatives to the observed harrier population, could easily be modified to form a traditional observation model for those data sets where harrier numbers are not known without error. Additionally, alternatives to the super-population are possible that would still introduce the ‘slack’ in the system needed to estimate the parameter values. One such alternative could be to include the uncertainty around the estimates for the harriers’ prey, the voles and pipits. The model could also be useful as a prediction tool, although this would require estimates
of the number of voles, pipits and grouse chicks to be present in the future. Since changing land use practices can affect harrier numbers and habitat use (Amar & Redpath, 2005), it would be necessary to predict harrier densities under different prey densities to try and determine the effect of these, and other, environmental changes.

The model, as described in Section 3.5, can be fit to hen harrier populations in mainland Scotland, England and Europe. It should be noted that the greatest exceptions to the model assumptions occur in the harrier population on Orkney. The population of hen harriers on this northern set of islands is different from those found elsewhere. Most notably, hen harriers in Orkney show a much higher rate of polygamy than any other population. This is due to an unusually high female to male ratio, rather than restricted male breeding (Picozzi, 1984). Additionally, female harriers show a higher survival rate, both as adults and as fledglings, than their male counterparts (Rothery et al., 1984). Harriers in Orkney also display different behaviour with regards to habitat use for hunting. They do not selectively choose the type of sub-habitat over which they hunt based upon prey availability; rather they hunt equally over the different types of habitat near to their nesting site. There are still some slight preferences between the sexes, probably due to their differing ability to catch certain prey types (Amar & Redpath, 2005). The higher rates of polygamy and the different hunting behaviour would require a different model to allow for accurate estimates of harrier numbers.

In the model, as it stands, the strong positive dependence of immigration \((\eta_t)\) on vole densities was somewhat unexpected, given that winter migration seems to be dependent on pipit densities (Watson, 1977). However, previous studies have found a relationship between the abundance of small mammals and harrier breeding densities (Redpath & Thirgood, 1997), so it is not the relationship, but rather its strength, that was unexpected. While harrier immigration will not halt in the absence of voles, it will decrease, limiting the number of harriers found in an area. This may be the cause of harriers’ declining use of conifer plantations as the age of the plantation increases (Thompson et al., 1988). Rodents are abundant in young plantations, encouraging
movement of harriers into the area. However, as the plantation grows older, the density of rodents decreases (Usher & Gardner, 1988), resulting in a lower rate of immigration. While alternate prey may be enough to sustain the site-loyal harriers that initially nested in the plantation, the densities would not be high enough to encourage young birds to settle in the area. Additionally, harriers are better adapted to hunting in open country (Watson, 1977), so as confier plantations become more closed, they will be less able to catch prey in the area. As a result, immigration would reduce to the point where the population size could not be maintained, since there would not be enough young harriers to replace the older birds lost to the population.

The other aspects of the model behaved as expected. Higher pipit densities resulted in greater harrier survival, but this did not adversely affect immigration due to the low territoriality of the hen harrier. When pipits are absent or at very low densities, but voles continue at high densities, it is possible that relatively large numbers of harriers could remain in an area. While survival would decrease, movement into an area would remain high, thus maintaining high densities of hen harriers even in the relative absence of pipits. This has implications for management, since it implies that the aggregative response of hen harriers to their prey may be a stronger determinant of population numbers than their numerical response.

It is encouraging that this model provides reasonable super-population and parameter estimates, as well as displaying good mixing and convergence. However, it does not fully represent harriers in a community context. Other research (e.g., Matthiopoulos et al., 2007) has shown that the effect of harriers on grouse densities may be determined, in part, by the density of other available prey. By extending the models to include the presence of multiple prey species it will be possible to obtain a better picture of the impact of hen harriers on red grouse, improving understanding of the inter-species dynamics.
Chapter 4

Red Grouse

“Red Grouse (Lagopus scoticus): One sunny morning a few months ago, as I stood on a mountain slope among bracken, ling, and furze, and scattered masses of grey rock, watching a small party of grouse near me, it struck me that I had never looked on a more beautiful creature than this bird: so finely shaped and richly coloured, and proud and free in carriage, and in such perfect harmony with the rough vegetation and that wild and solitary nature amid which it exists. It is not strange that this species should have a fascination above all others for the sportsman that he is willing to go farther and spend more in its pursuit; for it is not the bird only that draws him: the fascination is of that unadulterated nature of which the bird is a part, and the sense of liberty and savage life that returns to man in the midst of mountain and moorland scenery.”

- William Henry Hudson (1906)

4.1 History

The red grouse (Lagopus lagopus scoticus) was important as an early food source, with laws protecting the bird going back as early as the 15th century. Interest in the grouse has always focused on its value as a gamebird. However, in the 18th century
the reasons for hunting grouse shifted from sustenance to sport, and the needs of farming began to conflict with those of the grouse. Elaborate game preservation and predator controls on grouse moors were put into place by the middle of the 19th century, enabling continued grouse hunting. These preserves created a large increase in the number of red grouse on the moors, bringing the population to an estimated five million in the early 20th century. Grouse bags in the early part of the century totalled greater than 2 million birds. However, since World War II there has been a marked decline in the number of red grouse in the UK. This is likely due to a mix of reduced predator control and habitat loss as land use practices change and grouse shooting becomes less profitable (Hull, 2001; Marchant et al., 1990).

4.2 Life history

For those uninterested in sport hunting, the red grouse is most famous for its appearance on the Famous Grouse Whiskey bottle. It is a medium sized gamebird with reddish-brown feathers and notably tufted feet in a paler colour. Both males and females have a red comb, although it is more prominent on the males, where it plays a role in sexual signaling. Red grouse are a member of the family Tetraonidae and are related to other UK gamebirds such as the black grouse (Tetrao tetrix) and ptarmigan (Lagopus mutus). Red grouse are found almost exclusively on heather (Calluna vulgaris) moorlands, where young heather serves as the birds’ main food source and mature heather provides shelter and cover for their nests (Jenkins et al., 1963).

Red grouse are a territorial species, in which cocks that fail to establish territories in the autumn suffer considerably greater over-winter mortality than territory-holding cocks (Jenkins et al., 1967; Watson, 1985). Only territorial cocks will breed, so the autumn contests determine spring breeding densities. While red grouse are monogamous, they are not necessarily loyal to their partner, taking new mates on the death of the old one (Watson et al., 1994) and even changing partners within a year (Moss et al., 1988). Egg laying usually begins in late April, with hatching following in the next 20-25 days (Jenkins et al., 1963). It is at this point that the territorial system begins to break down (Watson, 1985). Individual brood sizes will range from one
to 12 chicks. Where the adults depend on heather for their main food source, chicks depend on arthropods for the first two weeks of life before they begin to eat the young heather shoots (Hudson, 1982).

The breeding success of red grouse is affected by the parasitic nematode *Trichostrongylus tenuis*. While the exact mechanism is unclear, red grouse with higher parasite burdens produce fewer young (Newborn & Foster, 2002). The uptake of the parasite is through the consumption of heather shoots eaten by the adult birds, so the chicks are not being affected directly by *T. tenuis*. Instead, it may be that a reduction in adult fitness reduces their ability to raise their young. The number of chicks fledged by the red grouse will also depend on predation, as the chicks provide a source of food for many predators. Some, such as the red fox (*Vulpes vulpes*), can be legally controlled, while others, such as the hen harrier (*Circus cyaneus*), cannot.

Those chicks that survive to fledge remain juveniles only until the autumn. Male juvenile birds take part in the autumn territorial contests; the young cocks that successfully obtain territories survive the winter and are recruited into the adult population, breeding that spring. Juvenile birds are site loyal, rarely dispersing far from their natal site. Therefore, those birds that fail to be adopted into the adult population have likely died over the winter, either because they have been pushed onto marginal habitat or have been lost to predation or shooting. Since females only survive when paired with a territorial male and the birds are monogamous, there is an approximately 1:1 sex ratio in the red grouse (Jenkins et al., 1963).

### 4.3 Cycles

Periodic fluctuations (cycles) in populations attract considerable research from both empiricists and theoreticians (Berryman & Turchin, 2000; Turchin, 2003). This is partly due to the lack of a single unifying theory for the causes of cycles, which has meant that mechanisms must be postulated for each species separately. Other species’ cycles can only provide a backdrop of information from which to develop possible hypotheses, creating ever-opening avenues of new research. To make things more
difficult, competing explanations for population cycles are abundant and often equally well-supported from both theory and empirical data. Even broad generalizations about population cycles are hard. Almost all species require extrinsic mechanisms to create periodic fluctuations. Yet, there is at least one species, the red grouse, whose population cycles can be driven by an intrinsic mechanism (Turchin, 2003).

Although the statistical properties of cycles in red grouse have been studied for many decades (Moran, 1952; Haydon et al., 2002), the cause of the fluctuations has been a topic of considerable debate. Several mechanisms, such as food quality or maternal nutrition, have been postulated to explain the cycles and most have been ruled out as being unable to drive the observed fluctuations (Hudson, 1992). Only two hypotheses remain; the intrinsic, ‘territorial behaviour’ hypothesis (Moss et al., 1996; Matthiopoulos et al., 1998, 2003, 2005; Mougeot et al., 2003) and the extrinsic, ‘parasite’ hypothesis (Dobson & Hudson, 1992; Hudson, 1992; Hudson et al., 1992b). There is empirical and theoretical support for both (Dobson & Hudson, 1992; Hudson, 1992; Hudson et al., 1992a,b, 1998; Matthiopoulos et al., 1998, 2000, 2002, 2003; Mougeot et al., 2003, 2005c), providing fuel for a long-running debate.

Red grouse population densities are driven by cock territory numbers. Cocks that fail to establish territories in the autumn suffer considerably greater over-winter mortality than territory-holding cocks (Jenkins et al., 1967; Watson, 1985). According to the territorial behaviour hypothesis, fluctuations in aggressiveness result in varying levels of juvenile recruitment into the territorial population. Theory and experiments have shown that the interactions between aggressiveness, recruitment and density can cause instability in red grouse populations. High aggressiveness occurs at peak densities, reducing recruitment. This decreases population density, lowering aggressiveness and allowing recruitment to rise (Moss et al., 1996; Matthiopoulos et al., 2003, 2005; Mougeot et al., 2003).

In contrast, according to the parasite hypothesis, the nematode *Trichostrongylus tenuis* reduces the grouses' chick-rearing success (Newborn & Foster, 2002). The number of successfully-reared chicks is lower in birds with higher parasite burdens (Dobson & Hudson, 1992; Hudson, 1992; Hudson et al., 1998). While there is evidence
that increased parasite burdens make adult grouse more vulnerable to predation, this has the same effect on grouse population size as random predation (Hudson et al., 1992a), so parasite burdens do not increase adult grouse mortality. Theory and experiments have shown that the interactions between parasites and density can also cause instability in red grouse populations, although parasites are not a requirement for cycles (Moss et al., 1993; Redpath et al., 2006a). As rearing rate is reduced, so are the numbers of young available for recruitment, causing grouse density to decline. As host numbers decline, so does the transmission rate, decreasing the average parasite burdens. With fewer parasites, grouse rear more young, resulting in increased grouse density. *T. tenuis* affects autumn densities by limiting the number of young reared per pair, so its influence is not gender-specific.

Recent research indicates a connection between aggressiveness and parasite loads (Fox & Hudson, 2001; Mougeot et al., 2005c, 2006; Redpath et al., 2006a; Seivwright et al., 2005), giving rise to a ‘combined’ hypothesis. Experiments have shown that parasites ultimately reduce territorial behaviour in male red grouse (Fox & Hudson, 2001; Mougeot et al., 2005b). Moreover, further experiments have shown that increased aggressiveness leads to high parasite intensities (Seivwright et al., 2005). The relationship between aggression and parasites can also be seen in comb size, which can be used as a proxy for aggression. Cocks with larger combs are more likely to gain territories. The larger comb may also be an indication of higher levels of immunocompetence, making them better able to cope with high levels of parasites (Mougeot & Redpath, 2004).

Matthiopoulos et al. (2007) demonstrated the effect of different model assumptions regarding the cause of red grouse cycles on the interactions between the grouse and a generalist predator, the hen harrier. They found that some predictions were robust to model and parameter uncertainty, while others, such as the maximum effect of harrier predation, were not. These differences highlighted the importance of model choice and specification, but comparisons could only be made between single-mechanism models (intrinsic, extrinsic, as well as a general phenomenological model) because no
Theoretical form of the combined hypothesis existed. The exact nature of the interaction between aggressiveness and parasites is still not completely understood, making its explicit inclusion in any model difficult. However, the ability of aggressiveness and parasites to act simultaneously in red grouse populations is unquestionable. Until now, deterministic models have aimed to uncover necessary and sufficient mechanisms for cyclic behaviour. Yet, finding out how these determine the detailed shape of the cycles is an equally legitimate next question. This can be achieved by confronting with field data a model in which both of these influential mechanisms co-exist. In this chapter I develop such a model.

4.4 Aggressiveness

Male red grouse have a range of agonistic behaviours, varying from being alert and watchful in the absence of predators to physically fighting with other males. Prolonged threat displays and vocal calls are used to define and defend territories. When protecting their territories, cocks shift rapidly between different postures and calls. The agonistic interactions are brief, as they are physically tiring. Pecking and clawing is part of the aggressive behaviour observed in territorial contests, but rarely ends in serious wounding. More important are the cocks’ combs, which remain erect during the aggressive displays. A slight lowering of the comb, or even outright fleeing, indicates the more submissive of the two cocks involved in the altercation (Watson & Jenkins, 1964).

The frequency of aggressive displays can be used to determine an index of aggression for red grouse, both in the field (e.g., Watson & Miller, 1971) and in captivity (Moss et al., 1979). A heritable trait (Moss et al., 1985), aggression is known to be positively correlated with territory size in the red grouse (Watson, 1964; Watson & Miller, 1971). In turn, the possession of a territory is a requirement for survival. Therefore, an increase in aggression results in larger territories, leading to smaller spring breeding densities. The observation that spring grouse densities seemed to be determined by the territorial contests the previous autumn (Jenkins et al., 1963) led to the formation of the territorial hypothesis as the cause of the red grouse cycles.
For territorial behaviour to change from year to year, the aggressiveness of the cock red grouse must also be changing. Testosterone is positively correlated with aggressiveness, especially in reproductive contexts. It may also play a role in regulating territorial aggressiveness, as it relates to breeding (Wingfield et al., 1987). While the red grouse territorial contests occur in the autumn, only those birds which gain territories survive to breed. Additionally, the aggressive behaviour continues through the winter up until the time of hatching (Watson, 1985), so autumn territorial aggression can be viewed in a reproductive context.

Changes in the levels of circulating testosterone in a bird’s bloodstream are regulated by environmental and social cues (Moss et al., 1979; Wingfield et al., 1987). Seasonal changes in aggressiveness can be observed in red grouse, as cocks first become aggressive when competing for territories in autumn, gradually increase their aggressiveness through winter, and become completely territorial in the spring (Jenkins et al., 1963; Watson & Jenkins, 1964). The exclusive territories are maintained until the chicks hatch, and testosterone levels then decrease for the summer, only to rise again in autumn (Watson, 1985). In most bird species where fathers show parental care, testosterone levels, and thus aggression, decreases with the hatching of the chicks. This helps chick survival as the parents devote more time to caring for their young than defending a territory (Wingfield et al., 1987).

While fluctuating levels of aggression in cock red grouse may drive the changing territory sizes, it is possible that aggression is not the cause of the cycles, but a symptom of a different underlying driver. It may be that the changing aggressiveness is simply the visible result of a change in the environment or grouse social structure. Given the regularity of the grouse cycles, environmental factors are unlikely to be the cause of changing aggression, although such factors may impact the relative levels of aggressiveness. Social factors are more likely to play an important role in determining the levels of aggression in a red grouse population. The dependency on territories for grouse survival, coupled with the fact that grouse are less aggressive to kin than non-kin (Watson et al., 1994), gave rise to the ‘kin-facilitation’ hypothesis.

According to the kin-facilitation hypothesis, changing levels of relatedness lead to
varying levels of aggression between individuals. Adult cocks benefit by allowing their offspring to be recruited into the population, and are therefore less aggressive towards their sons. However, the adult cocks would eventually reach a minimum territory size at which they are no longer willing to ‘share’ territories. Once the limit is reached, no further recruitment takes place, reducing the level of relatedness. Relatedness decreases because when an adult’s offspring fails to recruit into the breeding population the surviving male is increasing surrounded by non-kin, especially as the adult’s own father and brothers die. With a drop in the level of relatedness, aggression increases, leading to a corresponding increase in territory size. Territories eventually increase in size and adult males become more willing to recruit their offspring, starting the cycle again (Moss & Watson, 1985).

Other aspects of grouse behaviour, not just the dependency on territories for survival and differing aggression between kin and non-kin, support a kin-facilitation hypothesis. Young cock red grouse stay in their natal area to compete for territories, often settling near their fathers, even taking their father’s territory when he dies (Lance, 1978). Additionally, during the winter months, young cocks will often spend time in their father’s territory as well as their own (Hudson, 1992). The philopatric recruitment in red grouse encourages the formation of kin clusters (Watson et al., 1994; MacColl et al., 2000). This facilitates the recruitment of young into the population (MacColl et al., 2000), which is the main cause of population growth in the red grouse (Moss & Watson, 1991). Additionally, it has been noted that kin-clusters increase in size during high recruitment and shrink during times of low recruitment (Lock, 2003), which would be expected under the kin-facilitation hypothesis.

The kin-facilitation hypotheses has support from both theoretical work (Matthiopoulos et al., 1998, 2000, 2002), as well as the field experiments (Mougeot et al., 2005c) and observations (Moss & Watson, 1991; Watson et al., 1994; MacColl et al., 2000). However, it is by no means the only mechanism capable of driving changing levels of aggressiveness. Matthiopoulos et al. (2003, 2005) developed a non-mechanistic model for aggression as a cause of cycles in red grouse. This allows for the possibility of alternative mechanisms to the kin-facilitation hypothesis, as it builds a more
general premise for the relationship between aggression and red grouse cycles. Population studies of the red grouse in which aggression is manipulated, as opposed to kin-structure, also support fluctuating levels of aggression as a cause of red grouse cycles, regardless of the mechanism that drives the changing aggression (e.g., Moss et al., 1994).

In addition to affecting aggressiveness, it is also possible that the increased levels of testosterone may impact the bird's survival, either through increased injury during aggressive encounters, or reduced fitness (Dufty, 1989). Certainly in red grouse, aggressive behaviour has been noted to cause serious injury (Hudson, 1992), and lower survival has been observed of cocks with artificially increased testosterone (Moss et al., 1994; Redpath et al., 2006b). There is no contradiction in having cocks with increased testosterone being more likely to gain territories and yet have lower survival than cocks with sham implants. While possession of a territory is a requirement for survival, over-winter survival is not guaranteed by possession of a territory. Territorial birds that die over the winter will be replaced from the surplus non-territorial population (Watson, 1967; Watson & Jenkins, 1968). So, while higher levels of testosterone increase a cock’s chance of obtaining a territory, it decreases his chance of keeping it through the winter.

As well as the costs, there are also benefits to higher levels of testosterone. In red grouse, cocks with increased levels of testosterone have better breeding success, which is hypothesised to be due to their ability to get larger territories, and therefore better hens (Moss et al., 1994; Redpath et al., 2006b). However, an earlier study found that breeding success was not correlated with territory size (Watson & Miller, 1971), implying that it is some aspect of the increased testosterone that improves breeding. Testosterone stimulates the development of secondary sex characteristics, which are used for sexual signaling and aggressive displays (Witschi, 1961). In the case of red grouse, increased levels of testosterone increase the cocks’ comb size (Mougeot et al., 2005a), which would serve to make the implanted cocks more attractive to the hens. Increased likelihood of obtaining a territory and increased breeding success are short-term benefits of testosterone, which appear to outweigh the lower over-winter survival
(Redpath et al., 2006b). However, there is the possibility that increased testosterone can have long-term effects on fitness (Wingfield et al., 2001), especially considering that increased testosterone in red grouse makes them more susceptible to the parasite \textit{T. tenuis} (Mougeot & Redpath, 2004; Mougeot et al., 2005a).

4.5 Parasites

Parasitism is when one species, the parasite, lives in or on the body of another species, the host. For an organism to be a parasite, it must meet three criteria. The organism must 1) use the host as its habitat, 2) be nutritionally dependent on the host and 3) cause ‘harm’ to the host. The harm the parasite does can vary from being almost undetectable to the death of the host. However, those species which kill their host as a requirement to successfully develop are not parasites, but parasitoids (Anderson & May, 1978). The nematode \textit{Trichostrongylus tenuis} fits this definition of a parasite, their host being the red grouse.

\textit{T. tenuis} has a direct relationship with red grouse; there are no intermediate hosts. As an adult worm, \textit{T. tenuis} lives in the caecal walls of the grouse. The female worms are fecund, producing as many as 5,500,000 eggs per year (Hudson, 1992). The eggs pass from the grouse in the birds’ caecal droppings and can be used to accurately estimate the host’s worm burden (Seivwright et al., 2004). When free of the grouse, the eggs mature into an infective stage. As infective larvae, the parasite migrates to heather shoots, where they are ingested by feeding birds. Once inside the grouse, the larvae develop into adults in 12-14 days. The larvae are capable of remaining inside the grouse in an arrested state, hypobiosis, for as long as six months. More commonly, the larvae only enter arrestment only to survive the winter period, before developing into an adult (Hudson, 1992).

The transmission function, the rate at which infective larvae are ingested, is probably the most important aspect of host-parasite interactions, as well as one of the most difficult to quantify (Fenton et al., 2002). There are few data available on the rate of transmission (Dobson & Hudson, 1992), but it can be estimated indirectly
through changes in the intensity of parasite burdens. For red grouse, a problem with determining the transmission rate has been the difficulty in recovering the infective stage from the field. While *T. tenuis* is well adapted to its host, selectively migrating towards heather both horizontally (Saunders et al., 2001) and vertically (Saunders et al., 2000), the infective larvae are highly aggregated. This makes it hard to estimate the availability of infective stages and to predict *T. tenuis* outbreaks (Saunders et al., 1999).

Weather can give some indication of outbreaks in the relative intensities of *T. tenuis* infections in red grouse (Cattadori et al., 2005). Parasite recruitment is greatest in wet summers, with rainfall explaining much of the year to year variation in parasite burdens (Moss et al., 1993). Severe rainfall causes heather browning, reducing the shoots available for the grouse to eat. *T. tenuis* larvae may congregate on the eatable shoots in higher densities than they would during years when healthy heather is more widespread. This would increase the amount of infective larvae ingested by red grouse and consequently the parasite burden (Moss et al., 1990). In the case of severe weather, increases in parasite density need not be dependent on increases in host density (Moss et al., 1993). However, the density of red grouse does play a role in determining parasite burdens, as parasites are slightly aggregated with grouse density. Variations in parasite density are correlated with density of grouse in the previous July, as well as the intensity of the infection in adult grouse (Hudson et al., 1992b).

There is no contradiction or conflict in having the level of parasite intensity dependent on both the weather and grouse density from the previous year. The infective larvae cannot travel far from the caecal droppings (Saunders et al., 2001), so most worm burdens are increased through self-infection or infection from close relatives (Saunders et al., 1999). If grouse density is low, the birds will be too widely spaced for the parasites to spread easily. As densities get higher, the grouse become more crowded and are steadily exposed to more parasites. The weather will modify the magnitude of change in the parasite burdens, with wet summer weather potentially increasing parasite burdens dramatically.
The intensity of the parasitic infection increases throughout the lifespan of the red grouse (Hudson, 1992). Grouse show no ability to ‘self-cure,’ to build up a level of immunity to *T. tenuis*. Infection rates in juvenile, naïve grouse are the same as the re-infection rates in older grouse that have been treated with an anthelmintic to clear them of any infection. This indicates a lack of immunological memory, no heightened resistance to the parasite due to exposure. The possible size of the parasite burden increases further due to the lack of density-dependence acting on the parasites within the grouse. This allows the numbers of worms and eggs produced to continue to grow linearly; it is likely the host dies before density-dependence can regulate parasite numbers or reproduction (Hudson & Dobson, 1997). Due to the lack of density-dependence and immune-response, older birds should have higher parasite burdens than younger birds.

The parasitic nematode decreases the body condition of the red grouse, burrowing into the caecal mucosa, interrupting the function of the gut and causing internal bleeding (Hudson, 1992). There is some question as to whether the lower body condition increases the mortality of red grouse, either through ‘natural’ causes or increased vulnerability to predation. Hudson et al. (1992a) found birds killed by predators in spring had higher worm burdens than those shot by hunters in autumn. Additionally, those birds which died of ‘natural’ causes had higher worm burdens than those predated or shot. The authors therefore concluded that high worm burdens decreased the overall fitness and survival of red grouse. In contrast, Moss et al. (1990) found higher levels of parasites did not increase hen red grouse vulnerability to predation and found no evidence of ill-health, even with high worm burdens. Since *T. tenuis* burdens in red grouse increase with age, it is possible that those birds found dead by Hudson et al. (1992a) died of ‘natural’ causes having nothing to due with their parasite burden. Other factors may be the source of the observed differences between the studies; factors such as location, timing or the level of worm burdens. Slightly more recent work indicates there is no difference in survival, body condition or spring density between birds with experimentally reduced worm burden and those with parasite intensities at their natural level (Newborn & Foster, 2002).
Instead of decreasing survival, *T. tenuis* decreases breeding productivity of hen red grouse. While there is no difference in clutch size, experiments have shown that the number of chicks successfully reared by heavily parasitised red grouse hens is significantly lower than those of healthy birds (Hudson, 1986; Hudson et al., 1998; Newborn & Foster, 2002). It is unclear why high worm burdens would have an indirect effect, the decline in the number of chicks reared, as opposed to a more direct one, a decline in clutch or brood size. One possibility is the lower body condition of the hen reduces the energy available to invest in the care of young, resulting in fewer chicks surviving. Another possibility involves the effects of *T. tenuis* on the caeca. The parasite burrows into caecal walls, disrupting their function, including the ability to control the production of scent. During the breeding season hens usually stop producing caecal feces and produce less scent. High levels of *T. tenuis* inhibit this ability, making the birds easier to locate (Hudson et al., 1992a). While this does not increase the hens’ vulnerability to mammalian predators, it may increase their chicks’ vulnerability, as the nests will be easier to find than those of a healthy bird.

To help increase the survival of their chicks after fledging, hens may choose as mates cocks with ‘good genes;’ genetic disease resistance as advertised by traits which take health and vigour to express (Hamilton & Zuk, 1982). In red grouse, comb size is one such trait, serving as a measure of body condition and immune function, not *T. tenuis* burden. While having a large comb advertises the ability of a cock to withstand parasite infection, it also increases a cock’s susceptibility to the parasite, as testosterone, which controls comb size, has immunosuppressive effects (Mougeot & Redpath, 2004; Mougeot et al., 2005a). Those males who are better able to cope with parasites can afford to invest more in testosterone without decreasing their own survival or reproductive potential (Folstad & Karter, 1992). Their parasite burdens are therefore equivalent to those in birds with lower testosterone, but with more resources allocated to their immune response. Since comb size is heritable in red grouse (Moss et al., 1985), females would gain an advantage for their offspring by choosing mates with large combs.

Experimentally, cocks with artificially increased testosterone were more successful in
breeding and obtaining hens, but their parasite burdens were higher and their body condition lower (Mougeot et al., 2006; Seivwright et al., 2005). This may have been observed because, while all cocks were given increased levels of testosterone, not all would have had the ability to mediate the trade-offs between testosterone level and parasite resistance. It has been observed that relative parasite burdens in between individual birds stay the same across years, even as the population’s average worm burden fluctuates (Moss et al., 1993). Additionally, a bird’s initial parasite burden plays a role in determining its final parasite burden (Seivwright et al., 2005). Given these three aspects of the parasitic infection, it would imply that an individual’s parasite burden is a function of exposure to the parasite, testosterone level and some inherent resistance.

The different biological processes involved in a host-parasite association can have both stabilising and destabilising effects on the system. Stabilising biological processes include over-dispersion of parasites, density-dependent parasite mortality and a non-linear relationship between infection intensity and parasite-induced host mortality (Anderson, 1978). Within the red grouse- T. tenuis system, the only stabilising process observed is the slight over-dispersion of the parasitic nematode (Hudson et al., 1992b). However, this mild aggregation of the parasite is capable of having a strong stabilising effect. Of the other biological processes, there is no evidence of density-dependence acting on the parasite (Hudson & Dobson, 1997) or of any parasite-induced host mortality (Newborn & Foster, 2002).

The biological processes which lead to destabilisation are parasite induced reduction in host reproductive success, parasite reproduction within the host that directly increases parasite population size and time-delays in parasite transmission or reproduction (May & Anderson, 1978). While T. tenuis does not reproduce directly within red grouse, it does reduce breeding success (Hudson, 1986; Hudson et al., 1998; Newborn & Foster, 2002) and can have a time delay in the transmission phase of as long as six months (Hudson, 1992). Both of these, especially the time-delay, can have a strong destabilising effect on the host population dynamics. The balance and trade-offs between the differing biological processes contribute to the population dynamics of
the red grouse.

The pre-existing quantitative models for the grouse-\textit{T. tenuis} interactions are based on the framework built by Anderson & May (1978) and May & Anderson (1978), made biologically specific to \textit{T. tenuis} and red grouse. One of the strengths of these models is their ability to create cycles of different periods under a range of parameter values. This allows for differences in regions, environmental effects and other factors, making the models more biologically realistic (Dobson & Hudson, 1992).

In order to assess the accuracy of the models, it is necessary to test their predictions by manipulating the system. Of the two destabilising factors that contribute to the cycles, it is not possible to stop the infective stage of \textit{T. tenuis} from going into arrestment. However, parasite-induced reduction in host reproductive success is a reasonable mechanism for the observed fluctuations and it is possible to attempt to manipulate breeding success by treating the grouse to rid them of their parasite infection. In fact, experimental reduction of parasite burdens, either through direct dosing with anthelmintics or medicated grit, results in increased breeding success in hen red grouse (Hudson et al., 1992b) and reduces the tendency of the grouse population to cycle (Hudson et al., 1998). In this scenario, the density of parasites lags behind the density of grouse. This is expected in host-parasite fluctuations (Anderson & May, 1978) and is predicted by the red grouse-\textit{T. tenuis} models (Dobson & Hudson, 1992).

If a time-delay in reduction in breeding success is causing the observed fluctuations, then grouse populations treated for parasites should stop cycling. When red grouse populations were dosed to rid them of the nematode shortly before a predicted crash the tendency to cycle was reduced, but the cycles were not stopped. This was predicted in the model, as only an average of 20\% of grouse were treated for parasites; enough to stop the population from crashing, but not enough to halt the cycles themselves. Since the predictions of the model were met, the results were interpreted as proving that parasites were the cause of the observed cycles in red grouse (Hudson et al., 1998). In order to stop the cycles completely, it was estimated that at least 65\% of the population would need to be treated; a goal that was deemed to be unrealistic.
The validity of these results has not been questioned, but their interpretation has been the subject of much debate (e.g., Hudson et al., 1999; Lambin et al., 1999). Experiments have shown the nematode is necessary for cycles of the observed magnitude, but do not prove cycles are eliminated in the absence of *T. tenuis* (Tompkins & Begone, 1999). Parasites do not need to be causing the cycles to have a role in the population dynamics of their host. Their function may be to regulate the magnitude and timing of the observed cycles. Increased breeding success through reduced parasite burdens (Hudson et al., 1998, 1992b) and a climate-parasite interaction may control the magnitude and timing of the cycles. Climate plays a significant role, since it is a climate-parasite interaction that is believed to be the mechanism behind the intermittently observed synchronous cycles in northern England (Cattadori et al., 2005).

In the past, research into the parasite and territorial behaviour hypotheses had been in separate geographical regions. The parasite hypothesis was heavily researched in England, while the territorial behaviour hypothesis was focused in Scotland. This gave rise to the argument that there were spatial differences in the mechanisms causing the cycles (Turchin, 2003). The climate, grouse density and average parasite burden vary between the two regions, leading to the assumption that the various extrinsic and intrinsic factors may have different impacts on grouse dynamics in the two countries (Moss & Watson, 1985). Recent fieldwork, done jointly in Scotland and England, leaves no room for the contention that differences in the timing, methods or type of analysis were confounding the comparison of the two regions. Despite the inherent differences, the results of the study were the same across all areas. In Scotland and England an average of 67% of the grouse were treated with anthelmintics to reduce parasite burdens. In some populations as many as 81% of the grouse were treated, well above the predicted 65% needed to stop the cycles. The treatment was able to lessen the magnitude of the cyclic decline, but was unable to halt it completely. As a result, parasites cannot be the sole cause of the observed fluctuations. The parasitic nematode does have an important role in the cyclic dynamics of the red
grouse, especially in the start of the decline (Redpath et al., 2006a). *T. tenuis* may be capable of causing the abrupt change between tolerance and aggression needed for socially induced population cycles (Matthiopoulos et al., 2005).

### 4.6 Model development

#### 4.6.1 Aggression

Aggressiveness in grouse cocks affects population density by limiting the number of juvenile cocks that can be recruited into the territorial population. Aggressiveness and density are coupled because aggressiveness both modifies, and is dependent upon, density. Furthermore, experiments have shown that aggressiveness depends on both current density and density in the previous year (Mougeot et al., 2003, 2005c). These relationships were modeled on the basis of observations of within-year variation in aggressiveness by Matthiopoulos et al. (2003, 2005),

\[ a_{t+1} = a_t \left(1 - l + \frac{(1 + u)(\psi_t^C l)}{\psi_m^u u + \psi_m^l l}\right) \]

\[ \psi_t = wN_t + (1 - w)N_{t+1}, \]

where \(a_t\) is the aggressiveness of male grouse in year \(t\), \(N_t\) is the density of territorial cocks in year \(t\), \(w\) determines the time delay in the effects of density on aggressiveness, \(\psi_t\) is a dummy variable regulating the timing of density dependence, \(\psi_m\) is male density at equilibrium, \(u\) and \(l\) are the maximum and minimum annual increases in aggressiveness, respectively, and \(C\) is a shape parameter for the relationship between aggressiveness and density.

Due to its support in the literature and the existence of estimates for the various parameters involved, Eqn. 4.1 was originally used to model the aggressiveness of male red grouse. However, the equation does not limit the value for aggression, and, without data to inform it, the model was capable of predicting exponentially increasing levels of aggressiveness. This lack of biologically realistic behaviour led to the need to develop a different model for the annual changes in aggressiveness.
One attribute of the model presented in Matthiopoulos et al. (2003, 2005) was that it was modelled only on the basis of within-year observations due to the availability of just a few years of data. With a longer time series, it is possible to map aggressiveness across years according to the function,

\[ a_t = \frac{\exp\{\xi_0 + \xi_1 0.5G_{f,t} + \xi_2 0.5G_{f,t-1}\}}{1 + \exp\{\xi_0 + \xi_1 0.5G_{f,t} + \xi_2 0.5G_{f,t-1}\}}, \tag{4.2} \]

where \( a_t \) is now the aggressiveness index for year \( t \), constrained to lie between zero and one, and \( G_{f,t} \) is autumn grouse density in year \( t \) prior to hunting and recruitment, both of which occur in the autumn. Only male birds contribute to aggressiveness so, given the 1:1 sex ratio (Jenkins et al., 1963), autumn grouse density is halved in Eqn. 4.2. By constraining aggressiveness to lie between zero and one it was possible to avoid the exponential increase in aggression observed when Eqn. 4.1 is used in the model fitting process.

### 4.6.2 Parasites

The parasitic nematode \( T. tenuis \) reduces the ability of red grouse to rear their young (Newborn & Foster, 2002). Changes in average \( T. tenuis \) burden (\( W_t \)) per bird must therefore be tracked from spring to spring, when grouse start breeding (Jenkins et al., 1963). The yearly changes in spring parasite loads are due to density in the previous year (Hudson, 1992) and seasonal changes within a year, which must also be considered (McGladdery, 1984; Shaw & Moss, 1989).

Given a worm burden in year \( t \), an average number of eggs (\( E \)) are produced per worm. A percentage, \( \nu_s \), of these develop into infective larvae, which survive with probability \( \phi_p \). A portion of the infective larvae, \( \omega \), are then ingested by the adult grouse, where they establish as adult worms at the end of the summer. Assuming no adult worms die between spring and autumn, the average autumn worm burden per bird (\( W_{f,t} \)) is,

\[ W_{f,t} = W_t(1 + E\nu_s\phi_p\omega). \tag{4.3} \]

I have retained \( \nu_s, \phi_p \) and \( \omega \) as individual parameters because studies of \( T. tenuis \)
have focused on estimating these values separately (Dobson & Hudson, 1992; Hudson et al., 1992b; Shaw et al., 1989).

In the autumn the parasite reproduces again. The proportion of eggs that develop into infective larvae ($\nu_f$) is season-specific, while the number of eggs produced ($E$), the larvae’s survival ($\phi_p$) and their ingestion and establishment in red grouse ($\omega$), are not. Rather than establish as adult worms, the infective larvae ingested by the red grouse in autumn establish as arrested larvae. This gives the average number of arrested larvae per bird in the autumn ($A_t$),

\[ A_t = W_{f,t}E\nu_f\phi_p\omega. \]  (4.4)

In both Eqns. 4.3 and 4.4 we are assuming that worm egg production occurs in discrete time. In reality, worm reproduction is continuous, as modelled by (Dobson & Hudson, 1992).

Survival of the adult worms and arrested larvae occurs over the winter. While T. tenuis has been found in other game birds, the parasite’s life cycle is direct, without any intermediate hosts (Hudson, 1992), so the continued existence of the parasite depends on grouse. Additionally, parasite burdens are heterogeneous in the hosts, so the removal of a few highly-parasitised birds will have a disproportionately large effect on average worm burden (Hudson et al., 1992a). While the survival of parasites within a living bird is not affected by the death of another bird, the death does affect the average survival for the T. tenuis population, which is the parameter of interest. Thus, the average worm burden is affected by grouse’s overall survival. However, adult and juvenile birds survive at different rates, with juvenile survival varying yearly (see Eqns. 4.8 and 4.9). As a result, the combined over-winter survival of adult and juvenile grouse, which impacts worm survival, is handled in terms of the proportional change in grouse density from the autumn of time $t$ ($G_{f,t}$) to the spring of time $t + 1$
(\(G_{t+1}\)),

\[
\phi_{l,t} = \frac{\exp \left\{ \delta_l - \delta_0 \left( \frac{G_{t+1}}{G_f,t} \right) \right\}}{1 + \exp \left\{ \delta_l - \delta_0 \left( \frac{G_{t+1}}{G_f,t} \right) \right\}}
\]  \( (4.5) \)

\[
\phi_{w,t} = \frac{\exp \left\{ \delta_w - \delta_0 \left( \frac{G_{t+1}}{G_f,t} \right) \right\}}{1 + \exp \left\{ \delta_w - \delta_0 \left( \frac{G_{t+1}}{G_f,t} \right) \right\}},
\]

where \(\delta_l\) and \(\delta_w\) are a measure of the survival rates in the absence of any effect of changing grouse densities for arrested larvae and adult worms respectively and \(\delta_0\) is a measure of the effect of grouse density on survival. The model, as presented here, tracks the average parasite burden per bird, not the distribution of parasites across individuals, and assumes arrested larvae and adult worm survival have logistic relationships with grouse survival, as well as the constant presence of red grouse.

After the winter, the surviving larvae come out of arrestment and combine with the surviving adult worms to form the spring worm burden in time \(t+1\),

\[
W_{t+1} = W_{f,t} \phi_{w,t} + A_t \phi_{l,t}.
\]  \( (4.6) \)

### 4.6.3 Grouse

The punctuated nature of annual demographic events in a grouse population allows me to model its dynamics in discrete time. It is assumed that no immigration or emigration takes place within the population, which is reasonable, given that the birds rarely disperse or establish far from their natal territory (Jenkins et al., 1967). There is also the assumption that the grouse population’s boundary is defined by a feature of the natural habitat, such as farmland or pasture, which is often the case.

The discrete grouse model first suggested by Matthiopoulos et al. (2003) formalises only the intrinsic hypothesis. The continuous model, developed by Dobson & Hudson (1992), and based on a the prototype by Anderson (1978) examined the extrinsic hypothesis. To model both hypotheses simultaneously, I modified the Matthiopoulos et al. (2005) model as follows: The state variable \(G_t\) refers to the spring breeding
density of both cocks and hens. The variable $G_{f,t}$ is used as shorthand for autumn density prior to hunting and recruitment,

$$G_{f,t} = G_t + 0.5G_t\lambda_t,$$  \hspace{1cm} (4.7)

where $\lambda_t$ (Eqn. 4.10) is the rearing rate per grouse pair and $G_t\lambda_t$ is multiplied by 0.5, since while $\lambda_t$ is per pair, spring grouse density ($G_t$) includes both genders and needs to be halved. The modified model allows recruitment to vary with autumn cock density prior to territorial contests and hunting. When this autumn density is low, established cocks will not need to defend their territories against as many birds. Conversely, large numbers of young cocks means adult males are more vigorous in their territory defense, increasing aggressiveness even when adult cock density is low,

$$G_{t+1} = \left(\phi_a + 2 \left(\frac{0.25\lambda_t}{1 + (\kappa a_t 0.5G_{f,t})}\right)\right) G_t,$$  \hspace{1cm} (4.8)

where $\kappa$ regulates the strength of the density dependence and territory density (set at 0.1 by Matthiopoulos et al. (2007)). The equation tracks both male and female density, but recruitment during the territorial contest depends only on the males so autumn density ($G_{f,t}$) is multiplied by 0.5. As in Eqn. 4.7, the rearing rate ($\lambda_t$) is multiplied by 0.5, to convert spring density ($G_t$) to pairs. Additionally, recruitment only acts directly on the male young, so $\lambda_t$ is multiplied by 0.5 again, resulting in a constant of 0.25, giving the average number of male young reared per pair. The number of males recruited into the population is doubled to account for the hens with which they will pair.

Juvenile survival is equivalent to the recruitment of young cocks into the territorial population,

$$\phi_{j,t} = \frac{1}{1 + (\kappa a_t 0.5G_{f,t})},$$  \hspace{1cm} (4.9)

where the functional form of the equation is taken from Matthiopoulos et al. (2005) and constrains survival to be between zero and one, while still accounting for the appropriate biological details.
The average rearing rate ($\lambda_t$) per pair has also been modified to allow for yearly variation due to fluctuating spring parasite burdens,

$$\lambda_t = \exp\{\gamma_0 - \gamma_1 W_t\}, \quad (4.10)$$

where $\gamma_0$ is the natural log of average red grouse brood size and $\gamma_1$ measures the effect of the average worm burden on reducing the size of the brood reared.

Stochasticity was added to the models by assigning distributions to the rearing rate, the number of adults to survive and the number of juveniles recruited. For the rearing rate we have a Poisson distribution,

$$R_t \sim \text{Pois}(\lambda_t), \quad (4.11)$$

where $R_t$ is the average number of young reared per pair in year $t$ and $\lambda_t$ is calculated using Eqn. 4.10. The Poisson distribution was chosen for practical purposes, even though $R_t$ is used as the mean brood size. The number of juvenile males recruited and the number of surviving adults were drawn from a binomial distribution,

$$G_{a,t} \sim \text{Bin}(G_t, \phi_a)$$
$$G_{j,t} \sim \text{Bin}(G_{m,t}, \phi_{j,t}), \quad (4.12)$$

where $G_{a,t}$ and $G_{j,t}$ are the number of adult and juvenile cocks to survive the winter of year $t$, respectively, and $G_{m,t}$ is the number of male young reared in year $t$,

$$G_{m,t} = 0.25G_t\lambda_t. \quad (4.13)$$

The observation model for the red grouse needs to account for the fact that the gamekeepers only saw a proportion of the grouse present, $p_t$, according to the effort (number of drives, $d_t$) placed into counting the grouse in year $t$,

$$p_t = \frac{d_t}{d_t + c}, \quad (4.14)$$

where $c$ is an unknown constant to be estimated. Since only a proportion of the grouse where seen, the functional form of the equation was chosen to constrain $p_t$ to remain
between zero and one. While the proportion of grouse observed may depend on more
than just effort, information was not available for the other possible metrics, such as
the individual gamekeeper or skill of the dogs used to flush the grouse. Therefore,
only the number of drives was used as a proxy for effort to account for the proportion
of the grouse that were seen on the moor in year $t$.

The red grouse observations were modelled as a binomial distribution, which was
approximated using a normal distribution with the same mean and variance,

$$
\mu_t = G_{f,t}p_t
$$
$$
\sigma_t^2 = G_{f,t}p_t(1 - p_t)
$$

(4.15)

$$
G_{\text{Obs},t} \sim N(\mu_t, \sigma_t^2).
$$

A normal approximation was used for practical purposes, since runtime in WinBUGS
will increase when discrete distributions are used.

A summary of the states and parameters, and their definitions, can be found in Table
4.1.

4.7 Data

The data used for model fitting came from Langholm moor in Scotland from 1975-
1996. Each autumn, gamekeepers with trained dogs undertook counts of grouse prior
to shooting. The moor was divided into six beats (areas of the moor managed by
different gamekeepers) and data are available from four of these. The four beats for
which data are available are designated LC, LD, LM and LR. The counts represent
a proportion of the grouse on the estate. The proportion seen is thought to vary
between beats and with the amount of annual effort. From 1993, hen harriers, which
are capable of affecting grouse dynamics, were known to be successfully nesting on
the moor in numbers large enough to impact the grouse population. Thus, data past
1992 are excluded from the analysis to avoid any possible confounding with the effects
of predation on grouse cycles (Redpath & Thirgood, 1997; Thirgood et al., 2000c).
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E$</td>
<td>Average number of eggs produced per worm</td>
</tr>
<tr>
<td>$\nu_s$</td>
<td>Percentage of $T. tenuis$ eggs that develop into infective larvae in the spring</td>
</tr>
<tr>
<td>$\nu_f$</td>
<td>Percentage of $T. tenuis$ eggs that develop into infective larvae in the fall</td>
</tr>
<tr>
<td>$\phi_p$</td>
<td>Infective larvae survival</td>
</tr>
<tr>
<td>$\phi_l$</td>
<td>Over-winter survival of arrested larvae</td>
</tr>
<tr>
<td>$\phi_w$</td>
<td>Over-winter survival of adult worms</td>
</tr>
<tr>
<td>$\omega$</td>
<td>Proportion of infective larvae ingested by grouse</td>
</tr>
<tr>
<td>$\delta_l$</td>
<td>Measure of the survival rate of infective larvae</td>
</tr>
<tr>
<td>$\delta_a$</td>
<td>Measure of the survival rate of adult worms</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>Strength of density dependence</td>
</tr>
<tr>
<td>$\delta_0$</td>
<td>Effect of overall grouse survival on parasite survival</td>
</tr>
<tr>
<td>$\gamma_0$</td>
<td>Natural log of average brood size</td>
</tr>
<tr>
<td>$\gamma_1$</td>
<td>Effect of average worm burden on average brood size</td>
</tr>
<tr>
<td>$\xi_0$</td>
<td>Intercept parameter for the aggression model</td>
</tr>
<tr>
<td>$\xi_1$</td>
<td>Effect of grouse density in time $t$ on aggression</td>
</tr>
<tr>
<td>$\xi_2$</td>
<td>Effect of grouse density in time $t-1$ on aggression</td>
</tr>
<tr>
<td>$\phi_a$</td>
<td>Adult cock survival</td>
</tr>
<tr>
<td>$\phi_j$</td>
<td>Juvenile cock survival</td>
</tr>
<tr>
<td>$c$</td>
<td>Observation constant</td>
</tr>
<tr>
<td>$G_t$</td>
<td>Spring grouse density ($\text{km}^{-2}$) in time $t$</td>
</tr>
<tr>
<td>$G_{f,t}$</td>
<td>Autumn grouse density ($\text{km}^{-2}$) in time $t$, prior to hunting and recruitment</td>
</tr>
<tr>
<td>$G_{a,t}$</td>
<td>Adult cock density ($\text{km}^{-2}$) in time $t$</td>
</tr>
<tr>
<td>$G_{j,t}$</td>
<td>Juvenile cock density ($\text{km}^{-2}$) in time $t$</td>
</tr>
<tr>
<td>$G_{m,t}$</td>
<td>Male young ($\text{km}^{-2}$) reared in time $t$</td>
</tr>
<tr>
<td>$G_{\text{Obs},t}$</td>
<td>Observed autumn grouse density in time $t$</td>
</tr>
<tr>
<td>$\lambda_t$</td>
<td>Rearing rate per grouse pair in time $t$</td>
</tr>
<tr>
<td>$a_t$</td>
<td>Aggression index for time $t$</td>
</tr>
<tr>
<td>$W_t$</td>
<td>Average spring worm burden per bird in time $t$</td>
</tr>
<tr>
<td>$W_{f,t}$</td>
<td>Average autumn worm burden per bird in time $t$</td>
</tr>
<tr>
<td>$A_t$</td>
<td>Average number of arrested larvae per bird in autumn</td>
</tr>
<tr>
<td>$d_t$</td>
<td>Amount of gamekeeper effort (drives) in time $t$</td>
</tr>
<tr>
<td>$R_t$</td>
<td>Stochastic realization of $\lambda_t$</td>
</tr>
<tr>
<td>$p_t$</td>
<td>Proportion of grouse observed in time $t$</td>
</tr>
</tbody>
</table>

Table 4.1: The states and parameters found in the red grouse model, and their definitions.
The data from Langholm moor lack any numerical information regarding aggressiveness and parasites. However, the caeca of some shot birds were checked during the study, confirming the presence of *T. tenuis*. Similarly, while no data were collected on the aggressiveness, agonistic encounters between territorial cocks were repeatedly observed (Redpath & Thirgood, 1997).

4.8 Simulations

Two approaches were taken to estimating the parameters of the parasite and aggression models, given the lack of data. In the case of the *T. tenuis* model, parameter values were found in the published literature (Hudson, 1992; Hudson et al., 1992b; Hudson & Dobson, 1997; Dobson & Hudson, 1992; Gibbs, 1986; Shaw et al., 1989) that coincided with those parameters used in the model, $E, \phi_p, \nu_s, \nu_f, \omega, \delta_l$ and $\delta_w$ (Table 4.2). The only parameter for the parasite model that lacked any estimate from earlier research was $\delta_0$, the effect of changing grouse density on the survival of the parasitic nematode.

<table>
<thead>
<tr>
<th>$\Theta$</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E$</td>
<td>20000</td>
</tr>
<tr>
<td>$\nu_s$</td>
<td>0.0011</td>
</tr>
<tr>
<td>$\nu_f$</td>
<td>0.0156</td>
</tr>
<tr>
<td>$\phi_p$</td>
<td>0.66</td>
</tr>
<tr>
<td>$\omega$</td>
<td>0.025</td>
</tr>
<tr>
<td>$\delta_l$</td>
<td>0</td>
</tr>
<tr>
<td>$\delta_w$</td>
<td>-0.66</td>
</tr>
</tbody>
</table>

Table 4.2: Parameter values for the *T. tenuis* model that have been estimated in previously published literature.

The aggression model presented here does not have an equivalent theoretical form in the published literature. It was therefore necessary to determine possible parameter values using a different method from the parasite model. Additionally, while the parameter values for the parasite model are based on previous research, the model itself remained unproven in its ability to create the observed population fluctuations in red grouse. Therefore, simulations were run to determine the ability of the proposed
model to create cycles, as well as to establish a range of possible values for $\xi_0, \xi_1, \xi_2$ and $\delta_0$. The simulations were run over a range of previously estimated values for the remaining parameters $(\phi_a, \gamma_0, \gamma_1)$ to determine whether the model was capable of creating biologically realistic cycles and, if so, for which values of the unknown parameters. ‘Biologically realistic’ was defined as the ability to create cycles of the appropriate period (2-15 years (Haydon et al., 2002)) with densities that never exceeded the maximum recorded number of birds shot per km$^2$ on any moor in the autumn (750 birds km$^{-2}$ (Hudson & Watson, 1985)). While it is expected that more grouse would be present on the moor than are shot, records from shooting estates deal with the size of the grouse bags, not grouse density. The interest in the underlying density of grouse arose only when the birds’ numbers began to decline, making it difficult to establish a maximum possible density on a moorland estate. As a result, the maximum number of grouse recorded shot on a hunting estate was chosen as a conservative upper bound, as it should not be possible to shoot more grouse than are present on the moor. Parameter values that allowed for realistic periods for the grouse cycles did not come close to approaching the upper limit.

The model needed to be able to produce realistic cycles in a stochastic, as well as a deterministic, setting. Therefore, Eqns. 4.11 and 4.12 were used to add stochasticity to the simulations. A range of values were examined for adult survival ($\phi_a$), while recruitment ($\phi_{j,t}$) was calculated using Eqn. 4.9.

The range of values for $\xi_0, \xi_1, \xi_2$ and $\delta_0$ that were capable of producing biologically realistic grouse cycles were used to inform the priors for the state-space models (Table 4.3).

4.9 Priors

To account for variations in habitat quality between the four beats and the mostly sedentary nature of red grouse, parameters related to demography ($\phi_a, \gamma_0, \gamma_1$) were assumed to be beat-specific. However, the parameters pertaining to aggressiveness and parasites ($\xi_0, \xi_1, \xi_2, \delta_0$) were assumed to be beat-independent since these responses
Figure 4.1: The figures track grouse density in the spring and autumn (black), through time, as well as the corresponding average worm burdens (red) and aggression (blue). Worm burdens are associated with spring grouse density, while aggression is linked with grouse density in the autumn. The figures serve as an example of possible trajectories for grouse population dynamics using a deterministic form of the combined model.
Figure 4.2: The figures track grouse density in the spring and autumn (black), through time, as well as the corresponding average worm burdens (red) and aggression (blue). Worm burdens are associated with spring grouse density, while aggression is linked with grouse density in the autumn. The figures serve as an example of possible trajectories for grouse population dynamics using a stochastic model.

should apply to the entire species (Lambin et al., 2006). The values for the uniform priors (Table 4.3) were determined from the simulations described in Section 4.8.

<table>
<thead>
<tr>
<th>θ</th>
<th>Prior</th>
</tr>
</thead>
<tbody>
<tr>
<td>ξ₀</td>
<td>U(-4,-2)</td>
</tr>
<tr>
<td>ξ₁</td>
<td>U(0,0.02)</td>
</tr>
<tr>
<td>ξ₂</td>
<td>U(0.005,0.04)</td>
</tr>
<tr>
<td>δ₀</td>
<td>U(0,6)</td>
</tr>
</tbody>
</table>

Table 4.3: Priors for the red grouse parameters for which no previous biological information was available.

For the parameters γ₀ and γ₁ it was possible to use information available in the published literature to choose weakly informative means and variances for the priors. The parameter γ₀ is the log of base brood size of the grouse, and so could take both positive and negative values. A reasonably large variance was chosen, resulting in a N(0,10) prior. *T. tenuis* is known to reduce the grousers’ rearing rate, so the effect of parasites is constrained to be negative in the model itself (Eqn. 4.10). Therefore
\( \gamma_1 \) must be positive. Given that parasite burdens can be very high, up to as much as 25,000 worms in a single bird (Shaw & Moss, 1989), \( \gamma_1 \) must be small; otherwise no young would ever be produced by the grouse. As a result \( \gamma_1 \) was given a \( \Gamma(1,50) \) prior. With regards to adult survival, and in the case of the extrinsic model, juvenile survival, the prior was based solely on biological realism, resulting in the use of a beta prior on the survival parameters to constrain the values between zero and one (Table 4.4).

<table>
<thead>
<tr>
<th>( \Theta )</th>
<th>Prior</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \gamma_0 )</td>
<td>( N(0,10) )</td>
</tr>
<tr>
<td>( \gamma_1 )</td>
<td>( \Gamma(1,50) )</td>
</tr>
<tr>
<td>( \phi_a )</td>
<td>( \beta(1,1) )</td>
</tr>
<tr>
<td>( \phi_j^* )</td>
<td>( \beta(1,1) )</td>
</tr>
</tbody>
</table>

Table 4.4: Priors for the red grouse parameters for which previous biological information was available. (* Extrinsic model only)

Since \( \gamma_0 \) and \( \gamma_1 \) combine with the average parasite burden (\( W_t \)) to produce the rearing rate, \( \lambda_t \) (Eqn. 4.10), an implicit prior is formed. When the possible values for \( W_t \) are taken into account, the implicit prior on \( \lambda_t \) allows for extremely large values for the rearing rate (Fig. 4.3). While it is not biologically realistic to have a rearing rate in the thousands, the implicit prior does ensure that our choice of weakly informative priors on \( \gamma_0 \) and \( \gamma_1 \) is not unduly affecting \( \lambda_t \).

![Figure 4.3: An example of an implicit prior for \( \lambda_t \), where \( W_t \) is equal to 25,000](attachment:image.png)
A weak prior was chosen for the observation constant, \( c \) (Eqn. 4.14). This was because, while I am not explicitly defining a prior for \( p_t \), the value is calculated using an estimated parameter \( c \), resulting in an implicit prior on \( p_t \). The prior for \( c \) was therefore chosen to result in a reasonable implicit prior on \( p_t \), defined as a unimodal distribution on \( p_t \) for all levels of effort \( (d_t) \). A \( \Gamma(15,2) \) prior was chosen for \( c \), since this resulted in hill-shaped implicit priors on \( p_t \) that avoided spikes at zero or one (Fig. 4.4).

![Figure 4.4: An example of an implicit prior for \( p_t \), when \( d_t \) is equal to three.](image)

As well as priors for the different parameters used in the model, it was necessary to specify initial state priors for fall grouse density in year one, \( G_{f,1} \), and spring grouse density and parasite burdens in year two, \( G_2 \) and \( W_2 \), respectively (Table 4.5). The grouse process model began in year two to allow the first year’s data to inform the estimate of \( G_{f,1} \) needed in Eqn. 4.2 to calculate aggressiveness for year two. Otherwise, it would have been necessary to estimate a value for \( G_{f,0} \), for which no count data was available. Since density and \( T. tenuis \) burdens cannot be negative, gamma distributions were chosen for the priors to constrain the estimates to be positive. Weakly informative priors were chosen for the density estimates, where the mean was equal to the variance. For autumn density, a mean of 60 was used, as this was slightly less than double the observed counts. Assuming that the proportion of grouse seen during grouse counts does not vary with season, autumn counts have been observed to be approximately twice the size of counts which take
place the following spring (see Redpath & Thirgood, 1997). As a result, a mean of 30 grouse was used for the initial prior for $G_2$. Choosing a mean and variance for $W_2$ was more difficult, as there was no information in the data set on which to base the prior. Instead, the mean and variance were chosen based on general knowledge of possible parasite burdens. $T. tenuis$ begins to have negative effect on grouse rearing rate when 3000 or more worms are present in the bird (Redpath et al., 2006a). As a result, a mean of 3000 was chosen for the parasite initial value prior. It is also known that $T. tenuis$ loads in red grouse vary from six to 24,850 worms per bird (Shaw, 1988), so a large variance was chosen to allow for the possibility of large initial mean parasite burdens.

<table>
<thead>
<tr>
<th>Initial State</th>
<th>Prior</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G_{f,1}$</td>
<td>$\Gamma(60,1)$</td>
</tr>
<tr>
<td>$G_2$</td>
<td>$\Gamma(30,1)$</td>
</tr>
<tr>
<td>$W_2$</td>
<td>$\Gamma(3,0.001)$</td>
</tr>
</tbody>
</table>

Table 4.5: Initial state priors for autumn grouse density ($G_{f,1}$), spring grouse density ($G_2$) and average parasite burden ($W_2$).

4.10 Model fitting

The grouse model was fit in a state-space model, as described in Chapter 2. The stochastic realisations of the grouse population processes (Eqns. 4.11 and 4.12) were used in the process model, while the red grouse observations were modelled using Eqns. 4.14 and 4.15.

To compare the intrinsic and extrinsic hypotheses, three models were run. The first, as presented in Eqn. 4.8, incorporated both hypotheses. In the other two models the effects of either parasites or aggressiveness were switched off as follows: In the case of the intrinsic model, the rearing rate ($\lambda_t$) was modified to be a constant dependent solely upon $\gamma_0$, the log of average brood size of red grouse (see Eqn. 4.10). For the extrinsic hypothesis, juvenile survival ($\phi_j$) was estimated as a constant with a $\beta(1,1)$ prior, instead of being allowed to vary from year to year with autumn cock density and aggression, as it did in Eqn. 4.9.
Model selection is usually achieved through information criteria (see Chapter 2 Sec. 2.7). The BIC is not appropriate here, since the models are hierarchical and the effective number of parameters is not known (Spiegelhalter et al., 2002). However, the DIC also fails to be applicable, since it can result in negative dimensionality when used in conjunction with models involving missing data (Celeux et al., 2006). Given the lack of data on aggressiveness and parasites, the models for the different hypotheses were compared in three ways. First, the model fitting diagnostics were examined to assess convergence and mixing. While these cannot be used to select between the hypotheses, inference from a model that displays poor mixing and/or convergence would be questionable. The poor mixing and/or convergence could also be a result of poor implementation of the MCMC algorithm or parameter redundancy. Second, the model estimates for grouse density were examined to determine whether they were cyclic. Lastly, a selection of estimated model parameters were compared to those available in the literature, to determine if the models are capable of creating cyclic dynamics under biologically realistic circumstances.

4.11 Results

Each model took three to six hours to run three chains for 100,000 iterations on a 3.2 GHz processor. A burn-in of 10,000 iterations was used and only every tenth iteration was retained to reduce serial autocorrelation between MCMC trials and to help with the storage of the output from the MCMC chains. Trace plots were used to assess mixing and the Gelman-Rubin statistic was used as a quantitative diagnostic to assess the convergence of multiple chains to a target distribution (Brooks & Roberts, 1998). Autocorrelation plots for the grouse densities on each of the four beats in spring and autumn were investigated to determine the presence of cycles. Grouse fluctuations are variable, as peaks in population numbers can occur at irregular intervals (Potts et al., 1984; Williams, 1985; Hudson, 1992). Due to the inability to remember the phase, grouse cycles can be termed ‘phase-forgetting quasi-cycles,’ as opposed to those species that cycle with precise periods (Nisbet & Gurney, 1982). As a result, decisions on the cyclic nature of the grouse densities was determined by the presence
of ‘quasi-cycles.’

Correlations between the parameters were examined individually for each model. Given the relationships between the parameters, it would be reasonable to look for correlations among the aggression parameters \((\xi_0, \xi_1, \xi_2)\), the rearing rate parameters \((\gamma_0, \gamma_1)\), and the survival parameters \((\phi_a, \phi_j)\). Additionally, correlations between \(\gamma_1\) and \(\delta_0\) should be examined, as both parameters deal directly with parasite burdens. Finally, there is also conceivably a relationship between adult survival \((\phi_a)\) and the log of brood size \((\gamma_0)\), since high adult survival might reasonably be postulated to reduce the number of young reared per pair due to increased density dependence.

4.11.1 Prior sensitivity

The parameters for which it was possible to use informative priors based on previous biological knowledge \((\gamma_0, \gamma_1, \phi_a, \phi_j, c)\) were robust to the choice of prior. Given the lack of data to fit to the models for aggression and parasites, it is not surprising that the associated parameters \((\xi_0, \xi_1, \xi_2, \delta_0)\) showed prior sensitivity. The sensitivity to prior choice is not immediately apparent from the posterior-prior plots, as the posterior distributions for \(\xi_0, \xi_1, \xi_2\) and \(\delta_0\) have moved away from the prior. While there is still a degree of overlap between the distributions, the posteriors have moved away from the uniform distribution of the priors (Figs. 4.5, 4.6 and 4.7). It should be noted that the posteriors change significantly depending on the choice of priors. Due to the use of uniform priors, the measure of overlap between the prior and posterior distributions may be a reasonable indicator weak identifiability of parameters. However, the consistency of the threshold in cases where not all the priors are uniform is not clear, nor is the application of the threshold to cases other than mark-recapture-recovery data (Gimenez et al., 2008).

Due to the lack of data for the aggressiveness and parasite parameters, if truly uninformative priors are chosen, the posterior estimates tend towards values that would negate the affect of the two processes. Predictions of large values for \(\xi_0, \xi_1\) and \(\xi_2\) result in aggression levels maintained around a value of one; juvenile survival is then
essentially dependent solely on fall density (See Eqn. 4.2). Higher estimates of $\delta_0$ result in low parasite and arrested larvae survival (See Eqn. 4.5). Consequently, *T. tenuis* burdens become extremely low and therefore have little affect on grouse rearing rate (See Eqn. 4.10). Previous studies have shown the ability of parasites and aggression to affect red grouse (e.g., Hudson et al., 1992b; Mougeot et al., 2005c). Thus, given the processes are known to have an effect, it is necessary to include aggressiveness and parasites in the model, either as point estimates of the unknown parameters chosen to allow cycles, or else by providing informative priors. Since it is best to avoid choosing arbitrary parameter values, the simulations described in Section 4.8 were used to provide a range of values for the informative priors that were capable of creating biologically realistic dynamics.

Figure 4.5: Posterior (red) - prior (black) plots for the parameters in the intrinsic model for red grouse population dynamics.

For all three models, the estimates for the initial states are very sensitive to the choice
of prior (Fig. 4.8). While there does appear to be some information available for the initial values of $G_{f,2}$, it is not strong. Additionally, when gamma priors are chosen with different means, there is a corresponding shift in the initial value estimates. The change in the estimate for the initial value affects the grouse densities and parasite burdens predicted by the model. However, the pattern of the yearly fluctuations in grouse densities and parasite burdens remains the same. The estimated value is simply shifted upwards or downwards. Therefore, while the model would not be useful in predicting exact grouse densities, it is useful with regards to investigating red grouse population processes, the mechanisms behind their cycles and the affect of various impacts on grouse dynamics.

4.11.2 Intrinsic model

The red grouse model, in the absence of $T. tenuis$, displayed cyclic behaviour on all four monitored beats, starting during a cyclic increase and ending in a decline phase. Spring and fall densities followed the same pattern, with autumn density higher than
Figure 4.7: Posterior (red) - prior (black) plots for the parameters in the combined model for red grouse population dynamics.
Figure 4.8: Posterior (red) - prior (black) plots of the initial states for the combined model for red grouse population dynamics.

Spring density (Fig. 4.9). Aggressiveness peaked with, or just after, peak autumn densities, remaining high during the initial decline phase and only later allowing grouse densities to increase (Fig. 4.10). The intrinsic model converged for all the tracked parameters and states. Overall, the model displayed good mixing, although for some states, such as adult grouse density on beat LC and most of the estimates for the number of young reared per pair, mixing was generally poor in comparison to the other models.

Strong correlations can be seen between adult survival ($\phi_a$) and the log of brood size ($\gamma_0$). However, there is only a weak negative correlation among the aggression parameters ($\xi_0, \xi_1, \xi_2$) (Fig. 4.11).

4.11.3 Extrinsic model

The extrinsic model followed a similar pattern to the intrinsic model, with evidence for cyclic behaviour in both the spring and fall densities of the red grouse (Fig. 4.12). The predicted parasite densities lagged behind spring grouse densities, peaking just
Figure 4.9: Density of red grouse (km$^{-2}$) in autumn (black) and spring (brown) on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1992 for the intrinsic model. Estimates of spring grouse density start in 1976.

Figure 4.10: The relative timing of aggression (blue) and autumn grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1992 for the intrinsic model.
after grouse reached their peak and remaining low during the initial increase phase of
grouse cycles (Fig. 4.13). The predicted values for the worm burdens were comparable
across the beats and remained within the biologically realistic bounds of six to 24,850
worms per grouse (Shaw, 1988). The model converged for all the tracked parameters
and states. However, mixing for years two and three on beat LD was relatively poor
for adult, juvenile, chick and autumn density, as well as for adult (φₐ) and juvenile
(φⱼ) survival, excluding beat LC. Otherwise the model displayed good mixing for
most parameters and states.

For the extrinsic model, there are strong negative correlations between the survival
parameters (φₐ, φⱼ). In contrast to the intrinsic model, the negative correlations
between adult survival (φₐ) and the log of brood size (γ₀) are much weaker, even
becoming positive for beat LR. Additionally, there is only an extremely slight positive
correlation between the rearing rate parameters (γ₀, γ₁) and no correlation between
the parasite parameters (γ₁, δ₀) (Fig. 4.14).
Figure 4.12: Density of red grouse (km$^{-2}$) in autumn (black) and spring (brown) on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1992 for the extrinsic model. Estimates of spring grouse density start in 1976.

Figure 4.13: The relative timing of parasites (red) and spring grouse density (km$^2$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1992 for the extrinsic model.
4.11.4 Combined model

The combined model showed cyclic behaviour (Fig. 4.15). Aggression peaked with, or just after, peak autumn densities and parasites peaked just after peak spring densities (Figs. 4.16 and 4.17). Both aggression and parasite burdens remained high through the initial decline phase of the cycle and crashed shortly after the crash in grouse density, remaining low during the initial growth phase of the grouse population cycle. Parasite burdens were not as consistent across the beats, but remained biologically plausible (Fig. 4.17). The combined model converged and displayed good mixing.

In contrast to the intrinsic and extrinsic models, there are no strong correlations between parameters in the combined model. There is no real evidence for correlations between the parasite parameters \((\gamma_1, \delta_0)\) or between adult survival \((\phi_a)\) and the log of brood size \((\gamma_0)\). There are only weak positive correlations between the rearing rate \((\gamma_0, \gamma_1)\) and the aggression \((\xi_0, \xi_1, \xi_2)\) parameters (Fig. 4.18).
Figure 4.15: Density of red grouse (km$^{-2}$) in autumn (black) and spring (brown) on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1992 for the combined model. Estimates of spring grouse density start in 1976.

Figure 4.16: The relative timing of aggression (blue) and autumn grouse density (km$^2$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1992 for the combined model.
Figure 4.17: The relative timing of parasites (red) and spring grouse density (km², black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1992 for the combined model.

Figure 4.18: Correlation plots for the parameters in the combined model for red grouse population dynamics.
4.11.5 Model comparison

The only parameters to appear in all three models were the natural log of average brood size ($\gamma_0$), adult survival ($\phi_a$), juvenile survival ($\phi_j$) and the observation constant ($c$). The parameter estimates varied across the three models (Table 4.6) and were compared with ranges of values published in earlier literature. The range of posterior mean adult survival probabilities across the beats was lowest in the intrinsic model (25-44%) and highest in the extrinsic model (54-76%). The combined model, whose values fell between the other two (50-66%), was the only model to remain completely within the range of previous estimates for $\phi_a$ (34% (Jenkins et al., 1967) to 70% (Park et al., 2002)). The exponent of $\gamma_0$ gave mean brood size, which showed a similar pattern to $\phi_a$; the range of brood size across the beats was lowest in the intrinsic model (5.4-6.9 chicks) and highest in the extrinsic model (6.7-18.8 chicks). The values estimated from the combined model fell between the other two models (6.2-9.8 chicks). My estimates of $\gamma_0$, while less variable than individual brood sizes, should fall between the lowest (one (Jenkins et al., 1963)) and highest (12 (Moss et al., 1981)) observed individual broods. Only the estimates from the intrinsic and combined models are below 12. Juvenile survival varied from year to year in the combined and intrinsic models according to changing levels of aggression and grouse density (Eqn. 4.9). The estimates for the range of values across the beats from the intrinsic model (8-75%) were almost identical to those from the combined model (7-75%). Juvenile survival was a constant in the extrinsic model with much lower and less variable estimates (10-25%) across the beats, which fell below the previous estimate of 48% for $\phi_j$ (Hudson, 1992). The estimates for the observation constant, $c$, varied among the three models, but showed the same pattern in the relative values for the individual beats.

The parameter values for aggression ($\xi_0, \xi_1, \xi_2$) were similar between the combined and the intrinsic models (Table 4.7). The estimates related to the parasites ($\delta_0, \gamma_1$) varied slightly between the two models, with the values estimated by the combined model slightly lower than those for the extrinsic model (Table 4.8). Dobson & Hudson (1992) estimated the reduction in grouse fecundity per worm to be $5 \times 10^{-4}$. The estimates
<table>
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<th>Extrinsic</th>
<th>Combined</th>
<th>Previous Estimate</th>
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<td>1.8</td>
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<td>(3.1, 7.4)</td>
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Table 4.6: Posterior means and their 95% credible intervals for the red grouse parameters estimates, as well as their values from previously published literature (Jenkins et al., 1963, 1967; Moss et al., 1981; Hudson, 1992; Park et al., 2002). (* Estimates vary from year to year, ‡No previous estimate available, †Values are on the log scale)
for $\gamma_1$, the effect of *T. tenuis* on rearing rate, range from $2.8 \times 10^{-4}$ to $3.8 \times 10^{-3}$, across the two models. Given the lack of data on parasite burdens, the estimates of $\gamma_1$ were seen to fall within a reasonable range of the previously estimated value.

$$
\begin{array}{c|cc}
\Theta & \text{Intrinsic} & \text{Combined} \\
\hline
\xi_0 & -2.3 (-3.0, -2.1) & -2.3 (-2.9, -2.0) \\
\xi_1 & 0.014 (0.0036, 0.019) & 0.0158 (0.0042, 0.019) \\
\xi_2 & 0.032 (0.014, 0.039) & 0.029 (0.0099, 0.039) \\
\end{array}
$$

Table 4.7: Estimates and 95\% credible intervals for the red grouse parameters associated with aggression. No previous estimates of these parameters are available.

$$
\begin{array}{c|ccc|c}
\Theta & \text{Extrinsic} & \text{Combined} & \text{Previous Estimate} \\
\hline
\delta_0 & 5.7 & 5.3 & 5.0 \times 10^{-4} \\
& (5.02, 5.9) & (4.4, 5.9) & \\
\gamma_{1,LC} & 1.1 \times 10^{-3} & 2.9 \times 10^{-4} & \\
& (4.6 \times 10^{-5}, 5.1 \times 10^{-3}) & (4.1 \times 10^{-6}, 1.6 \times 10^{-3}) & \\
\gamma_{1,LD} & 3.8 \times 10^{-3} & 1.3 \times 10^{-3} & \\
& (4.9 \times 10^{-5}, 2.9 \times 10^{-2}) & (1.1 \times 10^{-5}, 6.9 \times 10^{-3}) & \\
\gamma_{1,LM} & 4.7 \times 10^{-4} & 3.1 \times 10^{-4} & \\
& (1.8 \times 10^{-5}, 2.6 \times 10^{-3}) & (8.2 \times 10^{-6}, 1.6 \times 10^{-3}) & \\
\gamma_{1,LR} & 3.4 \times 10^{-4} & 2.8 \times 10^{-4} & \\
& (4.3 \times 10^{-6}, 1.9 \times 10^{-3}) & (1.6 \times 10^{-6}, 1.5 \times 10^{-3}) & \\
\end{array}
$$

Table 4.8: Estimates and 95\% credible intervals for the red grouse parameters associated with parasite burdens. (‡No previous estimate available.)

Correlations between the various model parameters are more apparent in the intrinsic and extrinsic model, as compared with the combined model. The pattern of the correlations can be explained from a biological viewpoint. In the extrinsic model, an inverse relationship between juvenile and adult survival would be expected, as limited resources ensure that an increase in numbers in one requires a decrease in the numbers of the other. Interestingly, even when an informative prior implying high juvenile survival spiked at one is used for $\phi_j$ in the extrinsic model, the resulting posterior estimates of $\phi_j$ remain low and relatively unchanged. The slight positive correlation between the rearing rate parameters ($\gamma_0$, $\gamma_1$) can be explained, since increased brood sizes would allow for a larger effect of parasite burdens without reducing the rearing rate to biologically implausible values.

In the intrinsic model it would be reasonable, from a biological standpoint, to expect an inverse relationship between mean brood size and adult survival. If adults
are surviving longer, then fewer young may be produced, since there is a limit to the numbers of grouse an area can support. The lack of strong correlations in the combined model is due to the model’s increased number of parameters. The effect of shifting the value of any one parameter is diffused, as the impact of the change is spread across multiple parameters.

Checking the fit of the model to the data can be achieved by drawing samples from the posterior distribution and comparing these to the observed data (Gelman et al., 1995). In this case, the simulated trajectories from all three models (Fig. 4.19) capture the main features of the data. Individual predictions varied the most in the years where no data were available for autumn grouse density. In these years it was difficult to estimate the phase of the cycle, so estimates ranged from sharp peaks to steep declines. This is reflected in the uncertainty around the models’ estimates for autumn grouse density in those years. The data (dashed line) are consistently below the simulated trajectories because the model trajectories are estimates of the underlying ‘true’ grouse densities, while the data represent only a proportion of the grouse present on the estate (Eqn. 4.14).

With regards to the various states tracked by the model, the autumn densities estimated by the three models were similar, and all matched key features of the data (Fig. 4.20). The combined model provided the highest density estimates, followed by the intrinsic and then the extrinsic model, with exceptions on beats LD and LR. In beat LR, the intrinsic model estimated higher densities than the combined model for the entire time series.

Distinct differences among the models were seen in the estimated spring densities (Fig. 4.21). The values each model estimated for spring density showed little consistent pattern in their relationship to the other models, although the intrinsic model consistently estimated spring densities lower than the combined model for all four beats. In contrast, the spring densities estimated by the extrinsic model showed no regular pattern in relation to the other two models. In comparison to the other models, spring density on beat LM has less of a tendency to cycle in the extrinsic model.
Figure 4.19: Fifty simulated trajectories for autumn grouse density (km$^{-2}$) from the intrinsic (orange), extrinsic (green) and combined (black) models for each of the four beats on Langholm estate (LC, LD, LM, LR) from 1975-1992, as compared to the observed grouse densities (dashed line) for each of the beats in that time period.

Figure 4.20: Density of red grouse (km$^{-2}$) in autumn on each of four beats on Langholm moor (LC, LD, LM, LR) from 1975-1992 for the combined (black), intrinsic (orange) and extrinsic (green) models, in comparison to the observed data (dashed line).
Figure 4.21: Density of red grouse (km$^{-2}$) in spring on each of four beats on Langholm moor (LC, LD, LM, LR) from 1976-1992 for the combined (black), intrinsic (orange) and extrinsic (green) models.

The estimates for aggression level were almost identical for the combined and intrinsic models (Fig. 4.22). In contrast, T. tenuis burdens were higher for the combined model than the extrinsic model for all but beat LD. While the average worm burden per bird showed the same pattern of increase and decrease for the two models, the estimated values varied appreciably between them (Fig. 4.23).

4.12 Discussion

The need for parsimony and computationally tractability has meant that single-factor hypotheses have, until now, dominated the literature on population cycles (Turchin, 2003; Berryman, 2002). This is most apparent in the case of red grouse, where the debate between two single-factor hypotheses has also come to embody the debate on the relative importance of intrinsic and extrinsic mechanisms for population dynamics. I have addressed this by formulating an initial model of the ‘combined’ hypothesis.

A comparison between the proposed explanations requires that they are confronted
Figure 4.22: Aggression levels on each of four beats on Langholm moor (LC, LD, LM, LR) from 1975-1992 for the combined (black) and intrinsic (orange) models for red grouse population dynamics.

Figure 4.23: Average worm burdens on each of four beats on Langholm moor (LC, LD, LM, LR) from 1976-1992 for the combined (black) and extrinsic (green) models for red grouse population dynamics.
with field observations. The assumptions inherent in the use of these hypotheses are supported by field observations (e.g., Hudson et al., 1992b; Mougeot et al., 2003, 2006).

It is known from past theoretical work (Dobson & Hudson, 1992; Matthiopoulos et al., 1998, 2000, 2002, 2003) that each of the two single-factor hypotheses can, under realistic ranges of parameters, generate cycles with period and amplitude within the observed ranges. However, a more stringent test of the models’ validity is to fit them to data, since this enables us to express the quality of different models in likelihood terms and study the correlations between different parameters.

All three models produced similar estimates of autumn density, but differed in their estimates of spring density. The intrinsic model estimated spring densities consistently lower than the combined model, but the extrinsic model showed no apparent pattern in its relationship to the other models. The variation in spring densities among the models results from a combination of differences in parameter estimates and the interactions between density, aggression and parasite burdens.

The intrinsic model yielded the smallest estimates of adult survival, resulting in the estimated low spring densities. However, due to the absence of *T. tenuis* from that model, there is no reduction in the rearing rate. This allowed autumn densities to reach the same values as the other models, despite the low brood size. Maintaining relatively high autumn density produces aggression levels comparable with those of the combined model, resulting in more limited recruitment than would be expected from the spring densities alone. This reduction, combined with low adult survival, gives the low predictions of spring density for the intrinsic model.

In the extrinsic model, large brood size and high adult survival can produce high spring densities, but only when parasite burdens are low. Otherwise, the low juvenile survival combines with the reduced rearing rate to suppress spring density. Spring density impacts the estimates of *T. tenuis* levels, because the overall survival of grouse from autumn of year $t$ to spring of year $t + 1$ affects parasite survival (Eqn. 4.5). The spring parasite burden then modifies the rearing rate, and thus the number of young available to be recruited into next year’s breeding population. The extrinsic model’s different spring density estimates, combined with a slightly higher estimate for $\gamma_0$, 

result in the different predicted parasite burdens between the combined and extrinsic models.

In the combined model, it is possible to observe the indirect impacts between aggression and parasites. Autumn density controls aggression, determining the level of juvenile recruitment into the territorial population. Recruitment shapes grouse numbers, which affect parasite survival through changes in grouse density from autumn to spring. The shifting parasite burdens modify the rearing rate, impacting autumn density and aggression during the territorial contests. The estimates of adult survival and brood size are not as high as for the extrinsic model, but the fluctuating juvenile survival can allow for greater recruitment into the population and thus higher spring densities in many cases.

All three models fitted the data well, and all are capable of creating cyclic dynamics. While good convergence and mixing do not indicate model appropriateness, inference is unreliable if convergence and mixing are poor. In our case, all the models converged on stationary distributions, but only the combined model displayed good mixing for all MCMC chains. This is likely due to the strong correlations between parameters in the intrinsic and extrinsic models, which can slow mixing (Figs. 4.11, 4.14 and 4.18). Slow mixing means posterior densities may not accurately represent the target distribution, leading to questionable inference. However, outputs from multiple chains can be used to improve coverage of the parameter space.

Given that my first two methods of comparison, model diagnostics and the ability to create cycles, fail to show a distinct difference among the models, model choice is dependent on the biological plausibility of the parameter estimates. All three models generate fall grouse densities that fit the main features of the data (Fig. 4.20). However, only the combined model does so using biologically realistic parameter values. This may be due to the increased flexibility of the combined model. However, if the incorporation of both mechanisms led to an over-parameterized model, identifiability would tend to decrease, which may lead to an apparent lack of biological plausibility. On the contrary, the combined model was the only one to estimate biologically realistic parameter values in all cases, providing support for the combined hypothesis.
High levels of uncertainty in the parameters, $\gamma_0$ in particular, may be due to the lack of information on aggressiveness and parasites.

In contrast to earlier work that focused on management related to a single hypothesis, these results imply that efficient management of grouse populations requires both aggression and parasites be taken into account. Managing only for parasites increases the rearing rate (Newborn & Foster, 2002), eventually leading to increased aggression and continued cycles. If spring density is lowered to reduce the effects of aggression, parasite loads will still increase (Watson & Hudson, 1988). The density manipulations will keep the grouse population from crashing, so transmission of $T. tenuis$ will remain high. This results in a reduced rearing rate and the eventual continuation of the cycles. Potential field studies to test the combined hypothesis, in which there would be both a reduction of spring density and treatment with anthelmintics to reduce parasites, could be used to further test whether the combined hypothesis is the reason for persistent red grouse cycles. Such field tests could also be used to provide data to build a model for an ‘interaction’ hypothesis, where the direct relationships between aggressiveness and parasites are taken into account. The additional information could also be used to construct a model for the parasites that accounts for the distribution of $T. tenuis$ across individuals, rather than tracking the average worm burden per bird.

Although the models were fit to data from the Langholm estate, they could readily be applied to data from other grouse estates in the UK. Beat-specific demographic parameters ($\phi_a, \phi_j, \gamma_0, \gamma_1$), could be treated as region-specific, giving the model the ability to account for spatial variations in grouse cycles. Additionally, weather can give some indication of outbreaks in the relative intensities of $T. tenuis$ infections (Cattadori et al., 2005) and can affect parasite recruitment (Moss et al., 1993). Therefore, the parasite model could be adapted to incorporate local weather data, which may also explain some of the observed regional differences in grouse cycles.

As well as suggesting further field experiments and increasing understanding of the red grouse population dynamics, the models could be used to directly assess the effect of different management plans on grouse populations. Predictions into the future can
be made under alternative management scenarios, such as the one suggested for the field experiment. By using a Bayesian framework the level of uncertainty around management decisions can be quantified, allowing for choices to be made based on all the available information.

Additionally, the grouse-only model presented in this Chapter can be combined with the hen harrier model presented in Chapter 3. This creates a more biologically realistic representation of the grouse system, as harriers are known to predate the red grouse chicks (e.g., Redpath & Thirgood, 1997). If the goal of understanding the red grouse population processes is to inform management, then it is also necessary to have some understanding of the grouse’s interaction with their predators; most notably the hen harrier, which cannot be legally controlled by gamekeepers.

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Chapter 5

Grouse-Harrier Interactions

5.1 The conflict

The impact of human-wildlife conflict on ecosystems can be profound. People often deal with perceived pests by culling, both legally and illegally. As well as achieving the suppression of local populations, lethal control can result in species extinction within an area, or even for the species as a whole. The conflict between people and individual species does not exist in a vacuum; habitats and ecosystems are also affected. For instance, habitat destruction can be used to put a permanent end to human-wildlife conflict, but will result in the loss of many species not directly inconveniencing people. Additionally, the loss of a single species can have cascading effects, negatively impacting ecosystems and other species that may depend on the one that has been extirpated (Woodroffe et al., 2005c).

Some human-wildlife conflict occurs due to one animal’s predation on economically or culturally valuable game species. While the long held belief was that predators took only the ‘doomed surplus,’ more recent research shows that predators are capable of limiting prey populations (Thirgood et al., 2005). As mentioned in Chapter 3, the conflict between hen harriers (Circus cyaneus) and humans is a result of the negative impact the harriers’ presence is perceived to have on the economically valuable gamebird, the red grouse (Lagopus lagopus scoticus), and thus the income and livelihoods of many people in Scotland. The conflict is an old one; in the 1850’s as many as 310
harriers were killed on a single estate in Ayrshire in just four years (Elton, 1942). People’s concerns are not unfounded; the presence of both hen harriers and peregrine falcons (*Falco peregrinus*) on a grouse moorland has led to as much as a 50% decline in autumn grouse densities (Thirgood et al., 2000c). A decline this severe can lead to population densities too low to allow for driven shooting, resulting in reported losses of as much as $150,000 per year (Redpath & Thirgood, 1997). As a consequence, lethal control of hen harriers continues into the present day, despite the legal protection meant to halt the persecution (Etheridge et al., 1997).

Attempts have been made to mitigate the conflict between gamekeeper interests and hen harriers. Since the harrier exists in multi-use landscapes heavily exploited by humans, it is not possible to effectively conserve the raptor if coexistence with people is not possible (Woodroffe et al., 2005b). A stakeholder focus group, including raptor conservationists and gamekeepers attempted to address the issues arising from harrier predation on grouse. The resulting conclusion was that gamekeepers are not adverse to having hen harriers on the moorland, provided the red grouse are not negatively affected. Different options for conflict mitigation were explored, such as habitat manipulation and methods to deter harriers from feeding on grouse chicks. However, many of these options were not acceptable to both sides of the management debate; while raptor conservationists favour allowing hen harriers to reach their natural densities, gamekeepers reject this idea because of its strong negative impacts on the economic viability of the grouse moors. By the same token, the conservationists are unwilling to accept management actions that include the legal culling of hen harriers (Redpath et al., 2004).

Lethal control may have a role in wildlife conservation (Treves & Naughton-Treves, 2005), but it remains a topic of great debate, since it addresses ethical and conservation issues in modern society. Alone, lethal control is rarely enough to reduce the impacts of predation to a level acceptable to humans. The unacceptability of lethal control makes non-lethal methods necessary, which must be effective, acceptable, applicable and cost-effective (Breitenmoser et al., 2005). The human-harrier conflict is unusual, since the lethal control of the hen harrier has proven to be enough to
completely halt the effects of predation and maintain grouse shooting as a profitable enterprise (Thirgood et al., 2000a). Additionally, while the persecution of the hen harrier has slowed its recovery in the UK, it has not completely halted the birds’ re-colonisation of its traditional range (Thirgood & Redpath, 2005). Hen harriers, therefore, fit within two of the three criteria used to evaluate the feasibility of lethal control: the effectiveness of the method in reducing impact on human livelihoods and the continued viability of the species even when controlled. However, the third criterion, public and stakeholder participation, is not met due to declining public tolerance for hunting and culling in the UK (Treves & Naughton-Treves, 2005). While lethal control can be based on less controversial methods such as egg removal, as opposed to the destruction of adult harriers, it is still unlikely that this method of conflict-mitigation would ever have the political will and support needed to be implemented (Thirgood & Redpath, 2005; Woodroffe et al., 2005b), despite the ‘success’ of lethal control at increasing grouse density. While the culling of any raptor population is unlikely to gain public support, the removal of ‘problem’ individuals may still be permitted when the birds begin to have strong negative impacts on farmers. In contrast, the human-harrier conflict revolves around game hunting, a pastime seen as being limited to the privileged and wealthy, making any sort of legal control unacceptable.

Given that the legal eradication of harriers is not considered an acceptable management action, non-lethal methods must be used to mitigate the conflict. Many non-lethal methods have been developed for the protection of livestock, such as flock guarding, fences or repellents, and are not practical for game-species or avian predators (Breitenmoser et al., 2005; Woodroffe et al., 2005b). Techniques meant to provide compensation for losses to wildlife face a similar problem, since they are targeted towards the replacement of individual animals lost to predators, or towards people harmed by wildlife (Nyhus et al., 2005). The high costs and lack of political support make it unlikely that compensation schemes could work in the human-harrier conflict. Some non-lethal management strategies suggested for hen harriers are not feasible due to logistic or financial reasons (Thirgood & Redpath, 2005), while still others are not proven to be successful or may negatively impact other species on the moorland (Amar et al., 2004; Thirgood et al., 2002). Additionally, the mitigation
of the human-harrier conflict is made more difficult by the entrenched views of the stakeholders involved in the debate (Thirgood & Redpath, 2008).

The feasibility of some mitigation techniques remains to be tested. However, such field-based research is expensive, in terms of both money and time. For example, the recently instigated Langholm Moor Demonstration Project will look at many of the issues surrounding the human-harrier conflict and will cost £3 million over ten years. The project will examine the combined effects of habitat management, legal predator control and diversionary feeding on the grouse and harrier populations. Predator control for the hen harrier will take the form of ceilings on the numbers of hen harriers, after which birds attempting to settle in the area will be translocated to other places (Thirgood & Redpath, 2008). While the hen harrier meets the IUCN guidelines for species translocation, this mitigation method is unlikely to be completely successful. Movement of hen harriers from areas of conflict into areas of low harrier density can help establish new harrier populations and reduce human-harrier conflict in the short term (Watson & Thirgood, 2001). However, translocation would have to continue indefinitely to keep harriers at the set threshold density. Additionally, as populations of harriers establish, the sites available for translocation will decrease, even as the number of harriers available to move onto grouse moors will increase. Translocation may therefore serve as a short-term mitigation technique, but is unlikely to serve as a long-term solution to the problem (Treves & Naughton-Treves, 2005).

Another proposed solution to reduce human-harrier conflict is habitat alteration. Outside of increasing the total area covered by suitable heather moorland, there is little evidence that management of grouse habitat can increase the bird’s density (Hudson, 1992; Thirgood et al., 2002). Additionally, grouse susceptibility to predation seems to have little relation to exact composition of their habitat. This implies that habitat manipulation for the purpose of increasing grouse density may have limited success as a conflict mitigation technique (Thirgood & Redpath, 2005). The other option for habitat manipulation is to attempt to alter heather moorland to make it less favourable to the harriers. This would be achieved by trying to reduce the density of the harriers’ main prey species, meadow pipits (Anthus pratensis) and field voles
(Microtus agrestis). These species are most common on moors containing a mixture of heather and grass (Smith et al., 2001). Therefore, if the amount of heather is increased, it is possible that the density of harriers would decrease due to the lower availability of prey. In this case, the goal is to limit harrier density in an area, rather than the overall effect of their predation. However, the impacts of this type of management are unclear. Manipulating grouse habitat to increase heather could have consequences with regards to biodiversity, since it would affect other moorland species in addition to the meadow pipit and field vole. Additionally, even if habitat manipulation was successful in reducing the human-harrier conflict, it may not aid in the recovery of hen harriers. While fewer harriers in an area may result in less illegal persecution, it would not aid the raptors’ conservation status, since the amount of habitat suitable for harriers would be decreasing (Thirgood & Redpath, 2005).

The final mitigation technique that will be field tested in the Langholm Moor Demonstration Project will be diversionary feeding (Thirgood & Redpath, 2008). While not the preferred management action of either gamekeepers or conservationists, diversionary feeding was highly regarded as a potential management strategy by both stakeholder groups. Gamekeepers favour the idea since it would, conceivably, lessen the impact of harrier predation on grouse chicks. Raptor conservationists also support diversionary feeding, since it allows for the coexistence of hen harriers and red grouse, as well as stopping many destructive persecution methods, such as poisoned bait (Redpath et al., 2004).

While a popular idea in terms of management, the ability of diversionary feeding to achieve its aims is still questionable. Feeding only a portion of the harriers present in a study on Langholm moor failed to increase grouse densities. However, by feeding all the harriers on the moor it might have been possible to increase grouse densities, since the number of grouse chicks brought to fed harrier nests was significantly lower than those brought to unfed harrier nests. Given the expense of providing supplementary food for all hen harrier nests on the moor, estimated at £11,000 per year (Redpath et al., 2001b), it would be beneficial to know whether diversionary feeding is capable of achieving its proposed aims. Additionally, if a goal of moorland management is to
maximise the density of both red grouse and hen harriers, the price of supplementary feeding can only increase as harrier numbers rise. While this could be lessened through translocation of the extraneous hen harriers, translocation has associated financial and logistical costs that are unlikely to be less than those connected to diversionary feeding. Finally, even should diversionary feeding initially achieve its aims, there may be a threshold density over which it would no longer act as a mitigating technique. At high harrier densities the combined effects of reduced predation by individual harriers may still be enough to limit grouse density. This is of particular concern to hunters, who also worry that the presence of supplementary food will attract other predators to the grouse moor (Thirgood & Redpath, 2005).

Models of hen harrier-red grouse interactions can provide a background against which to test the theories behind the field studies currently under way. In this chapter I will initially address the ability of hen harriers to suppress grouse cycles, comparing a model in which hen harriers are absent to one in which they are actively predating grouse chicks. I will then investigate the ability of diversionary feeding to serve as a mitigation technique. I will look first at a model that mimics the Langholm study, in which only a portion of the hen harriers were provided with supplementary food (Redpath et al., 2001b), comparing my results with those achieved by the study. Finally, I will examine a model in which all harrier nests present on the moor are provided with supplementary food, to try and determine whether diversionary feeding can serve as a feasible mitigation technique.

It is always possible that a combination of different techniques, as suggested in the Langholm Moor Demonstration Project (Thirgood & Redpath, 2008), can reduce the impact of harrier predation on red grouse densities, where one action alone is not enough. Indeed, no mitigation technique discussed in this chapter should be considered mutually exclusive. The combination of different management actions may alleviate some of the concerns of the different stakeholders involved, making them more willing to accept management actions that had previously caused them concern (Thirgood & Redpath, 2005; Woodroffe et al., 2005b).
5.2 The model

To model the interactions of the hen harrier and red grouse it is necessary to combine
the models presented in Chapters 3 and 4 that track the changes in hen harrier nests
\((H_t)\) and spring grouse density per square kilometre \((G_t)\) from year to year,
\[
G_{t+1} = \left(\phi + 2 \left(\frac{0.25\lambda_t}{1 + (\kappa a_t G_{f,t})}\right)\right) G_t \tag{5.1}
\]
\[
H_t = H_{t-1}\phi_{t-1} + \eta_t, \tag{5.2}
\]
where the rearing rate, \(\lambda_t\), is dependent on average parasite \((Trichostrongylus tenuis)\)
burden per bird \((W_t)\) and the aggressiveness of red grouse cocks \((a_t)\) is dependent on
their autumn density prior to hunting and recruitment \((G_f)\) from years \(t\) and \(t-1\).
Hen harrier survival \((\phi_{t-1})\) is increased by pipit density \((P_t)\), and harrier movement
\((\eta_t)\) into an area is dependent on the density of voles \((V_t)\) and pipits in an area (See
Chapters 3 and 4 Secs. 3.5 and 4.6 for the equations describing \(\eta_t, \phi_t, \lambda_t, W_t,\) and \(a_t\)
in detail).

The interaction between hen harriers and red grouse occurs when the harriers consume
red grouse chicks. Hen harriers eat the chicks in the spring and summer when they
themselves are rearing their young. The consumption rate of the grouse chicks will
depend on the harriers’ multi-species functional response (MSFR) as described by
Asseburg (2005) and Asseburg et al. (2006),
\[
f_{i,t} = \frac{k_i N_{i,t}^{m_i}}{1 + \sum_{j=1}^{N} k_j h_j N_{j,t}^{m_j}}, \tag{5.3}
\]
where \(k\) is the attack rate on species \(i\), \(N\) is the density of species \(i\) in year \(t\), and
\(i = meadow \pipits (mp), field \voles (v) or red \grouse (g)\). The parameter \(m_i\) alters
the curvature of the response for species \(i\), relating the manner in which predators’
attacks change with prey density, \(h_j\) is the handling time required for each species
\(j\), and \(f_i\) gives the consumption rate of species \(i\) per hour per harrier pair in year \(t\).
Just like the SSFR, the MSFR described in Eqn. 5.3 is capable of reflecting the prey
switching that is believed to be a part of harrier predation.
Harrier predation on the grouse chicks will reduce the number of young reared. However, while *T. tenuis* is known to reduce grouse rearing success (Newborn & Foster, 2002) the exact mechanism is unknown. Since it was only possible to model the effect of the parasitic nematode, not the mechanism (see Chp. 4), it was not possible to have the effect of parasites and predation occurring simultaneously. As a result, we are using the rearing rate (*λ*<sub><em>t</em></sub>) from Eqn. 5.1 to calculate the grouse chick density (*N*<sub><em>g</em></sub>) in year *t* for the MSFR,

\[
N_g = 0.5G_t\lambda_t,  \tag{5.4}
\]

where spring grouse density (*G*<sub><em>t</em></sub>) is halved to account for the fact that *λ*<sub><em>t</em></sub> is estimated per pair of red grouse, while *G*<sub><em>t</em></sub> is the density of grouse as a whole.

During the spring, each harrier pair will hunt for up to 15 hours a day (Watson, 1977) for 60 days (Redpath & Thirgood, 1997). Traditionally, the overall effect of harrier predation, the number of chicks eaten per km<sup>2</sup> in year *t* (*E*<sub><em>t</em></sub>), has been estimated by scaling the consumption rate per hour for grouse chicks in year *t* (*f*<sub><em>g,t</em></sub>) upwards according to the equation (Redpath & Thirgood, 1997),

\[
E_t = \frac{f_{g,t}H_t \times 15 \times 60}{L},  \tag{5.5}
\]

where *L* is the area of the grouse moor in km<sup>2</sup>, *f*<sub><em>g,t</em></sub> is calculated using the MSFR (Eqn. 5.3) and *H*<sub><em>t</em></sub> is the number of harrier nests in year *t* (Eqn. 5.2). Eqn. 5.5 overestimates the effect of predation, since it assumes the same chick density will be available for consumption over the full 60 days. However, chicks eaten by a pair of harriers on day one will no longer be available for consumption on the second day. Nor will those chicks that have been consumed by one pair be available to the other harriers. It is therefore necessary to alter the way consumption is modelled.

I model consumption by reducing the density of grouse chicks available to a pair of hen harriers during a single day by the number of grouse chicks already consumed by other harrier pairs on the same day. This is done by modelling the consumption of individual harrier pairs sequentially, within a day. The first harrier pair is ‘allowed’ to hunt and the number of chicks consumed by the pair is subtracted from the grouse chick density.
The reduced density is then used in the MSFR to calculate the consumption of the next harrier pair. The chick density is consistently reduced for each harrier pair, until all the pairs have hunted on day \(d\),

\[ N_{g,t,d,p+1} = N_{g,t,d,p} - \frac{15f_{g,t,d,p}}{L}, \tag{5.6} \]

where \(N_{g,t,d,p}\) is the density of grouse chicks available to harrier pair \(p\) on day \(d\) in year \(t\) and \(f_{g,t,d,p}\) is the number of grouse chicks consumed per hour by harrier pair \(p\) on day \(d\) in year \(t\). The new grouse chick density, \(N_{g,t,d,p+1}\), is then used in the MSFR (Eqn. 5.3) to find the consumption rate of harrier pair \(p + 1\) (\(f_{g,d,t,p+1}\)). The total number of grouse chicks consumed on day \(d\), per km\(^2\), for all harrier pairs \(p\) in year \(t\) (\(E_{t,d}\)) is therefore,

\[ E_{t,d} = \sum_{p=1}^{H_t} \frac{15f_{g,d,t,p}}{L}. \tag{5.7} \]

Once each pair of harriers has hunted on day \(d\), the density of grouse chicks available to be hunted by the first harrier pair on day \(d + 1\) is needed (\(N_{g,t,d+1}\)). However, Eqn. 5.7 gives the total number of chicks consumed. I therefore find \(N_{g,t,d+1}\) by subtracting the chicks that were eaten from the remaining density,

\[ N_{g,t,d+1} = N_{g,t,d} - E_{t,d}. \tag{5.8} \]

\(N_{g,t,d+1}\) becomes the grouse chick density used in the MSFR for the first harrier pair to hunt on day \(d + 1\), and the process of allowing each harrier pair to hunt sequentially, by day, begins again. This continues for all 60 days in which the harriers can hunt grouse chicks. The total number of consumed grouse chicks in year \(t\) (\(E_t\)) is then,

\[ E_t = \sum_{d=1}^{60} E_{t,d}. \tag{5.9} \]

Again, this gives the total number of chicks consumed over the hen harriers’ hunting period, while I am really interested in the number of chicks that survive to take part in recruitment in the autumn. I therefore calculate the proportion of chicks to survive despite the presence of harriers (\(\pi_t\)) in year \(t\),

\[ \pi_t = \frac{N_{g,t} - E_t}{N_{g,t}}, \tag{5.10} \]
where \( N_{g,t} \) is the chick density prior to predation (Eqn. 5.4). In Chapter 4 I defined \( \lambda_t \) to be the number of chicks successfully reared per grouse pair in year \( t \). Therefore, all chicks in \( N_{g,t} \) are certain to survive until the autumn territorial contest, unless otherwise eaten by a harrier. This slightly exaggerates the effect of harrier predation, since it assumes that chick mortality due to hen harriers is completely additive. However, while some harrier induced mortality may be compensatory, the majority of their impact must be additive, otherwise they would not suppress grouse cycles.

The model for the red grouse population dynamics (Eqn. 5.1), is now modified to account for the proportion of successfully reared chicks not consumed by hen harriers \((\pi_t)\), as well as adult \((\phi_a)\) and juvenile \((\phi_{j,t})\) survival,

\[
G_{t+1} = \left( \phi_a + 2 \left( \frac{0.25\lambda_t\pi_t}{1 + (\kappa_a 0.5G_{f,t})} \right) \right) G_t.
\] (5.11)

To include diversionary feeding the model, it is necessary to modify harrier consumption to account for the fact that harriers provided with supplementary food eat fewer grouse chicks. Redpath et al. (2001b) estimated that fed harrier pairs brought, on average, 3.2 fewer grouse chicks to their nests, per 100 hours. This is equivalent to 0.48 chicks per day per pair. I therefore modified Eqn. 5.6 to account for the pairs that were fed,

\[
N_{g,t,d,p+1} = N_{g,t,d,p} - \frac{15f_{g,t,d,p} - \Delta 0.48}{L},
\] (5.12)

where \( \Delta \) is equal to one, if the harrier pair has been provided with supplementary food, but is zero otherwise. Diversionary feeding is accounted for on a per pair basis. Those harrier pairs provided with additional food are ‘allowed’ to hunt first, ensuring that each successive harrier pair has the maximum possible chick density from which to hunt. This may result in slightly higher estimates of chick consumption than if pairs not provided with supplementary food are ‘allowed’ to hunt first. The higher estimates of chick consumption are due to higher chick densities being available to more pairs, so the rate of consumption can remain high. However, the greater availability of chicks is more likely to mimic reality, since birds provided with supplementary food would not catch as many young grouse, leaving higher densities available for the remaining pairs.
As with the model that deals with only the red grouse, stochasticity needs to be included in the grouse-harrier model. Stochasticity acts on a beat-specific basis, rather than for the moorland as a whole. The same distributions as described in Chapter 4 are used for the model presented here. In addition, a binomial distribution was used to include the effect of harrier predation on chick survival,

\[
R_t \sim \text{Pois}(\lambda_t)
\]

\[
G_{a,t} \sim \text{Bin}(G_t, \phi_a)
\]

\[
G_{y,t} \sim \text{Bin}(G_{c,t}, \pi_t)
\]

\[
G_{j,t} \sim \text{Bin}(G_{m,t}, \phi_{j,t})
\] (5.13)

where \(R_t\) is the average number of grouse chicks reared per pair, \(G_{a,t}\) and \(G_{j,t}\) are the densities of adult and juvenile cocks, respectively, to survive the winter in time \(t\), \(G_{y,t}\) is the density of young grouse present in autumn after harrier predation, but prior to hunting and recruitment, \(G_{c,t}\) is the density of grouse chicks in year \(t\) and \(G_{m,t}\) is the density of young males prior to hunting and recruitment in the autumn of time \(t\). Again, a Poisson distribution was chosen for reasons of convenience, as opposed to any theoretical arguments. In contrast to Chapter 4, the density of young males prior to hunting and recruitment \((G_{m,t})\) is now found according to the equation,

\[
G_{m,t} = 0.5G_{y,t},
\] (5.14)

and the density of grouse chicks \((G_{c,t})\) is found using the number of grouse chicks reared per pair \((R_t)\),

\[
G_{c,t} = 0.5G_tR_t.
\] (5.15)

The same observation model, a normal approximation of a binomial distribution, was used for the grouse as described in Chapter 4,

\[
\mu_t = G_{f,t}p_t
\]

\[
\sigma_t^2 = G_{f,t}p_t(1 - p_t)
\] (5.16)

\[
G_{f,\text{Obs},t} \sim \text{N}(\mu_t, \sigma_t^2),
\]
where, \( p_t \) is the proportion of grouse seen according to the effort (drives, \( d_t \)) in year \( t \) and \( c \) is a constant to be estimated,

\[
p_t = \frac{d_t}{d_t + c}.
\] (5.17)

For the hen harrier, since numbers were believed to be known without error, the super-population model used in Chapter 3 was implemented,

\[
\begin{align*}
\sigma_t^2 &= H_{t-1}\phi_{t-1}(1 - \phi_{t-1}) + \eta_t \\
\mu_t &= H_{t-1}\phi_{t-1} + \eta_t \\
\beta_{\Gamma,t} &= \frac{\mu_t}{\sigma_t^2} \\
\alpha_{\Gamma,t} &= \mu_t\beta_{\Gamma,t} \\
H_{\text{Obs},t} &\sim \Gamma(\alpha_{\Gamma,t}, \beta_{\Gamma,t}).
\end{align*}
\] (5.18)

In addition, instead of including grouse chick density as a covariate as was done in Chapter 3, an observation model was included for those years where chick counts were available (1992-1999). A log-normal distribution with a mean equal to the log of the estimated chick density was used,

\[
G_{c,\text{Obs},t} \sim \text{LN}(\log(G_{cavg,t}), \sigma_c^2),
\] (5.19)

where \( G_{c,\text{Obs},t} \) is the observed density of grouse chicks in year \( t \), \( G_{cavg,t} \) is the average density of grouse chicks estimated in year \( t \) (Eqn. 5.20) and \( \sigma_c^2 \) is the variance of the observation model and is to be estimated. Data on grouse chick densities were found for the entire estate, rather than the individual beats. This was due to the fact that the chick data was collected to study the hen harriers’ functional response, and while grouse are constrained to live within a given area, hen harriers are capable of hunting over the entire estate. Therefore, the average grouse chick density \( (G_{cavg,t}) \) was calculated as,

\[
G_{cavg,t} = \frac{\sum_{b=1}^{B} 0.5G_{b,t}R_{b,t}}{B},
\] (5.20)

where \( G_{b,t} \) and \( R_{b,t} \) are the spring grouse density and rearing rate in year \( t \) for beat \( b \), respectively, and \( B \) is the total number of beats on the estate for which data are
available. Since hen harriers hunt over the entire estate, the chick density calculated in Eqn. 5.20 needs to be used in the MSFR, rather than the $N_{g,t}$ found in Eqn. 5.4,

$$N_{g,t} = G_{cavg,t}. \quad (5.21)$$

The values for the parameters in the MSFR model (Eqn. 5.3), $m$, $k$ and $h$, were taken from Asseburg (2005), and are assumed to be know without error (Table 5.1). The use of point estimates for the parameter values reduces some of my ability to account for uncertainty. However, this is balanced by the inclusion of the MSFR model itself, which provides for greater biological realism than a single-species functional response (SSFR) model or the simple use of a set consumption rate. At this point, vole and pipit densities are still included as covariates. However, this will be changed in Chapter 6.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>$m$</th>
<th>$k$</th>
<th>$h$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grouse</td>
<td>4.51</td>
<td>$1.89 \times 10^{-6}$</td>
<td>2.16</td>
</tr>
<tr>
<td>Vole</td>
<td>1.04</td>
<td>$2.52 \times 10^{-2}$</td>
<td>1.24</td>
</tr>
<tr>
<td>Pipit</td>
<td>1.14</td>
<td>1.33</td>
<td>1.85</td>
</tr>
</tbody>
</table>

Table 5.1: Parameter values for the MSFR model for each species, $j$.

### 5.3 The data

The data available to fit the model was the same at that used in Chapters 3 and 4. The full time series of data from Langholm moor, from 1975-1996 was used, as were the chick counts that were available from 1992-1999. There was also information available for 1998 and 1999 with regards to the number of hen harrier nests that were provided with supplementary food.

### 5.4 Priors

The same priors were used for the grouse-harrier model as in the single-species harrier and grouse models (see Chapters 3 and 4 Tables 3.1, 4.3 and 4.4). An additional prior
was needed in the grouse-harrier model to account for the variance \( (\sigma^2_c) \) in the grouse chick observation process model (Eqn. 5.19). However, the log-normal distribution in WinBUGS is modelled using the inverse of the variance, so the prior used was actually for the precision, \( \tau_c \), where,

\[
\tau_c = \frac{1}{\sigma^2_c}
\]

(5.22)

The parameter showed a high level of sensitivity to the choice of prior. As a result, after the investigation of different choices for the prior on \( \tau_c \), a \( \Gamma(2.5,0.1) \) prior was chosen. The decision to use this prior was based on a combination of computational efficiency and biological realism. Interestingly, while the choice of prior for \( \tau_c \) influenced the estimated density of grouse chicks, it also affected the estimates and convergence for parasite burdens. The \( \Gamma(2.5,0.1) \) prior allowed for both the convergence of states associated with the parasite \( T. tenuis \), as well as mostly realistic estimates of the average parasite burden and grouse chick density, without being too restrictive on the estimates of grouse chick density.

### 5.5 Model fitting

The grouse-harrier models were fit in the Bayesian state-space framework described in Chapter 2. The stochastic realisations of the grouse processes (Eqn. 5.13) were used in the grouse process model. Red grouse observations were modelled using Eqns. 5.16, 5.17 and 5.19, while the harrier super-population model was fit using Eqn. 5.18.

To investigate whether hen harriers did in fact suppress grouse numbers as advocated by gamekeepers and hunters, two models were run. The first model, the predation model, looked for evidence of hen harrier suppression of grouse numbers, allowing harriers to hunt over the full time series in which they were present (1992-1999), without taking supplementary feeding into account. Next, I fit a prediction model to provide estimates for grouse density in the absence of hen harriers. Harrier numbers were set to zero for the last two years of the study and the chick data from this time period was removed to avoid any possible confounding with information contained in
the data with regards to hen harrier predation, as well as other, unknown, factors that were believed to be effecting chick density during this time (Redpath et al., 2001b). In these models the MSFR used the chick densities calculated using Eqn. 5.7.

The remaining two models examined whether supplementary feeding was an efficient method of mitigating the effects of hen harrier predation. The partial supplementary feeding model mimicked the Langholm field study by ‘providing’ supplementary food only to the same number of harrier nests that were actually fed during the experiment. Finally, to determine the effects of different levels of supplementary feeding, all harriers present on the moor were ‘provided’ with supplementary food in the fourth model. The supplementary feeding models were fit using Eqn. 5.12 to calculate the grouse chick densities needed for each pair’s MSFR.

5.6 Results

The models were run for three chains of 100,000 iterations, with a burn-in of 10,000 for all models except the full supplementary feeding model, which had a burn-in of 30,000. All the chains were thinned by taking every 10th iteration to reduce autocorrelation in the MCMC chain and allow for storage of the chains without encountering memory problems. The models took approximately three to four days to run on a 3.2 GHz computer processor. Trace plots were used to assess mixing and multiple chains with different starting points, and the Brooks-Gelman-Rubin statistic was used to assess convergence.

Correlations between the parameters were examined for each of the four models presented here. As well as the relationships examined in Chapters 3 and 4, I also examined possible correlations between the precision parameter for the grouse chick observation model, \( \tau_c \), and the natural log of grouse brood size, \( \gamma_0 \), since the prior sensitivity on \( \tau_c \) suggested a possible relationship between the parameters.

The correlations between the parameters related to the grouse population process model were similar for all four models. No parameters showed strong correlations,
although there was a slight negative correlation between adult grouse survival ($\phi_a$) and the natural log of grouse brood size ($\gamma_0$), as well as between between the aggression parameters $\xi_1$ and $\xi_2$ (Figs. 5.1-5.4).

Figure 5.1: Correlation plots for the grouse parameters in the predation model for grouse-harrier population dynamics.

The correlations between the parameters for the hen harrier super-population model were also similar for all four models. There was a strong negative correlation between the hen harrier survival parameters, $\alpha_0$ and $\alpha_1$, although this relationship was weaker in the prediction model. The parameters corresponding to harrier movements in response to voles and pipits, $\beta_0$ and $\beta_1$, respectively, also showed a strong negative correlation. Finally, there was a positive correlation between the effect of vole density on hen harrier movement, $\beta_0$, and the limiting effect of surviving harriers on movement into an area, $\beta_2$ (Figs. 5.5-5.8).
Figure 5.2: Correlation plots for the grouse parameters in the prediction model for grouse-harrier population dynamics.
Figure 5.3: Correlation plots for the grouse parameters in the partial supplementary feeding model for grouse-harrier population dynamics.
Figure 5.4: Correlation plots for the grouse parameters in the full supplementary feeding model for grouse-harrier population dynamics.
Figure 5.5: Correlation plots for the harrier parameters in the predation model for grouse-harrier population dynamics.

Figure 5.6: Correlation plots for the harrier parameters in the prediction model for grouse-harrier population dynamics.
Figure 5.7: Correlation plots for the harrier parameters in the partial supplementary feeding model for grouse-harrier population dynamics.

Figure 5.8: Correlation plots for the harrier parameters in the full supplementary feeding model for grouse-harrier population dynamics.
5.6.1 Prior sensitivity

Prior sensitivity was briefly examined to determine if the reliance of the estimates on the choice of prior distribution had changed from the single-species models. While the grouse model now incorporates the effects of hen harrier predation, there was no change in the prior sensitivity of the previously estimated grouse parameters. Comparing the four models for harrier-grouse interactions, the posterior-prior relationship for beat-dependent grouse parameters \((\gamma_0, \gamma_1, \phi, c)\) were nearly identical for all four models, none of which showed strong prior sensitivity (Fig. 5.9).

As in the grouse-only model, it was the beat-independent parameters related to aggression and parasites \((\xi_0, \xi_1, \xi_2, \delta_0)\) that showed prior sensitivity (see Chapter 4). Additionally, as mentioned in Sec. 5.4, the new parameter for the grouse chick observation model \((\tau_c)\) showed a significant amount of prior sensitivity. As a result, the final choice of prior for \(\tau_c\) was dependent on the efficiency of the MCMC algorithm and the biological realism of the resulting estimates.

There are differences in the posterior-prior relationships among the four models for parameters \(\xi_2\) and \(\tau_c\). In the grouse-only model the posterior for \(\xi_2\) had a mode at the upper limit of the prior (see Chapter 4), however, it now forms a more bimodal distribution, with modes at both the upper and lower limits, although this is least pronounced in the prediction model. The bimodal distribution may be due to the fact that, while the chains converge, mixing is poor, so that the posterior distribution should actually be fairly flat. For \(\tau_c\) the posterior from the prediction model shows greater uncertainty than the others (Fig. 5.10), as result of fewer years of grouse chick data being included in this model.

Among the hen harrier parameters, the only parameter to show prior sensitivity was \(\alpha_1\), the measure of the effect of pipit density on harrier survival (see Chapter 3). This was also the only parameter to display a difference in the posterior-prior relationships amongst the four models, with the prediction model having a posterior that has only narrowed slightly from the prior (Fig. 5.11). Again, this is due to two years of hen harrier data being excluded from the model, so less information is available to
Figure 5.9: Plots of the posterior distributions for the beat-dependent grouse parameters ($\gamma_0, \gamma_1, \phi_a, c$) for the predation (red), prediction (blue) and partial (green) and full (orange) supplementary feeding models for grouse-harrier population dynamics, in comparison to each parameter’s prior distribution (black).
Figure 5.10: Plots of the posterior distributions for the beat-independent grouse parameters ($\xi_0, \xi_1, \xi_2, \delta_0, \tau_c$) for the predation (red), prediction (blue) and partial (green) and full (orange) supplementary feeding models for grouse-harrier population dynamics, in comparison to each parameter’s prior distribution (black).
estimate an already sensitive parameter.

Figure 5.11: Plots of the posterior distributions for the hen harrier parameters $(\alpha_0, \alpha_1, \beta_0, \beta_1, \beta_2)$ for the predation (red), prediction (blue) and partial (green) and full (orange) supplementary feeding models for grouse-harrier population dynamics, in comparison to each parameter’s prior distribution (black).

5.6.2 Predation model

The predation model for the grouse-harrier interactions showed cyclic dynamics, in both spring and autumn, for the first 18 years of the study (Figs. 5.12 and 5.13). This was the time period in which harriers were known not to be present on the study site in numbers large enough to affect grouse density. From 1993, grouse dynamics showed suppressed fluctuations in autumn grouse density (Fig. 5.12). Spring density is also suppressed after 1992, although not to the extent seen in the autumn. The exception is beat LC, which appears to peak in 1998 (Fig. 5.13). The model converged for all tracked parameters and states, although mixing for some states, such as juvenile grouse density, $G_{j,t}$, was slow compared to the other tracked values within the model.
Figure 5.12: The relative timing of aggression (blue) and autumn grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1999 for the predation model. Harrier numbers were high enough to impact grouse density from 1993.

*T. tenuis* burdens on the four beats also show cyclic dynamics, peaking just after peak grouse densities. After 1992, when the grouse are no longer cycling, the parasite burdens begin to decline steadily, reaching low values, especially in comparison to their peaks (Fig. 5.13). Aggression shows a similar pattern to parasites, cycling so long as grouse densities are fluctuating, but stabilising at low values when the population is suppressed after the introduction of the hen harriers. Again, the exception is on beat LC, where aggression increases more than on the other beats (Fig. 5.12).

The estimates for the expected number of successful hen harrier nests fit very closely with the observed values, indicating a good relationship between the super-population model and the observed population (Table 5.2). Additionally, the estimates are very similar to those from the harrier-only model. The super-population estimate is the most dissimilar from the observed number of nests in 1996, where the estimate is five nests less than the observed number and the credible interval does not come close...
Figure 5.13: The relative timing of parasite burdens (red) and spring grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1999 for the predation model. Harrier numbers were high enough to impact grouse density from 1993.

to capturing the true value. As in the harrier-only model, the low estimates from the super-population model appear to be a result of low densities of voles and pipits limiting the survival and immigration of harriers into the area.

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<thead>
<tr>
<th>Year</th>
<th>Observed</th>
<th>Estimated</th>
</tr>
</thead>
<tbody>
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<td>1993</td>
<td>5</td>
<td>8.7 (5.9, 12.2)</td>
</tr>
<tr>
<td>1994</td>
<td>11</td>
<td>10.88 (8.5, 13.9)</td>
</tr>
<tr>
<td>1995</td>
<td>8</td>
<td>11.12 (9.6, 12.8)</td>
</tr>
<tr>
<td>1996</td>
<td>14</td>
<td>8.82 (7.1, 10)</td>
</tr>
<tr>
<td>1997</td>
<td>20</td>
<td>19.32 (14.4, 25.8)</td>
</tr>
<tr>
<td>1998</td>
<td>17</td>
<td>16.37 (13.8, 18.7)</td>
</tr>
<tr>
<td>1999</td>
<td>13</td>
<td>13.22 (10.9, 15.3)</td>
</tr>
</tbody>
</table>

Table 5.2: The observed numbers and super-population estimates for the hen harrier population with their corresponding 95% credible intervals from the predation model for grouse-harrier population dynamics.

Survival estimates for the hen harriers in the predation model fit the same pattern as observed for harrier survival in Chapter 3, although the estimates and corresponding credible intervals are slightly higher. The estimates ranged between 71-86%, which
includes the previous point estimate of 78% and are well within the previously estimated 95% confidence interval (57%, 90%) (Etheridge et al., 1997). However, the upper limits of the intervals can fall above the previously estimated range (Table 5.10).

The estimates for harrier movement onto the moor ($\eta_t$), varied significantly from year to year, depending on the densities of their alternate prey (Table 5.11). The density of field voles appears to have had the largest effect on harrier movement, since the greatest immigration occurs at the peak densities of this prey species, even when the corresponding meadow pipit density was low. The number of harriers surviving from the previous year ($H_{t-1}\phi_{t-1}$) has little impact on immigration ($\beta_2$: 0.031, 95% CI: (9.8 x10^{-4}, 0.1)).

5.6.3 Prediction model

During the first 18 years of the study, when hen harriers were known to be absent, the prediction model for grouse-harrier interactions showed cyclic dynamics with respect to both spring and autumn densities (Figs. 5.14 and 5.15). From 1993, the grouse population shows an extended decline phase in both seasons on all four beats, although the trough is less pronounced on beat LD. After 1997, when harriers are ‘removed’ from the area, autumn grouse density increases, reaching previously observed peaks on beats LC and LM (Fig. 5.14). Spring densities also increase once harriers are absent from the system, but only beat LC reaches a peak equivalent to those seen earlier in the time series (Fig. 5.15), although there is still the possibility that higher peaks could be reached in the future. All states and parameters converged, although mixing was slow for most tracked values, in comparison to the other models.

The estimated worm burdens showed cyclic dynamics for all four beats until hen harriers were introduced to the system in 1993. $T.\ tenuis$ then showed a steady decline, with little evidence for an increase when harriers are ‘removed’ from the system. Additionally, the parasite burdens for beat LC exceed the levels of biological realism (Fig. 5.15). The aggressiveness of cock red grouse shows the expected behaviour, peaking
Figure 5.14: The relative timing of aggression (blue) and autumn grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1999 for the prediction model. Harrier numbers were high enough to impact grouse density from 1993, but were ‘removed’ from the system in 1998 and 1999.
just after peak grouse densities when the grouse population is cycling, remaining at low levels when the population is suppressed by harrier predation, and then increasing again when harriers are not present in the system. The less pronounced suppression of the red grouse cycles on beat LD results in little observable effect of harrier predation on aggressiveness (Fig. 5.14).

Figure 5.15: The relative timing of parasite burdens (red) and spring grouse density (km⁻², black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1999 for the prediction model. Harrier numbers were high enough to impact grouse density from 1993, but were ‘removed’ from the system in 1998 and 1999.

In the prediction model there are only five years in which harriers are considered to be present on the moor. The estimates of the expected number of successful hen harrier nests for the prediction model follows the same pattern as for the predation model, being similar to the observed nests. The largest discrepancy between the observed number of nests and the super-population model is still observed in 1996 and remains about five nests (Table 5.3).

Survival estimates for the hen harriers in the prediction model were lower than those previously observed, although the range of point estimates, 67-83%, is still realistic,
Table 5.3: The observed numbers and super-population estimates for the hen harrier population with their corresponding 95% credible intervals from the prediction model for grouse-harrier population dynamics.

<table>
<thead>
<tr>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Obs.</td>
<td>5</td>
<td>11</td>
<td>8</td>
<td>14</td>
<td>20</td>
<td>17</td>
<td>13</td>
</tr>
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<td>Est.</td>
<td>8.82</td>
<td>10.93</td>
<td>10.82</td>
<td>8.52</td>
<td>19.13</td>
<td>-</td>
<td>-</td>
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<tr>
<td>CI</td>
<td>(6, 12.4)</td>
<td>(8.5, 14.1)</td>
<td>(8.5, 12.9)</td>
<td>(6.7, 10.3)</td>
<td>(13.9, 25.7)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

since it falls within the previous 95% confidence interval (57%, 90%) (Etheridge et al., 1997). However, the estimates of harrier survival are more uncertain, with much wider 95% credible intervals, in which both the upper and lower limits on the yearly survival can fall outside the previously estimated range (Table 5.10). This increase in uncertainty is due to the loss of two years of data on the hen harrier.

The estimates for harrier movement onto the moor ($\eta$), for the five years harriers were present, varied significantly, depending mostly on the density of field voles, although meadow pipits did contribute slightly to the harriers’ movement (Table 5.11). However, even when the corresponding meadow pipit density was at its peak, harrier immigration was not as high as for equivalent vole densities. There was little evidence for density dependence as a limiting factor on harrier movement ($\beta_2$: 0.031, 95% CI: $9 \times 10^{-4}$, 0.1)).

5.6.4 Partial supplementary feeding model

From 1975 to 1992, in the absence of hen harriers, the red grouse showed cyclic dynamics in the spring and autumn. Harrier predation began to affect grouse density in 1993, when they suppressed grouse fluctuations (Figs. 5.16 and 5.17). In 1998 and 1999 some of the hen harrier nests present on the moor were provided with supplementary food. However, the diversionary feeding failed to significantly increase grouse numbers (Fig. 5.16). Spring density also failed to recommence cycling, although this is less pronounced on beat LC (Fig. 5.17). The model showed good mixing and convergence for all tracked states and parameters. However, in comparison to other values within the model, the state $G_j$ displayed slow mixing for some years, $t$, as did $G_a$. 
Figure 5.16: The relative timing of aggression (blue) and autumn grouse density (km\(^{-2}\), black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1999 for the partial supplementary feeding model. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in 1998 and 1999.
Aggression cycled as expected when harriers were absent from Langholm, peaking with or just after peak autumn densities, lowering in value when harriers were suppressing the cycles. There was a slight increase in aggression when partial supplementary feeding took place, but not enough to allow for the cycling of the grouse population (Fig. 5.16). The parasitic nematode also showed the expected cyclic dynamics on all for beats until 1991, peaking just after peak grouse densities. Parasite burdens then declined to a low level when harriers were suppressing the grouse population through predation. Even when supplementary feeding occurred in the last two years of the study, parasite burdens remained low. The estimated parasite burdens stay just within the realm of biological plausibility on beat LC (Fig. 5.17).

![Figure 5.17](image_url)  

Figure 5.17: The relative timing of parasite burdens (red) and autumn grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1999 for the partial supplementary feeding model. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in 1998 and 1999.

Again, the estimates of the expected number of successful hen harrier nests fit very closely with the true values (Table 5.4), indicating a super-population not too far off of the observed population. The year 1996 is the most dissimilar, with the super-population value estimated as almost nine nests, while 14 nests were really observed.
Survival estimates for the hen harriers in the partial supplementary feeding model were almost identical to those in the predation model, ranging from 72-86%, with 95% credible intervals whose upper limits fall outwith the previously estimated 95% confidence interval, (57%, 90%) (Etheridge et al., 1997), but whose lower limits stay within those bounds (Table 5.10).

The estimates for harrier immigration into the existing population ($\eta_t$) were variable, depending strongly on the densities of their alternate prey (Table 5.11). The density of meadow pipits had a limited effect on harrier movement. Instead, immigration appears to be driven by field vole density. The number of harriers remaining in the area from one year to the next ($H_{t-1}\phi_{t-1}$) has little overall effect on immigration ($\beta_2$: $0.031$, 95% CI: (9.6 x10$^{-4}$, 0.097)).

### 5.6.5 Full supplementary feeding model

Grouse densities in spring and autumn showed cyclic dynamics for the first 18 years of the study when there were not enough hen harrier pairs present on the moor to affect the grouse population. When harriers re-colonised the moor in 1992 a prolonged decline phase was visible in both seasons for all four beats. During the last two years of the model, when all the hen harrier nests on the moor were provided with supplementary food, there was not an immediately noticeable increase in grouse density. Autumn densities remained below their previous peaks, although there did

<table>
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<th>Year</th>
<th>Observed</th>
<th>Estimated</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>5</td>
<td>8.72 (6, 12.2)</td>
</tr>
<tr>
<td>1994</td>
<td>11</td>
<td>10.9 (8.4, 14)</td>
</tr>
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<td>1996</td>
<td>14</td>
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<td>1997</td>
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<td>1998</td>
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</tr>
<tr>
<td>1999</td>
<td>13</td>
<td>13.2 (10.9, 15.3)</td>
</tr>
</tbody>
</table>

Table 5.4: The observed numbers and super-population estimates for the hen harrier population with their corresponding 95% credible intervals from the partial supplementary feeding model for grouse-harrier population dynamics.
appear to be some evidence of a slight increase in spring density in 1999, especially on beats LC and LM (Figs. 5.18 and 5.19). All tracked states and parameters displayed good mixing and convergence.

Figure 5.18: The relative timing of aggression (blue) and autumn grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1999 for the full supplementary feeding model. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in years 1998 and 1999.

Aggressiveness in the autumn on all four beats behaved as expected, peaking with, or just after peak grouse densities before declining, remaining at low levels when the population density was suppressed and raising slightly when supplementary feeding took place (Fig. 5.18). T. tenuis burdens also followed the expected pattern, fluctuating with the red grouse cycles, and then declining significantly and staying at low levels even when the population increases due to supplementary feeding. The estimate for peak parasite load of beat LC falls above the previously observed maximum worm burden (Fig. 5.19).

There is little change in the estimates of the expected number of successful hen harrier nests, which remain close to the true values (Table 5.5), indicating a good
Figure 5.19: The relative timing of parasite burdens (red) and autumn grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1999 for the full supplementary feeding model. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in years 1998 and 1999.
relationship between the super-population and the observed number of nests. The largest discrepancy remains 1996, with the super-population value estimated as being slightly more than five nests lower than the observed value. The disparity is most likely due to low nest numbers in the previous year as well as lower densities of field voles and meadow pipits than seen in other years.

<table>
<thead>
<tr>
<th>Year</th>
<th>Observed</th>
<th>Estimated</th>
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</thead>
<tbody>
<tr>
<td>1993</td>
<td>5</td>
<td>8.72 (6, 12.3)</td>
</tr>
<tr>
<td>1994</td>
<td>11</td>
<td>10.89 (8.5, 14)</td>
</tr>
<tr>
<td>1995</td>
<td>8</td>
<td>11.12 (9.6, 12.7)</td>
</tr>
<tr>
<td>1996</td>
<td>14</td>
<td>8.82 (7.7, 10)</td>
</tr>
<tr>
<td>1997</td>
<td>20</td>
<td>19.3 (14.4, 25.8)</td>
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<td>1998</td>
<td>17</td>
<td>16.37 (13.8, 18.7)</td>
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<tr>
<td>1999</td>
<td>13</td>
<td>13.21 (10.8, 15.3)</td>
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</tbody>
</table>

Table 5.5: The observed numbers and super-population estimates for the hen harrier population with their corresponding 95% credible intervals from the full supplementary feeding model for grouse-harrier population dynamics.

Yearly estimates for the survival of hen harriers in the full supplementary feeding model fit the same pattern as observed for harrier survival in Chapter 3. While the estimates and corresponding credible intervals are slightly higher, they still ranged between 71-86%. This includes the previous point estimate of 78% and is well within the 95% confidence interval (57%, 90%) (Etheridge et al., 1997), although the upper limits of the intervals can fall above the previously estimated range, as does the lower limit in year 24 (Table 5.10).

The estimates for harrier movement onto the moor ($\eta_t$), vary from one to eight pairs, depending strongly on the densities of the harriers’ alternate prey, most especially field voles (Table 5.11). There was little evidence for density-dependent limits on the harrier population, since the number of harrier nests surviving from the previous year ($H_{t-1}\phi_{t-1}$) had little impact on immigration ($\beta_2$: 0.031, 95% CI: $9.2 \times 10^{-4}$, 0.097)).

5.6.6 Model comparison

Until the last two years of the time series, the grouse density estimates in both spring and autumn are essentially identical for the four models. From 1998, I investigated
the impact of hen harriers on grouse densities under different scenarios. There is little difference among the estimates from the predation and supplementary feeding models, especially on beat LM, although there is a slight increase in spring and fall grouse densities when nests are provided with supplementary food. This difference is mildly more pronounced in the full supplementary feeding model, which predicts slightly higher densities. However, even when all the nests are fed, grouse densities do not reach the peaks they would have obtained in the absence of harrier predation. For all the models, the cycles displayed until 1991 match key features of the observed data (Figs. 5.20 and 5.21).

From 1992, information on red grouse population dynamics is provided through grouse chick densities, as opposed to autumn counts of the grouse present on the moor. For the estimates of grouse chick density, the models are not as successful in following key features of the data. While the models capture the initial increase in chick density,
Figure 5.21: The comparison of autumn grouse density estimates (km$^{-2}$) from the predation (black), prediction (blue) and partial (green) and full (orange) supplementary feeding models in relation to each other for each of the four beats (LC, LD, LM, LR) from 1975-1999. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding occurred in 1998 and 1999. In the prediction model, harriers were ‘removed’ from the system in 1998 and 1999.
they show a decline prior to the one observed in the data and increase again, even when the observed densities continue to show a decline. The steep increases in the last two years in the prediction model are a result of the data on chick density being excluded from the model for these two years to avoid any confounding in the model predictions (Fig. 5.22). The different estimates of chick density are a result of the four models each using a different estimate for \( \tau_c \) in the grouse chick observation model (Table 5.7), as opposed to any effect of harrier predation.

![Figure 5.22: The comparison of grouse chick density estimates (km\(^{-2}\)) from the predation (black), prediction (blue) and partial (green) and full (orange) supplementary feeding models for grouse-harrier population dynamics in relation to each other and the data (dashed line) from 1992-1999.](image)

The parameter estimates provided by the four models are very similar. The differences observed are a result of the failure to use the full time series of observations to estimate the needed values. The decrease in the amount of data available causes an increase in the uncertainty around certain parameters. Therefore, the parameter estimates from the prediction model are the most dissimilar to the other three models, which show the same relationship among themselves.

For the beat-dependent parameters, there is little difference among four models. However, the estimates from the prediction model, while close, were just slightly higher in almost all cases. Interestingly, adult survival (\( \phi_a \)) estimates for two of the beats,
LC and LM, are now below the lowest previously estimated value for the parameter
(0.34, (Jenkins et al., 1967)) for the predations and supplementary feeding models,
but not the prediction model (Table 5.6).

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Table 5.6: Posterior means and their 95% credible intervals for the beat-dependent
grouse parameter estimates for all four models describing the grouse-harrier popula-
tion dynamics. (Parameter values were estimated on the log scale)

The estimates for three of the beat-independent grouse parameters ($\xi_0, \xi_1, \delta_0$) were
practically identical, even the credible intervals, for all four models. The estimate for
the parameter $\xi_2$ was slightly higher for the prediction model, as a result of its more
unimodal prior (Fig. 5.10). The remaining parameter, $\tau_c$, the precision parameter for
the grouse observation model, was different for all four models. The higher value and
wider credible interval in the prediction model is a result of the decreased amount
of information available in this model. Interestingly, the full supplementary feeding
model has the lowest value and the narrowest credible interval, despite the fact that it is not an accurate representation of the actual data (Table 5.7).

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Table 5.7: Estimates and 95% credible intervals for the beat-independent grouse parameters for each of the four models describing the grouse-harrier population dynamics.

The proportion of the successfully reared grouse chicks that reach the autumn territorial contest (π_t) is dependent on the intensity of harrier predation. When harrier densities are low, π_t is high. However, once the estimated number of harrier nests is in the teens (from 1997), π_t decreases markedly. For the first five years harriers are present in the system, the estimates of the proportion of successfully reared grouse chicks to reach the autumn territorial contest are similar across the four models. Differences between the models only occur once I manipulate the presence of harriers in the system. When only a portion of the harrier nests are fed, π_t increases slightly compared to the predation model. However, when all the nests are fed in the full supplementary feeding model, π_t is essentially unchanged in the first year, but is much higher in the second year of supplementary feeding (Table 5.8). The unexpectedly low estimate of π_t in 1998 is likely due to the slightly higher estimated chick density (Fig. 5.22), which would allow for a higher rate of consumption.

The hen harrier movement parameters (β_0, β_1, β_2) are essentially the same for all four models. However, the estimates for the harrier survival parameters (α_0, α_1) from the prediction model are different from the other three models. The estimate for α_0 is much lower and has a wider credible interval, while the estimate for α_1 is slightly higher (Table 5.9). The difference in the estimates is due to the reduced amount of
Table 5.8: Yearly estimates for the proportion of successfully reared grouse chicks to reached the autumn territorial contest in the presence of harrier predation ($\pi_t$, %), with their corresponding 95% credible intervals for each of the four models describing the grouse-harrier population dynamics.

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Table 5.9: Estimates and 95 % credible intervals for the hen harrier parameters for each of the four models describing the grouse-harrier population dynamics.

Due to the differences in the $\alpha$ parameters for the prediction model, the estimates of hen harrier survival ($\phi_t$) from the model are lower than in the other three. However, even with this change, the estimates for $\phi_t$ remain similar across all four models, with the estimates from the remaining three models being nearly identical (Table 5.10).

Hen harrier movement ($\eta_t$) showed similar patterns across all four models, with immigration being higher in years of high vole density. While pipits contribute to immigration, their impact is minimal, since harrier movement is at its highest in a year.
Table 5.10: Yearly hen harrier survival estimates ($\phi_t$, %) with their corresponding 95% credible intervals for each of the four models describing the grouse-harrier population dynamics.

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of low pipit density. The estimates for $\eta_t$ are practically the same for all four models, although the estimates from the prediction model are slightly higher (Table 5.11). This was unexpected, since the estimates for the movement parameters ($\beta_0, \beta_1, \beta_2$) are effectively identical for all four models (Table 5.9). However, the differences in the estimates for $\eta_t$ are possibly due to the slightly wider credible intervals on the super-population estimates from the prediction model (Table 5.3).

### 5.7 Effects of multi-species modelling

The processes models used for the hen harrier and red grouse in the multi-species model were defined, in detail, in Chapters 3 and 4, respectively. Model selection was not required for the hen harriers’ population model, but the state process model for the red grouse was chosen based on the ability of the model for the combined hypothesis to create cycles under biologically realistic parameter values. There is no need to undergo a model selection process for the four models presented in this chapter. The predation, prediction and full supplementary feeding models are all exploratory to investigate the grouse-harrier interactions under different, theoretical conditions. Only the partial supplementary feeding model describes the system based
Table 5.11: Yearly estimates for hen harrier movement ($\eta_t$), with their corresponding 95% credible intervals, for each of the four models describing the grouse-harrier population dynamics, as well as the vole and pipit densities for each year (km$^{-2}$).

The grouse-only model used data from the first 18 years of the Langholm study to avoid confounding estimates with the later effects of harrier predation, which began to have a noticeable impact in 1993. For this initial time period, spring grouse densities from the single- and multi-species models follow the same pattern of peaks and troughs. However, the estimates from the multi-species model were consistently lower than those from the single-species model for all but beat LD (Fig. 5.23). There is almost no difference between the two models with regards to the estimated autumn grouse density for the first 18 years of the study, and both models follow key features of the data (Fig. 5.24).

The two models also showed the same pattern for the estimates of aggressiveness and parasite burdens. However, where aggression tends to be lower for the multi-species model, parasite burdens can be noticeably higher. The exception in both cases is beat LD, whose estimates for aggressiveness and $T. tenuis$ loads are almost the same for
Figure 5.23: The relative timing of parasite burdens (red) and spring grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1999 for the grouse-only (solid line) and partial supplementary feeding (dashed line) models. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in 1998 and 1999.
Figure 5.24: The relative timing of aggression (blue) and spring grouse density (km$^{-2}$, black) in relation to each other and the observed data (purple) on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1999 for the grouse-only (solid line) and partial supplementary feeding (dashed line) models. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in 1998 and 1999.
the two models (Figs. 5.23 and 5.24).

The effect of the inclusion of hen harriers in the model on the beat-specific red grouse parameters is mixed. The estimates for the natural log of average brood size \( (\gamma_0) \) are very close; estimates from the partial supplementary feeding model are slightly lower, with marginally narrower credible intervals. However, for beat LM the estimate provided by the multi-species model is not only significantly lower, but also has a much narrower credible interval that only just includes the estimate from the grouse-only model. In contrast, estimates for adult grouse survival \( (\phi_a) \) are more variable in the multi-species model; the estimates vary among the beats and have wider credible intervals compared to the estimates from the single-species model. For the observation model constant \( (c) \), the two models were very similar, with the exception of beat LD, whose estimate was notably higher in the partial supplementary feeding model. Given the higher estimates for \( T. tenuis \) burdens in the multi-species model, the estimates for the effect of parasites on the rearing rate \( (\gamma_1) \) were lower in the multi-species model for all but beat LD (Table 5.12). The exception is due to the fact that the estimates for the parasitic nematode on that beat were the same for the two models (Fig. 5.23).

There is very little difference between the multi- and single-species models in the estimates and credible intervals for the beat-independent grouse parameters (Table 5.13). Even the estimate for the aggressiveness parameter \( \xi_2 \) is only slightly lower, despite the bi-modality (Fig. 5.9).

The hen harrier super-population estimates provided by the two models are very similar, although the estimates from the partial supplementary feeding model are slightly higher (Table 5.14). The similarity is not surprising, given that the grouse do not play a direct role in hen harrier population dynamics and have minimal impact on the raptor.

The slightly higher super-population estimates in the multi-species model are due to the increased effect of meadow pipits on hen harrier dynamics. Of the hen harrier parameters, only the two associated with pipit density, \( \alpha_1 \) and \( \beta_1 \), show any difference
Table 5.12: Posterior means and their 95% credible intervals for the beat-dependent grouse parameter estimates for the partial supplementary feeding and grouse-only models. (†Parameter estimated on the log scale)
<table>
<thead>
<tr>
<th>$\Theta$</th>
<th>Partial</th>
<th>Grouse-only</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\xi_0$</td>
<td>-2.2 (-2.6, -2.0)</td>
<td>-2.3 (-2.9, -2.0)</td>
</tr>
<tr>
<td>$\xi_1$</td>
<td>0.013 (0.002, 0.019)</td>
<td>0.016 (0.0042, 0.019)</td>
</tr>
<tr>
<td>$\xi_2$</td>
<td>0.023 (0.006, 0.039)</td>
<td>0.029 (0.0099, 0.039)</td>
</tr>
<tr>
<td>$\delta_0$</td>
<td>5.4 (4.6, 6.0)</td>
<td>5.3 (4.4, 5.9)</td>
</tr>
</tbody>
</table>

Table 5.13: Estimates and 95% credible intervals for the beat-independent grouse parameters for the partial supplementary feeding and grouse-only models.

<table>
<thead>
<tr>
<th>Year</th>
<th>Observed</th>
<th>Partial</th>
<th>Harrier-only</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>5</td>
<td>8.7 (6, 12.2)</td>
<td>8.2 (5.6, 11.6)</td>
</tr>
<tr>
<td>1994</td>
<td>11</td>
<td>10.9 (8.4, 14)</td>
<td>10.4 (8.1, 13.3)</td>
</tr>
<tr>
<td>1995</td>
<td>8</td>
<td>11.1 (9.6, 12.7)</td>
<td>10.9 (9.4, 12.5)</td>
</tr>
<tr>
<td>1996</td>
<td>14</td>
<td>8.8 (7.7, 10)</td>
<td>8.6 (7.5, 9.8)</td>
</tr>
<tr>
<td>1998</td>
<td>17</td>
<td>16.4 (13.9, 18.7)</td>
<td>16.2 (13.6, 18.5)</td>
</tr>
<tr>
<td>1999</td>
<td>13</td>
<td>13.2 (10.9, 15.3)</td>
<td>13.1 (10.7, 15.2)</td>
</tr>
</tbody>
</table>

Table 5.14: The observed numbers and super-population estimates for the hen harrier population with their corresponding 95% credible intervals for the partial supplementary feeding and harrier-only models.
between the two models. The estimates for the two parameters are slightly higher in the partial supplementary feeding model, increasing the harriers’ survival through $\alpha_1$ and immigration through $\beta_1$ (Table 5.15).

<table>
<thead>
<tr>
<th>$\Theta$</th>
<th>Partial</th>
<th>Harrier-only</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_0$</td>
<td>0.37</td>
<td>0.37</td>
</tr>
<tr>
<td>(-0.65, 1.25)</td>
<td>(-0.60, 1.23)</td>
<td></td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>$2.7 \times 10^{-3}$</td>
<td>$2.49 \times 10^{-3}$</td>
</tr>
<tr>
<td>(7.1 $\times 10^{-4}$, 6.2 $\times 10^{-3}$)</td>
<td>(6.6 $\times 10^{-4}$, 5.7 $\times 10^{-3}$)</td>
<td></td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>$1.3 \times 10^{-3}$</td>
<td>$1.3 \times 10^{-3}$</td>
</tr>
<tr>
<td>(5.8 $\times 10^{-4}$, 1.9 $\times 10^{-3}$)</td>
<td>(6.1 $\times 10^{-4}$, 1.9 $\times 10^{-3}$)</td>
<td></td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>$1.1 \times 10^{-3}$</td>
<td>$9.4 \times 10^{-4}$</td>
</tr>
<tr>
<td>(7.6 $\times 10^{-5}$, 2.6 $\times 10^{-3}$)</td>
<td>(5 $\times 10^{-5}$, 2.4 $\times 10^{-3}$)</td>
<td></td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>0.031</td>
<td>0.031</td>
</tr>
<tr>
<td>(9.6 $\times 10^{-4}$, 0.097)</td>
<td>(9.8 $\times 10^{-4}$, 0.099)</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.15: Estimates and 95 % credible intervals for the hen harrier parameters for the partial supplementary feeding and harrier-only models.

The effects of the increased value for $\alpha_1$ can be seen in the estimates for yearly hen harrier survival ($\phi_t$). The multi-species model gives higher estimates of $\phi_t$, although there is not much change in the width of the credible intervals (Table 5.16). There are only estimates for hen harrier survival for the first seven years harriers are present in the system, since the harrier state process model uses $\phi_{t-1}$ to find the number of harrier nests surviving to year $t$ (Eqn. 5.2).

The slightly higher estimates of hen harrier immigration ($\eta_t$) to the moor can also be explained by the increased impact of pipits on $\eta_t$, through the higher estimate for $\beta_1$. The effect is noticeable, since the largest differences between the two models occur in the first two years when pipit densities are at their highest (Table 5.17).

5.8 Discussion

Reducing human-wildlife conflict is an important goal of management. The nature of the conflict, and thus the possible solutions, are dependent on the specific species involved. Some conflicts involve direct physical contact between humans and animals, such as when the presence of tigers places human lives at risk. Other conflicts consist
<table>
<thead>
<tr>
<th>Year</th>
<th>Partial</th>
<th>Harrier-only</th>
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</thead>
<tbody>
<tr>
<td>1992</td>
<td>79.2</td>
<td>73.8</td>
</tr>
<tr>
<td></td>
<td>(66.1, 90.5)</td>
<td>(64.7, 89.7)</td>
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<tr>
<td>1993</td>
<td>85.6</td>
<td>84.6</td>
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<td></td>
<td>(72, 96.5)</td>
<td>(70.5, 95.7)</td>
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<tr>
<td>1994</td>
<td>85.5</td>
<td>84.4</td>
</tr>
<tr>
<td></td>
<td>(71.8, 96.3)</td>
<td>(64.8, 89.8)</td>
</tr>
<tr>
<td>1995</td>
<td>79.4</td>
<td>78.4</td>
</tr>
<tr>
<td></td>
<td>(66.2, 90.6)</td>
<td>(62.3, 87.4)</td>
</tr>
<tr>
<td>1996</td>
<td>78.3</td>
<td>77.3</td>
</tr>
<tr>
<td></td>
<td>(65.2, 89.5)</td>
<td>(63.8, 88.7)</td>
</tr>
<tr>
<td>1997</td>
<td>72.7</td>
<td>71.9</td>
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<tr>
<td></td>
<td>(58.8, 84.7)</td>
<td>(57.8, 84.1)</td>
</tr>
<tr>
<td>1998</td>
<td>71.6</td>
<td>70.9</td>
</tr>
<tr>
<td></td>
<td>(57.3, 84.0)</td>
<td>(56.5, 83.4)</td>
</tr>
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</table>

Table 5.16: Yearly hen harrier survival estimates ($\phi_t$, %) with their corresponding 95% credible intervals for the partial supplementary feeding and harrier-only models.

<table>
<thead>
<tr>
<th>Year</th>
<th>Partial</th>
<th>Single</th>
<th>Vole</th>
<th>Pipit</th>
</tr>
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<tbody>
<tr>
<td>1993</td>
<td>7.1</td>
<td>6.6</td>
<td>1050.4</td>
<td>575.2</td>
</tr>
<tr>
<td></td>
<td>(4.3, 10.7)</td>
<td>(4, 10.1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td>6.6</td>
<td>6.1</td>
<td>1060.8</td>
<td>570.1</td>
</tr>
<tr>
<td></td>
<td>(4.1, 9.8)</td>
<td>(3.8, 9.2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>1.7</td>
<td>1.6</td>
<td>280</td>
<td>385.7</td>
</tr>
<tr>
<td></td>
<td>(0.81, 2.9)</td>
<td>(0.79, 2.7)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>2.5</td>
<td>2.4</td>
<td>535.6</td>
<td>358.8</td>
</tr>
<tr>
<td></td>
<td>(1.6, 3.5)</td>
<td>(1.6, 3.3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>8.4</td>
<td>8.2</td>
<td>1648.4</td>
<td>239.4</td>
</tr>
<tr>
<td></td>
<td>(3.3, 15.2)</td>
<td>(3.3, 14.9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>1.9</td>
<td>1.8</td>
<td>598</td>
<td>219.1</td>
</tr>
<tr>
<td></td>
<td>(0.74, 2.8)</td>
<td>(0.71, 2.7)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>1.1</td>
<td>1.0</td>
<td>104</td>
<td>216.5</td>
</tr>
<tr>
<td></td>
<td>(0.41, 1.7)</td>
<td>(0.39, 1.6)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5.17: Yearly estimates for hen harrier movement ($\eta_t$), with their corresponding 95% credible intervals, for the partial supplementary feeding and harrier-only models, as well as the vole and pipit densities for each year (km$^{-2}$).
of damage to human property, such as when elephants trample crops. Finally, the conflict can be indirect, resulting from the presence of one species of wildlife interfering with peoples’ ability to exploit another species, such as when wolves prey on deer and elk in areas used for hunting instead of farming (Woodroffe et al., 2005a). The human-harrier conflict falls into this last category.

Given the seemingly conflicting goals of grouse moor management, from conservation to economics, it is important to have tools to help assess the potential impacts of management plans on the ecosystem. Actions such as diversionary feeding bear different expenses, from the purely monetary to time and political costs. Providing all harrier nests with supplementary food places an additional burden on the gamekeepers, who take a larger risk by acting on a management plan whose final outcome is highly uncertain. If the method fails to meet all expectations, conservationists have lost nothing but an idea and the cost of the food for the time period of the study. However, should diversionary feeding increase harrier numbers, but not grouse density, the gamekeepers would face not only the cost of the supplementary food, but also the economic costs associated with higher harrier predation limiting the ability of driven shooting to take place. One goal of the models presented in this chapter is to help determine whether diversionary feeding can mitigate the human-harrier conflict by reducing harrier predation on red grouse chicks.

No matter the species involved or the nature of the conflict, all stakeholders want to lessen the risks associated with any action taken to reduce the strife between humans and wildlife. As a result, theoretical modelling has come to play an important role in management. In order for modelling to be successful, it is necessary to capture individual characteristics of the species involved in the conflict. Many times this involves using species-specific parameters in general models such as the Lotka-Volterra. However, it is also possible to build mechanistic models specific to the individual species. The problem with these models has been the complexity of the model fitting and the difficulty in including uncertainty in the modelling process. In this chapter I present a multi-species state-space model for the hen harrier-red grouse interactions that allows for the individual dynamics of the involved species to be taken into account,
while simultaneously including the uncertainty around the population processes and observations.

From a statistical perspective, there was no difficulty, other than increased costs in time, in running a multi-species state-space model. The process models were linked through harrier predation on the red grouse chicks, and while the hen harrier did not have an observation model, the grouse population had two. The state estimates from the grouse-harrier interaction model were similar to those from each individual species’ model, which was encouraging, since it implies that the model fitting process has not undergone any radical change to accommodate the increased complexity of the model. The differences in red grouse spring density estimates were a result of lower estimates for adult grouse survival in the multi-species model. However, the decrease in aggressiveness estimated by the multi-species model allows the two models to have nearly identical estimates of autumn grouse density for the first 18 years of the study. The lowering of aggressiveness is achieved by increasing the estimates for *T. tenuis* burdens, which reduces the number of young grouse available to be recruited in the fall.

Other than the natural log of brood size and adult grouse survival, there was little change in the parameter estimates or credible intervals between the single- and multi-species models. The change in the brood size parameter for the grouse-harrier model is a result of the inclusion of additional data on grouse chick density, which decreased the level of uncertainty around the parameter. In contrast, the estimates of adult grouse survival estimates showed increased uncertainty. This may be because the cessation of hen harrier persecution on the moor also benefited other grouse predators that had been harmed by non-species specific harrier eradication methods such as poisoned bait (Redpath et al., 2001b). The resulting increase in predation on adult grouse would mean that their survival before and after the reappearance of hen harriers would be different and not captured by my model. I did not estimate post-harrier red grouse survival parameters, since this would have meant estimating an additional four parameters with only eight years of data.

The results from my multi-species model fit with what would be expected based on
a previous study of the effect of hen harrier predation on red grouse on Langholm moor (Redpath et al., 2001b). The presence of the hen harrier suppressed the cycles, especially in comparison to what was predicted in the absence of harrier predation. Additionally, while the partial supplementary feeding of the hen harriers slightly increased the proportion of otherwise successfully reared chicks to reach the autumn territorial contests, the increase was not enough to raise grouse densities to anything resembling those predicted in the absence of harriers. The exclusion of data on grouse chick densities from the last two years of the time series in the prediction model resulted in much higher estimates of grouse chick density than were observed in the other models. The provision of all nests with supplementary food resulted in only a slight increase in grouse density that was mildly more pronounced in the spring. This would indicate that supplementary feeding is unlikely to be successful either for conservation or as a mitigating technique, especially on its own. However, it remains possible that supplementary feeding, in conjunction with other management actions may serve to reduce the human-harrier conflict.

For supplementary feeding to work as a standalone mitigation technique it would need to be much more effective than is suggested by my models. Autumn grouse densities increase slightly after hen harriers begin impacting the population in 1993. However, by 1996 all the beats show either a decrease or levelling off of grouse densities (see Fig. 5.21). This coincides with a 20% decrease in the estimates of \( \pi_t \). In the full supplementary feeding model, the proportion of chicks to survive the impact of harriers is 5% higher than in the predation model. Yet autumn grouse densities do not increase noticeably. Yet, in 1994, \( \pi_t \) is estimated as low as 85%. This would imply that supplementary feeding would need to be able to increase \( \pi_t \) by at least 10%. Additionally, the non-linear relationship between hen harriers and red grouse means that it is possible that the supplementary feeding of hen harriers may have different levels of effectiveness, depending on the respective densities of the two species. Further investigation would need to be undertaken to determine the exact level of effectiveness required, and at which densities, for supplementary feeding to be sufficient, on its own, to stop the hen harriers’ suppression of grouse densities.
The conclusions regarding the effectiveness of supplementary feeding need to be treated with caution. The inability to account for other possible sources of grouse mortality due to the lack legal predator control means that the effectiveness of supplementary feeding could be underestimated. This would occur because the only flexibility in the estimates of grouse survival occurs in juvenile survival. Since $\phi_j$ varies with grouse density, and adult survival is fixed, it is the proportion of chicks that would have otherwise successfully reached the autumn territorial contest that is driving the estimates of $\phi_j$. Therefore, since adult survival is fixed, if overall grouse densities are declining due to increased predation from animals other than harriers, the only way for the population to decline is if young are not being recruited into the adult population. As a result, supplementary feeding would be estimated to be ineffective, since it would be forced to incorporate mortality from sources other than the harriers.

As well as being concerned over the direct impact of diversionary feeding on grouse chick predation, gamekeepers are concerned with its possible effects on harrier survival and movement into an area. While Redpath et al. (2001b) did not note an increase in hen harrier immigration or site fidelity as a result of the provision of supplementary food, gamekeepers remain concerned, since the study was only performed over two years and was unable to address the long term effects of diversionary feeding on hen harrier populations. Although this question was not addressed here, it would be possible to modify the model to allow for the conceivable effects of supplementary food on hen harrier immigration and survival. The impacts on hen harrier life history processes, under different scenarios, could then be investigated. In this way, gamekeepers could make informed decisions with regards to the long-term risks involved in providing supplementary food to hen harriers.

Overall, this model has the potential to be useful for both management specific to the grouse-harrier debate, as well as having wider implications with regards to multispecies modelling. Supplementary feeding can be tested in field studies and the results presented here can provide insight on the possible outcomes of the management plan, allowing more informed decisions to be made. For those researchers outside
the grouse-harrier debate, the modelling method indicates that complex community interactions need not be simplified or limited to the inclusion of covariates, but can be expanded to model detailed interactions with relatively little increase in uncertainty.

5.9 Acknowledgements

I would like to thank the Reading Terminal Market, in particular Tommy DiNic’s, for their material support during the writing of this chapter.
Chapter 6

Community Interactions

6.1 Meadow pipit

The meadow pipit (*Anthus pratensis*) is a small, brown, inconspicuous bird that is identified in the field by its characteristic call, flight patterns and creeping walk. Males and females are similar, but juveniles can be identified by their shorter tails, which may cause them to be confused with other small passerines in the same family. In Britain, meadow pipits are found in a range of grasslands, moorlands, heaths and fens. A ground dweller, the pipit prefers open areas of fairly low, mostly complete ground cover, avoiding open areas. While the birds also avoid tall, dense vegetation (Cramp & Simmons, 1980), they do very well in young conifer plantations, although their numbers will decrease as the age of the plantation increases (Patterson et al., 1995).

Meadow pipits winter in their breeding grounds if conditions are favourable, but otherwise migrate to similar habitats in slightly warmer climes. Outside the breeding season, the pipits are found in loose flocks, but are territorial during the breeding season. Young hatch in late spring and will usually leave the nest within two weeks, even though they are not yet capable of flying. During the next fortnight the parents will show decreasing care for the young as they fledge. The fledged juveniles often stay near their parents' territory until September, when migration takes place. After one year, juveniles enter the breeding population, showing a strong tendency to return to their natal sites to breed (Cramp & Simmons, 1980).
The meadow pipit is the most common upland passerine in the UK, with as many as 3 million pairs in the summer, and approximately half that over the winter. However, the species has been in a mild decline since the 1980's (Marchant et al., 1990; Hull, 2001), possibly due to the fact that the insectivorous bird can be negatively affected by overgrazing in the British uplands, likely due to a decrease in their food availability (Evans et al., 2005). Since meadow pipits are the main passerine prey of the hen harrier (Circus cyaneus) in Scotland (Redpath & Thirgood, 1999), the meadow pipit decline has implications for harrier densities. In North America, harriers switch the focus of their predation to small passerines when the juveniles become available in the spring (Barnard et al., 1987), the high energy content of which may aid in hen harrier survival. Furthermore, recent research has raised the possibility that harrier numbers can limit meadow pipit density, which may, in turn, limit harriers through decreased breeding density (Amar et al., 2008) resulting from lower adult harrier survival. This is in contrast to the earlier assumption that harrier predation did not increase meadow pipit mortality, but does fit with evidence that harriers can show synchrony with their prey (Hamerstrom, 1979; Simmons et al., 1986).

### 6.2 Field vole

Field voles (Mictrotus agrestis) are an extremely common species, with a lower bound of annual production estimates for Britain being over 600 million a year (Dyczkowski & Yalden, 1998). Despite a decline due to increased agricultural practices (Harris et al., 1995), the vole is found throughout the UK and Europe, inhabiting mostly meadows, marshland and grassland, although they are also found in young conifer plantations. A small mammal, usually no longer than 13 cm in length, field voles have short grey-brown fur. They live for no more than two years, feeding on green leaves and grasses (Corbet & Southern, 1964). However, despite their short life span, field voles are prolific, capable of producing 4-6 young every 35 days from March to October, and even until December if weather conditions allow (Dyczkowski & Yalden, 1998).

Outbreaks of vole numbers were first officially recorded in the late 19th century in
Scotland. At the time, the outbreaks were partially blamed on the lower number of vole predators, which had been reduced by human persecution. This conclusion was based on the observation that predator numbers increased quickly following the vole outbreak, then declined again when vole density decreased. The weather was also hypothesised to play a role in the vole outbreaks. Prior to the explosion of vole numbers there had been a series of unusual weather events that provided conditions favourable to the vole reproduction and survival (Elton, 1942). Given the conflicting hypotheses at the time, the debate behind vole cycles can be argued to be at least 120 years old.

Despite the research that has occurred in the intervening years, vole cycles are not completely understood. Their population dynamics are complex, even more so than those of the red grouse (*Lagopus lagopus scoticus*). Voles fluctuate on shorter cycles (3-5 years) than grouse, but with higher amplitude. While there are still multiple different hypotheses for the cause of vole cycles, the general consensus is that they are most likely driven by maternal fitness, predation or food (Turchin, 2003). Each of these hypotheses has theoretical and empirical support (Stenseth et al., 1977; Batzli, 1983; Laine & Henttonen, 1983; Mihok & Boonstra, 1992; Inchausti & Ginzberg, 1998; Turchin & Batzli, 2001; Korpimaki et al., 2002, 2004).

The maternal effect hypothesis states that phenotypic individual quality is passed to the offspring through the mother’s ability to raise and provide for her young. Therefore, the environment in which the parents lived will affect the demographic rates of their offspring, creating the delayed density dependence needed to generate cycles (Inchausti & Ginzberg, 1998). The predation hypothesis proposes that the different patterns in vole population dynamics, from cycles to stability, can be explained by different abundances of vole predators (Hanski & Korpimaki, 1995). Specialist predators on voles, such as stoats (*Mustela erminea*), are capable of imposing the necessary delayed density dependence on mortality that generates cycles, while generalist predators, such as short-eared owls (*Asio flammeus*), can stabilise cycles by responding quickly to small-scale changes in vole densities (Korpimaki et al., 2002).
Finally, the food hypothesis postulates that vole cycles will occur when food availability remains low even after the population peaks, limiting survival and reproduction, generating delayed density dependence (Turchin & Batzli, 2001).

While support for each hypothesis exists, the body of accumulated evidence for and against them is complicated. For example, research has shown that changes in survival, as opposed to reproduction are the main demographic change driving vole cycles (Korpimaki et al., 2004), which would tend to exclude the hypothesis of maternal nutrition as a mechanism behind vole cycles. Yet, reproduction would also be affected by limited food availability. However, it is unlikely that food limitations alone are capable of driving vole cycles. Instead, interactions with other mechanisms, such as predation, are needed to explain the periodic fluctuations (e.g., Hansson, 1987), since experiments attempting to manipulate vole cycles through food quality and availability have not been successful in halting a decline or causing a population to expand rapidly (Krebs & DeLong, 1965). This leads to one of the difficulties in choosing a single ‘correct’ hypothesis for vole cycles: the different mechanisms may be acting independently, or in concert, to create the observed cycles (Klemola et al., 2000; Korpimaki et al., 2004). Finally, while only the three main hypotheses are discussed here, there are over 20 different possibilities recorded in the vole literature (Turchin, 2003), making vole dynamics difficult to model.

As well as the complexity of the different mechanisms and their possible interactions, there is the added difficulty that vole dynamics have proven to vary across different regions and not all vole populations cycle. Field vole populations in southern England do not oscillate (Turchin, 2003), although they do in Scotland, where the population dynamics are similar to those observed in Scandinavia (Dyczkowski & Yalden, 1998). This can have implications for the multi-species modelling of hen harriers and their prey, since models used for interactions in England may need to be different from those used in Scotland, depending on the nature of the data available.

Although harriers have been noted to cycle in synchrony with their rodent prey (Hamerstrom, 1979; Simmons et al., 1986), the absence of voles does not exclude harriers from a given area (Redpath et al., 2002a). Harrier survival and nest fidelity
are high (Watson, 1977), so a population can persist even when immigration is low due to a decline in vole density. Additionally, voles are not the only prey item to affect movement; pipits also play a role in determining immigration (see Chapter 3). Therefore, a brief decline in vole density will not result in harriers abandoning an area.

6.3 The model

There are only indirect interactions between the red grouse and the hen harriers’ alternate prey. No direct relationship has been found between grouse and meadow pipit abundance (Smith et al., 2001), and vole abundance fluctuates with very different periods; three to five years for voles, as opposed to four to ten year cycles for grouse (Turchin, 2003). While the three species may interact through other indirect methods, we are modelling grouse density as only being affected by vole and pipit density through hen harrier predation. Since we are using a multispecies functional response (MSFR) to model hen harrier consumption (see Chapter 5, Eqn. 5.3 for more detail), shifting densities of the harriers’ alternate prey will result in different rates of consumption of the red grouse chicks. This, in turn, will affect the number of juveniles available for recruitment in the fall. However, at no point do voles or pipits appear explicitly in the grouse model.

The relationships between hen harriers, meadow pipits and field voles are assumed to be one-way interactions. The density of harriers’ main prey species determines the raptors’ movement into an area \( \eta_t \), as well as influencing the harriers’ survival \( \phi_t \),

\[
\eta_t = \exp(\beta_0 V_t + \beta_1 P_t - \beta_2 H_{t-1} \phi_{t-1}) \tag{6.1}
\]

\[
\phi_t = \frac{\exp(\alpha_0 + \alpha_1 P_t)}{1 + \exp(\alpha_0 + \alpha_1 P_t)}, \tag{6.2}
\]

where \( \beta_0, \beta_1 \) and \( \beta_2 \) measure the effect of vole density \( (V_t, \text{km}^{-2}) \), pipit density \( (P_t, \text{km}^{-2}) \) and surviving harrier nests \( (H_{t-1} \phi_{t-1}) \) on harrier immigration, respectively, \( \alpha_0 \) is a measure of hen harrier survival and \( \alpha_1 \) measures the impact of pipit density.
on $\phi_t$. The reasoning behind the relationships described by Eqns. 6.1 and 6.2 is discussed in detail in Chapter 3. In contrast to the models in Chapters 3 and 5, the vole and pipit densities ($V_t$ and $P_t$) in Eqns. 6.1 and 6.2 are now estimates from the state-space model, rather than previously calculated covariates with no corresponding measure of uncertainty.

I will be assuming that the population dynamics of voles and pipits are not directly impacted by hen harriers. For the meadow pipits, I will be assuming that harrier predation on the small passerine is compensatory. While there is a negative correlation between hen harrier and meadow pipit densities on Langholm, meadow pipit densities remained at levels comparable with other upland areas despite the decline (Amar et al., 2008). Additionally, there are other factors that may have contributed to the decrease in pipit density. The authors did not investigate the effect of the abundance of other meadow pipit predators, such as gulls ($\textit{Larus sp.}$), competitors, such as cuckoos ($\textit{Cuculus canorus}$), or the possible effect of unusually cold weather, which would increase nestling mortality (Pedroli, 1978). Additionally, the effects of hen harrier predation on meadow pipits are confounded with the impact of changing moorland management during this time period, requiring further study (Baines et al., 2008). Given the lack of replication in the study and the limited data available, I maintained the assumption that hen harriers do not add to meadow pipit mortality. Instead, the raptors’ impact on pipit survival is incorporated into the passerine’s population dynamics through the growth parameter, $r$. The assumption is primarily due to the limitations of the data, but can easily be relaxed or eliminated in future models when more information is available.

I have therefore chosen to fit a simple logistic growth model to the pipit data,

$$P_{t+1} = P_t \exp \left( r \left( 1 - \frac{P_t}{K} \right) \right),$$

(6.3)

where $P_t$ is the density of meadow pipits in time $t$ and $r$ and $K$ are the growth rate and carrying capacity for pipits, respectively. If more data were available, $r$ could be modified to allow for the possible negative effects of hen harriers on meadow pipits. However, only eight years of data are available for the pipits and there are already five
parameters related to the pipits \((r, K, \sigma^2_p, \alpha_1 \text{ and } \beta_1)\). While an additional parameter could be added to Eqn. 6.3 to account for harrier predation and Bayesian methods are capable of fitting over-parameterised models (Gelman et al., 1995), it is not advisable to have almost as many parameters as data points.

The observation process for the pipits is lognormal, where the mean is equal to the log of estimated pipit density \((P_t)\) in year \(t\),

\[
P_{Est,t} \sim \text{LN}(\log(P_t), \sigma^2_p),
\]

where \(P_{Est,t}\) is the estimated density of meadow pipits in year \(t\) and \(\sigma^2_p\) is the variance of the pipit observation model and is to be estimated. The choice of a lognormal distribution for the observation model was based on the state-space model for distance sampling described in Buckland et al. (2004a).

The harriers’ relationship with small mammals, voles in particular, can be complex. However, in this case I will be assuming that harriers’ predation on voles is compensatory. This assumption is reasonable because, although harriers have been shown to synchronise with vole densities (Hamerstrom, 1979; Simmons et al., 1986), there is limited evidence of such behaviour on Langholm over the time period of the study. As with the meadow pipits, this assumption can be relaxed when more data become available.

Fitting mechanistic models to the vole dynamics that are capable of producing the observed vole dynamics is not within the remit of this PhD, especially given their complexity and the number of competing hypotheses. I therefore used an empirical approach to vole dynamics by implementing first and second order autoregressive models. However, as with the possible extensions to the meadow pipit model, almost as many parameters as data points would have been needed to match the observed behaviour. When fit in WinBUGS, the parameters being estimated for the autoregressive models failed to have posterior distributions different from their priors. Additionally, the vole densities estimated in these models failed to match any key features of the data. Therefore, rather than attempting to model the population processes of
the field voles, only an observation model was implemented. In this way I still incorporated the uncertainty around the estimates for voles density, but avoided making any broad assumptions about their population dynamics. A lognormal distribution was used, with the mean equal to the log of the observed vole density ($V_{\text{Obs},t}$) in year $t$,

$$V_t \sim \text{LN}(\log(V_{\text{Obs},t}), \sigma_v^2),$$  \hspace{1cm} (6.5)

where $V_t$ is the estimated vole density in year $t$ and $\sigma_v^2$ is the variance of the field vole observation model and is to be estimated. With a longer time series of data, or more consensus on the cause of vole cycles, it would be possible to fit a population process model to voles in the future.

It is possible that the inclusion of uncertainty around the estimate of $V_t$ absorbs some of the lack of fit in the model describing harrier immigration into an area (see Chap. 3 Eqn. 3.2). By the same token, it is possible that some of the lack of fit of the movement model may result from incorrect estimates of vole density, so the argument is somewhat circular. However, the main goal of this Chapter is to demonstrate the ability of the multi-species state-space modelling to incorporate more than two species, so an observation model for the voles was included, despite its potential impacts.

### 6.4 The Data

The data described in Chapters 3 and 4 were used to fit the multi-species model described in this chapter. For the red grouse, autumn grouse counts on Langholm moor, from 1975-1996 were used, as well as estimates of the chick density from 1992-1999. Hen harrier nest numbers were believed to be known without error from 1992-1999, and information was available on the number of nests provided with supplementary food in the last two years of the study, 1998 and 1999. Distance sampling techniques were used to estimate pipit density, and vole density estimates were based on an index according to the effective number of trap-nights.
6.5 Priors

I used the same priors for the red grouse \((\gamma_0, \gamma_1, \phi_0, \delta_0, \xi_0, \xi_1, \xi_2, \tau_c, \xi)\) and hen harrier parameters \((\alpha_0, \alpha_1, \beta_0, \beta_1, \beta_2)\) that were used in Chapter 5. An additional four parameters, \(K, r, \tau_p\) and \(\tau_v\), have been added to the model to account for the pipit and vole population models. While Eqns. 6.4 and 6.5 use \(\sigma_p^2\) and \(\sigma_v^2\), respectively, in the pipit and vole observation models, WinBUGS defines the lognormal distribution according to its precision, \(\tau\), so that is the parameter provided with a prior distribution where,

\[
\tau_v = \frac{1}{\sigma_v^2} \quad (6.6)
\]

\[
\tau_p = \frac{1}{\sigma_p^2}
\]

Three of the new parameters \((K, r, \tau_p)\) are associated with meadow pipits, while only one \((\tau_v)\) is connected to the field voles. All of the parameters’ posterior estimates were found to be sensitive to the choice of prior. This is a result of a combination of over-parameterisation and lack of information. There are eight years of data on vole and pipit density. Yet, with the inclusion of a state process model for pipits, there are five parameters \((K, r, \tau_p, \alpha_1, \beta_1)\) dependent on the pipit data for information. While the vole data only need to inform two parameters \((\tau_v, \beta_0)\), the complexity of the voles’ cyclic dynamics makes eight years of data not enough to fully capture the behaviour of the population.

Gamma distributions were used for all the priors to constrain the parameters to positive values (Table 6.1). As well as affecting the posterior density, the choice of prior influenced the ability of the fitting algorithm to move through the iterations, even failing to converge under certain scenarios. As a result, the priors were chosen carefully and were kept as uninformative as possible. Therefore, for the precision parameters a \(\Gamma(0.01,0.01)\) was used, while a \(\Gamma(3,4)\) was chosen for \(r\). The carrying capacity parameter was particularly important, since it would determine the estimated density of pipits. We used a \(\Gamma(200,1)\), for its large variance and because pipit density was observed to decline steadily towards 200 km\(^{-2}\) after reaching their peak earlier in the time series (Table 6.4).
6.6 Model fitting

In the community model, the partial supplementary feeding model developed in Chapter 5 was used for the grouse-harrier interactions. However, where the partial supplementary feeding model incorporated vole and pipit densities through the use of covariates, the community model estimates these values through the use of process and observation models (Eqns. 6.3-6.5), introducing additional uncertainty. However, no stochasticity was added to the pipit or vole models. The model was fit using the state-space modelling framework described in Chapter 2.

6.7 Results

The models took three and a half days to run three chains for 100,000 iterations on a 3.2 GHz processor. A burn-in of 10,000 iterations was used and only every tenth iteration was retained to reduce serial autocorrelation between MCMC trials and allow for storage of the MCMC output without encountering memory problems. Trace plots were used to visually assess mixing and the Gelman-Rubin statistic was used as a quantitative diagnostic to assess the convergence of multiple chains to a target distribution (Brooks & Roberts, 1998). All the tracked parameters and states converged and displayed good mixing.

Correlations between the parameters were examined for each model. As well as the relationships investigated in Chapters 3, 4 and 5, we also examined possible correlations between all of the new pipit parameters \( (K, r, \tau_p) \) and the precision parameters for voles and pipits \( (\tau_v, \tau_p) \).

Table 6.1: Prior distributions for the meadow pipit and field vole parameters in the community model.

<table>
<thead>
<tr>
<th>( \Theta )</th>
<th>Priors</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K )</td>
<td>( \Gamma(200,1) )</td>
</tr>
<tr>
<td>( r )</td>
<td>( \Gamma(3,4) )</td>
</tr>
<tr>
<td>( \tau_v )</td>
<td>( \Gamma(0.01,0.01) )</td>
</tr>
<tr>
<td>( \tau_p )</td>
<td>( \Gamma(0.01,0.01) )</td>
</tr>
</tbody>
</table>
The inclusion of models for the voles and pipits impacted the relationships between the parameters in the grouse and harrier models. For the grouse parameters, while the relationships themselves remained unchanged, a number of the correlations grew in strength, such as that between adult survival ($\phi_a$) and the natural log of brood size ($\gamma_0$) on beat LM (Fig. 6.1).

![Figure 6.1](image)

Figure 6.1: Correlation plots for both the beat-independent and beat-dependent parameters associated with the red grouse ($\gamma_0, \gamma_1, \phi_a, \tau_c, c, \delta_0, \xi_0, \xi_1, \xi_2$) in the community model.

In contrast, there was a significant difference in the hen harrier parameters, with only those parameters related to survival ($\alpha_0$ and $\alpha_1$) retaining a strong relationship. The previous strong correlation between the effect of vole density on harrier movement ($\beta_0$) and the limiting effect of surviving harriers ($\beta_2$) is weaker, and there is no longer any evidence for a relationship between the parameters measuring the effect of vole and pipit densities on harrier movement ($\beta_0$ and $\beta_1$, respectively) (Fig. 6.2).
Figure 6.2: Correlation plots for the parameters associated with hen harriers \((\alpha_0, \alpha_1, \beta_0, \beta_1, \beta_2)\) in the community model.
As for the parameters specific to the harriers’ alternate prey, there was no relationship between the precision parameters or the growth rate and carrying capacity. However, there is a slight positive correlation between pipit carrying capacity and precision, as well as a stronger negative relationship between pipit growth rate and precision (Fig. 6.3).

Figure 6.3: Correlation plots for the parameters associated with meadow pipits and field voles ($K, r, \tau_p, \tau_v$) in the community model.

As well as changes in the correlations between the parameters, the addition of models for the meadow pipits and field voles altered some of the prior sensitivities. The parameters related to the red grouse were the least affected, with the beat-specific grouse parameters remaining unchanged in their prior sensitivities from Chapters 4 and 5 (Fig. 6.4). The only beat-independent parameter to show a change in prior sensitivity is the aggression parameter $\xi_2$, which, while still showing the bi-modality observed in Chapter 5, is closer to mimicking the prior than was previously observed (Fig. 6.5).
Figure 6.4: Posterior (red) - prior (black) plots for the beat-dependent red grouse parameters in the community model.
Figure 6.5: Posterior (red) - prior (black) plots for the beat-independent red grouse parameters in the community model.
The hen harrier parameter most impacted by the inclusion of vole and pipit dynamics in the state-space model was the hen harrier survival parameter $\alpha_0$, whose posterior is now only slightly narrower than its prior. The relationship between the other parameters and their priors remain unchanged, although the posteriors are slightly wider than observed in Chapter 5 (Fig. 6.6).

The posterior distributions for the pipit process model parameters, $K$ and $r$, are completely dependent on the choice of priors. The precision parameters for the vole and pipit observation models, $\tau_v$ and $\tau_p$, while sensitive to prior choice, do show posterior distributions that have updated from the prior (Fig. 6.7).

Harriers were known to be absent from Langholm, in numbers large enough to impact grouse densities, for the first 18 years of the study. During this time the community model showed cyclic dynamics for the red grouse with respect to both their spring and autumn densities. Harriers begin to impact grouse dynamics from 1993, after which
Figure 6.7: Posterior (red) - prior (black) plots for the vole and pipit parameters in the community model. Due to the priors of the precision parameters, $\tau_v$ and $\tau_p$, tending towards infinity as $x$ goes to zero, the plots have been truncated so the posteriors could be shown in more detail.
the grouse population shows an extended decline phase in both seasons on all four beats, although beats LC and LM do show a slight increase in density at the end of the time period. Partial supplementary feeding occurs in 1998 and 1999, which may be the source of the increased density on beats LC and LM. However, the remaining two beats show no apparent effect resulting from the diversionary feeding of the hen harriers (Figs. 6.8 and 6.9).

Figure 6.8: The relative timing of aggression (blue) and autumn grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1999 for the community model. Harrier numbers were high enough to impact grouse density from 1993 and partial supplementary feeding took place in 1998 and 1999.

Aggressiveness in cock red grouse displays the expected behaviour, peaking with, or just after peak grouse densities when the grouse population is cycling, then remaining at low levels when the population is suppressed by harrier predation. Beats LC and LM both show a slight increase in aggressiveness at the end of the time series as a result of their slight increase in grouse densities (Fig. 6.8). The parasitic nematode, *Trichostrongylus tenuis* also showed cyclic dynamics for all four beats, until hen harriers were introduced to the system in year 19. After this point *T. tenuis* declined steadily, with no evidence of any effect of supplementary feeding on the worm burden.
Only beat LD shows a peak in parasite burdens after the suppression of grouse cycles, although it too, then declines rapidly to low levels. All of the beats remain within the realm of biological realism (Fig. 6.9).

![Graphs showing parasite burdens and spring grouse density](image)

Figure 6.9: The relative timing of parasite burdens (red) and spring grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1999 for the community model. Harrier numbers were high enough to impact grouse density from 1993 and partial supplementary feeding took place in 1998 and 1999.

The estimates of the expected number of successful hen harrier nests fit closely with the true values, indicating a good relationship between the super-population model and the observed population. The years 1993 and 1995 were the most dissimilar, with the super-population estimate being higher by approximately three nests in both cases (Table 6.2).

Survival estimates for the hen harriers in the community model were lower than those previously observed, although the range of point estimates, 72-79%, is still realistic, since it falls within the previous 95% confidence interval (57%, 90%), and includes the original point estimate of 78% (Etheridge et al., 1997). However, the estimates of harrier survival are uncertain, with 95% credible intervals whose lower limits fall...
<table>
<thead>
<tr>
<th>Year</th>
<th>Observed</th>
<th>Partial</th>
<th>Community</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>5</td>
<td>8.7</td>
<td>7.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6, 12.2)</td>
<td>(4.2, 11.7)</td>
</tr>
<tr>
<td>1994</td>
<td>11</td>
<td>10.9</td>
<td>11.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(8.4, 14)</td>
<td>(7.3, 16.5)</td>
</tr>
<tr>
<td>1995</td>
<td>8</td>
<td>11.1</td>
<td>10.58</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(9.6, 12.7)</td>
<td>(8.7, 13.2)</td>
</tr>
<tr>
<td>1996</td>
<td>14</td>
<td>8.8</td>
<td>11.66</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(7.7, 10)</td>
<td>(8.2, 18.5)</td>
</tr>
<tr>
<td>1997</td>
<td>20</td>
<td>19.4</td>
<td>19.11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(14.4, 25.8)</td>
<td>(13.9, 26.4)</td>
</tr>
<tr>
<td>1998</td>
<td>17</td>
<td>16.4</td>
<td>16.98</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(13.9, 18.7)</td>
<td>(14.1, 20.0)</td>
</tr>
<tr>
<td>1999</td>
<td>13</td>
<td>13.2</td>
<td>13.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(10.9, 15.3)</td>
<td>(11.5, 16.4)</td>
</tr>
</tbody>
</table>

Table 6.2: The observed numbers and super-population estimates for the hen harrier population with their corresponding 95% credible intervals for the partial supplementary feeding and community models.

outside the previously estimated range in each year (Table 6.3).

The estimates for harrier movement onto the moor ($\eta_t$) were varied, peaking with high vole densities, although meadow pipits did contribute slightly to the harriers’ movement (Table 6.4). There was little evidence for density dependence as a limiting factor on harrier movement ($\beta_2$: 0.08, 95% CI: (1.5 x10^{-3}, 0.30)).

The estimates of field vole density came from a model that assigned all the variation around the data to errors in the observations. The estimated values followed the same pattern as the observed densities, showing two peaks, one at the start of the time series in 1994 and another three years later in 1997. However, there was a great deal of uncertainty around the population estimates (Table 6.5).

Meadow pipits were modelled using both a process and observation model. However, unlike the voles, the pipit model failed to capture the dynamics of the observed data, which are determined solely by the choice of priors. This is an indication of poor model choice, and indicates that our assumptions about pipit dynamics need to be reconsidered. Where the observations show an initial increase in density before declining, the estimates of pipit density decline steadily from 1993 until 1999 when
<table>
<thead>
<tr>
<th>Year</th>
<th>Partial</th>
<th>Community</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>79.2 (66.1, 90.5)</td>
<td>78.9 (53.5, 93.5)</td>
</tr>
<tr>
<td>1993</td>
<td>85.6 (72.9, 96.5)</td>
<td>72.5 (44.6, 88.3)</td>
</tr>
<tr>
<td>1994</td>
<td>85.5 (71.8, 96.3)</td>
<td>72.9 (47.6, 87.5)</td>
</tr>
<tr>
<td>1995</td>
<td>79.4 (66.2, 90.6)</td>
<td>72.1 (46.6, 86.8)</td>
</tr>
<tr>
<td>1996</td>
<td>78.3 (65.2, 89.5)</td>
<td>72.1 (47.1, 86.6)</td>
</tr>
<tr>
<td>1997</td>
<td>72.7 (58.8, 84.7)</td>
<td>71.7 (46.5, 86.4)</td>
</tr>
<tr>
<td>1998</td>
<td>71.6 (57.3, 84)</td>
<td>71.7 (46.8, 86.3)</td>
</tr>
</tbody>
</table>

Table 6.3: Yearly hen harrier survival estimates ($\phi_t$, %) with their corresponding 95% credible intervals for the partial supplementary feeding and community models.

<table>
<thead>
<tr>
<th>Year</th>
<th>Partial</th>
<th>Community</th>
<th>Vole</th>
<th>Pipit</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>7.1 (4.3, 10.7)</td>
<td>6.0 (2.6, 10.2)</td>
<td>1050.4</td>
<td>575.2</td>
</tr>
<tr>
<td>1994</td>
<td>6.6 (4.1, 9.8)</td>
<td>7.5 (3.5, 13.1)</td>
<td>1060.8</td>
<td>570.1</td>
</tr>
<tr>
<td>1995</td>
<td>1.7 (0.8, 2.9)</td>
<td>2.6 (0.33, 6.6)</td>
<td>280.0</td>
<td>385.7</td>
</tr>
<tr>
<td>1996</td>
<td>2.5 (1.6, 3.5)</td>
<td>5.9 (2.1, 12.8)</td>
<td>535.6</td>
<td>358.8</td>
</tr>
<tr>
<td>1997</td>
<td>8.4 (3.3, 15.2)</td>
<td>9.0 (3.5, 16.8)</td>
<td>1648.4</td>
<td>239.4</td>
</tr>
<tr>
<td>1998</td>
<td>1.9 (0.74, 2.8)</td>
<td>2.6 (0.089, 7.6)</td>
<td>598.0</td>
<td>219.1</td>
</tr>
<tr>
<td>1999</td>
<td>1.1 (0.41, 1.7)</td>
<td>1.8 (0.066, 5.8)</td>
<td>104.0</td>
<td>216.5</td>
</tr>
</tbody>
</table>

Table 6.4: Yearly estimates for hen harrier movement ($\eta_t$), with their corresponding 95% credible intervals, for the partial supplementary feeding and community models, as well as the observed (black) and estimated (blue) vole and pipit densities for each year ($\text{km}^{-2}$).
they reach the estimated carrying capacity ($K$: 203.1, 95% CI: (176.0, 232.1)). Additionally, the pipit density estimates are consistently lower than the observed data, by more than 250 birds km$^{-2}$ in some cases (Table 6.6).

The estimates for the parameters in the meadow pipit’s process model, $K$ and $r$, were completely dependent on the choice of prior. In contrast, while the precision parameters from the vole and pipit observation models are sensitive to the choice of prior, their estimates have moved away from the prior mean and variance (Table 6.7).

### 6.8 Effects of community modelling

The process and observation models for the partial supplementary feeding model were described in detail in Chapter 5. In the current chapter I expand upon that framework by building a community model that includes an observation model for

<table>
<thead>
<tr>
<th>Year</th>
<th>Observed $V_t$ km$^{-2}$</th>
<th>Estimate $V_t$ km$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>1054.4</td>
<td>744.5 (49.8, 1436)</td>
</tr>
<tr>
<td>1994</td>
<td>1060.8</td>
<td>1033.0 (159, 2142)</td>
</tr>
<tr>
<td>1995</td>
<td>280.0</td>
<td>278.9 (17.6, 682.9)</td>
</tr>
<tr>
<td>1996</td>
<td>535.6</td>
<td>909.8 (200.8, 2503)</td>
</tr>
<tr>
<td>1997</td>
<td>1648.4</td>
<td>1884.0 (548.9, 4566)</td>
</tr>
<tr>
<td>1998</td>
<td>598</td>
<td>629.8 (51.9, 1585)</td>
</tr>
<tr>
<td>1999</td>
<td>104</td>
<td>125.3 (10.9, 8396.6)</td>
</tr>
</tbody>
</table>

Table 6.5: The observed densities and yearly estimates for field voles ($V_t$, km$^{-2}$), with their corresponding 95% credible intervals from the community model.

<table>
<thead>
<tr>
<th>Year</th>
<th>Observed $P_t$ km$^{-2}$</th>
<th>Estimate $P_t$ km$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>382.4</td>
<td>301.2 (268.6, 336.8)</td>
</tr>
<tr>
<td>1993</td>
<td>575.2</td>
<td>219.6 (124.5, 294.5)</td>
</tr>
<tr>
<td>1994</td>
<td>570.1</td>
<td>222.9 (180.6, 279.9)</td>
</tr>
<tr>
<td>1995</td>
<td>385.7</td>
<td>213.2 (171.6, 267.7)</td>
</tr>
<tr>
<td>1995</td>
<td>358.8</td>
<td>213.0 (178.8, 261.8)</td>
</tr>
<tr>
<td>1997</td>
<td>239.4</td>
<td>208.8 (174.9, 252.6)</td>
</tr>
<tr>
<td>1998</td>
<td>219.1</td>
<td>209.0 (177.8, 249.8)</td>
</tr>
<tr>
<td>1999</td>
<td>216.5</td>
<td>206.6 (175.5, 243.6)</td>
</tr>
</tbody>
</table>

Table 6.6: The observed densities and yearly estimates for meadow pipits ($P_t$, km$^{-2}$), with their corresponding 95% credible intervals from the community model.
### Table 6.7: The estimated values and 95% credible intervals for the meadow pipit and field vole parameters from the community model.

<table>
<thead>
<tr>
<th>( \Theta )</th>
<th>Prior</th>
<th>Posterior</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K )</td>
<td>200</td>
<td>203.1</td>
</tr>
<tr>
<td></td>
<td>(173.2, 228.7)</td>
<td>(176.0, 232.1)</td>
</tr>
<tr>
<td>( r )</td>
<td>0.75</td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td>(0.15, 1.8)</td>
<td>(0.11, 1.7)</td>
</tr>
<tr>
<td>( \tau_p )</td>
<td>( \frac{1}{3.5 \times 10^{-159}, 4.7} )</td>
<td>3.3</td>
</tr>
<tr>
<td></td>
<td>( (0.74, 8.7) )</td>
<td>( (0.13, 134.4) )</td>
</tr>
<tr>
<td>( \tau_v )</td>
<td>( \frac{1}{3.5 \times 10^{-159}, 4.7} )</td>
<td>18.5</td>
</tr>
</tbody>
</table>

field voles and a full state-space model for meadow pipits. I will compare the estimates from the partial supplementary feeding model and the community model to try and determine the effects of community modelling.

Spring and autumn grouse densities appear unaffected by the inclusion of vole and pipit dynamics in the model, as do the estimates of aggressiveness in cock red grouse (Figs. 6.10 and 6.11). The community model still matches key features of the data. The estimates are consistently higher than the observed data (Fig. 6.10), since the observation model for the red grouse states that only a proportion of the grouse present on the moor are seen, dependent on the amount of effort each year (see Chapter 4). However, there is a noticeable difference in the estimated *T. tenuis* burdens in the red grouse, with the estimates from the community model being consistently lower than those from the partial supplementary feeding model (Fig. 6.11). The estimated grouse chick densities, which still fail to match the key features of the data, are also different for the two models (Fig. 6.12). This is likely due, in part, to the differences in the average worm burdens between the two models.

Implementing the community model had no apparent effect on the parameters related to the red grouse. Both the beat-dependent and beat-independent parameters showed no significant changes in their estimates or credible intervals from the partial supplementary feeding model (Tables 6.8 and 6.9).

However, while the parameters that affect only the red grouse remain unchanged, those that involve the hen harrier have been impacted by the inclusion of vole and
Figure 6.10: The relative timing of parasite burdens (red) and spring grouse density (km$^{-2}$, black) in relation to each other on each of the four beats (LC, LD, LM, LR) on Langholm from 1976-1999 for the community (solid line) and partial supplementary feeding (dashed line) models. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in 1998 and 1999.
Figure 6.11: The relative timing of aggression (blue) and spring grouse density (km$^{-2}$, black) in relation to each other and the observed data (purple) on each of the four beats (LC, LD, LM, LR) on Langholm from 1975-1999 for the community (solid line) and partial supplementary feeding (dashed line) models. Harrier numbers were high enough to impact grouse density from 1993 and supplementary feeding took place in 1998 and 1999.

Figure 6.12: The comparison of grouse chick density estimates (km$^{-2}$) from the community (black) and partial (green) supplementary feeding models in relation to each other and the data (dashed line) from 1992-1999.
<table>
<thead>
<tr>
<th>Θ</th>
<th>Partial</th>
<th>Community</th>
</tr>
</thead>
<tbody>
<tr>
<td>γ₀,LC †</td>
<td>1.8</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>(1.1, 2.3)</td>
<td>(1.1, 2.3)</td>
</tr>
<tr>
<td>γ₀,LD †</td>
<td>2.2</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>(1.5, 2.8)</td>
<td>(1.5, 2.8)</td>
</tr>
<tr>
<td>γ₀,LM †</td>
<td>1.7</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>(1.1, 2.3)</td>
<td>(1.0, 2.3)</td>
</tr>
<tr>
<td>γ₀,LR †</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>(0.96, 2.3)</td>
<td>(0.95, 2.2)</td>
</tr>
<tr>
<td>φ₀,LC</td>
<td>0.31</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>(0.03, 0.57)</td>
<td>(0.05, 0.58)</td>
</tr>
<tr>
<td>φ₀,LD</td>
<td>0.51</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>(0.23, 0.70)</td>
<td>(0.25, 0.69)</td>
</tr>
<tr>
<td>φ₀,LM</td>
<td>0.32</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>(0.03, 0.60)</td>
<td>(0.04, 0.60)</td>
</tr>
<tr>
<td>φ₀,LR</td>
<td>0.50</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>(0.17, 0.73)</td>
<td>(0.19, 0.75)</td>
</tr>
<tr>
<td>cₐ,LC</td>
<td>6.7</td>
<td>6.5</td>
</tr>
<tr>
<td></td>
<td>(4.6, 9.1)</td>
<td>(4.5, 9.0)</td>
</tr>
<tr>
<td>cₐ,LD</td>
<td>10.1</td>
<td>9.8</td>
</tr>
<tr>
<td></td>
<td>(6.6, 14.1)</td>
<td>(6.5, 13.6)</td>
</tr>
<tr>
<td>cₐ,LM</td>
<td>5.6</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>(3.7, 8)</td>
<td>(3.5, 7.7)</td>
</tr>
<tr>
<td>cₐ,LR</td>
<td>5.1</td>
<td>5.0</td>
</tr>
<tr>
<td></td>
<td>(3.2, 7.6)</td>
<td>(3.1, 7.5)</td>
</tr>
<tr>
<td>γ₁,LC</td>
<td>9.1 x10⁻⁵</td>
<td>1.0 x10⁻⁴</td>
</tr>
<tr>
<td></td>
<td>(7.8 x10⁻⁷, 5.6 x10⁻⁴)</td>
<td>(8.2 x10⁻⁷, 6.4 x10⁻⁴)</td>
</tr>
<tr>
<td>γ₁,LD</td>
<td>1.13 x10⁻³</td>
<td>1.2 x10⁻³</td>
</tr>
<tr>
<td></td>
<td>(9.3 x10⁻⁶, 6.6 x10⁻³)</td>
<td>(1.0 x10⁻⁵, 7.0 x10⁻³)</td>
</tr>
<tr>
<td>γ₁,LM</td>
<td>8.8 x10⁻⁵</td>
<td>9.2 x10⁻⁵</td>
</tr>
<tr>
<td></td>
<td>(5.3 x10⁻⁷, 5.0 x10⁻⁴)</td>
<td>(5.2 x10⁻⁷, 5.4 x10⁻⁴)</td>
</tr>
<tr>
<td>γ₁,LR</td>
<td>8.8 x10⁻⁵</td>
<td>1.0 x10⁻⁴</td>
</tr>
<tr>
<td></td>
<td>(3.4 x10⁻⁸, 5.8 x10⁻⁴)</td>
<td>(6.0 x10⁻⁸, 6.8 x10⁻⁴)</td>
</tr>
</tbody>
</table>

Table 6.8: Posterior means and their 95% credible intervals for the beat-dependent grouse parameter estimates for the partial supplementary feeding and community models. (†Parameter estimated on the log scale)
Table 6.9: Estimates and 95% credible intervals for the beat-independent grouse parameters for the partial supplementary feeding and community models.

<table>
<thead>
<tr>
<th>Θ</th>
<th>Partial</th>
<th>Community</th>
</tr>
</thead>
<tbody>
<tr>
<td>ξ₀</td>
<td>-2.2</td>
<td>-2.2</td>
</tr>
<tr>
<td></td>
<td>(-2.6, -2.0)</td>
<td>(-2.7, -2.0)</td>
</tr>
<tr>
<td>ξ₁</td>
<td>0.013</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>(0.002, 0.019)</td>
<td>(0.001, 0.02)</td>
</tr>
<tr>
<td>ξ₂</td>
<td>0.023</td>
<td>0.024</td>
</tr>
<tr>
<td></td>
<td>(0.006, 0.039)</td>
<td>(0.006, 0.04)</td>
</tr>
<tr>
<td>δ₀</td>
<td>5.4</td>
<td>5.5</td>
</tr>
<tr>
<td></td>
<td>(4.6, 6.0)</td>
<td>(4.6, 6.0)</td>
</tr>
</tbody>
</table>

pipit dynamics. The proportion of otherwise successfully reared grouse chicks to reach the autumn territorial contest (\(\pi_t\)) is markedly lower than those from the partial supplementary feeding model for the first four years of the study in which harriers are present in the system. The three remaining years have similar estimates, with \(\pi_t\) being slightly higher in the community model when supplementary feeding is taking place. The level of uncertainty around the estimates of \(\pi_t\) is higher in the community model, but only from 1993 to 1996. For the last three years of the time series, the credible intervals remain relatively unchanged between the two models (Table 6.10). The wider credible intervals are due to the uncertainty around the vole and pipit density estimates, which affects the harriers’ MSFR. This impacts the number of grouse chicks consumed, and thus the proportion of otherwise successfully reared chicks to reach the autumn territorial contest. The uncertainty around the estimates for \(\pi_t\) remains relatively unchanged for the last two years of the study because the uncertainty associated with supplementary feeding is greater than that associated with the estimates of alternate prey densities.

The level of uncertainty around the super-population estimates for hen harrier numbers in the community model also increases, but not dramatically. The increase in uncertainty results in the credible intervals including the real values in 1993 and 1996, where the partial supplementary feeding model fails to include the observed values. Additionally, while 1996 was the most dissimilar in all the previous harrier models (see Chapters 3 and 5), that is not the case in the community model, whose estimate
Table 6.10: Yearly estimates for the proportion of successfully reared grouse chicks to reach the autumn territorial contest in the presence of harrier predation ($\pi_t$, %), with their corresponding 95% credible intervals for the partial supplementary feeding and community models.

<table>
<thead>
<tr>
<th>Year</th>
<th>Partial</th>
<th>Community</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>94.5 (87.6, 98.2)</td>
<td>87.7 (72.5, 96.5)</td>
</tr>
<tr>
<td>1994</td>
<td>87.1 (74.5, 95)</td>
<td>72.0 (53.8, 87.9)</td>
</tr>
<tr>
<td>1995</td>
<td>92.2 (80.5, 98.0)</td>
<td>84.6 (66.1, 96.3)</td>
</tr>
<tr>
<td>1996</td>
<td>94.4 (86.9, 98.4)</td>
<td>85.9 (66.5, 96.4)</td>
</tr>
<tr>
<td>1997</td>
<td>70.6 (46.2, 90.5)</td>
<td>69.8 (45.2, 89.5)</td>
</tr>
<tr>
<td>1998</td>
<td>76.7 (46.7, 96.0)</td>
<td>77.5 (46.8, 96.1)</td>
</tr>
<tr>
<td>1999</td>
<td>78.8 (48.5, 97.4)</td>
<td>79.5 (47.5, 97.3)</td>
</tr>
</tbody>
</table>

for that year is off by just over two nests. The biggest discrepancies in the community model are in 1993 and 1995, which estimate approximately three more nests than were actually observed (Table 6.2).

With the exception of $\beta_0$, the effect of vole density on harrier movement, all the hen harrier parameters differed notably between the community model and the partial supplementary feeding model. The increase in the estimates for the effects of pipit density on harrier survival ($\alpha_1$) and movement ($\beta_1$) are likely a result of the lower estimates of pipit density. The change in the remaining harrier survival parameter, $\alpha_0$, is therefore not surprising, since it is highly correlated with $\alpha_1$ (Fig. 6.2). Interestingly, although still a low value, the effect of surviving harriers on movement into an area has more than doubled, possibly due to the higher credible bounds on the super-population estimates (Table 6.11).

Although the estimate for $\alpha_1$ has increased, the combination of low estimates for both pipit density and $\alpha_0$ in the community model has resulted in estimates of harrier survival ($\phi_t$) that do not follow the same pattern as the estimates of $\phi_t$ from the partial supplementary feeding model. The estimates from the community model start at a
Table 6.11: Estimates and 95% credible intervals for the hen harrier parameters for the partial supplementary feeding and community models.

peak in 1992, and then decline steadily until the end of the time series. In contrast, the survival estimates from the partial supplementary feeding model follow the observed pipit data, peaking in 1993 and 1994, before declining steadily to levels comparable to the community model. Additionally, the estimates of $\phi_t$ from the community model show more uncertainty throughout the whole time series (Table 6.3). The wider credible intervals are a result of the uncertainty around the estimates for pipit density, which plays a role in harrier survival (Eqn. 6.2).

The estimates for harrier movement into an area ($\eta_t$) are higher in the community model, for all but 1993. This single low value is a result of the estimates of both vole and pipit density being lower than the observed densities in that year. However, despite the difference in estimates, the pattern of movement is the same for both models, being greatest in years with high vole densities. Nonetheless, pipit density does play a role in harrier movement, as can be seen in 1994 where the higher estimate of $\beta_1$ increased the impact of pipit density on movement, resulting in a larger estimate of $\eta_t$ in 1994, despite the lower estimates of vole and pipit density in the community model. Even so, it is the higher estimates of vole density that are likely to be the root of the greater estimates of $\eta_t$ in the community model. Due to the uncertainty around the vole and pipit densities in the community model, the model’s estimates of $\eta_t$ also have wider credible intervals than are observed in the partial supplementary feeding model (Table 6.4).
6.9 Discussion

Understanding the interactions between species in a community is an important part of ecology. No species exists in complete isolation, and must therefore interact with the surrounding ecosystem. Ignoring these interactions, or assuming they are known, will lead to over-confidence in our understanding of community dynamics. This can, in turn, led to mis-management and detrimental effects for the entire community involved. The detailed modelling of community dynamics has been avoided due to lack of data and the complexity involved in attempting to model multiple species simultaneously. In this chapter I present a framework that allows for community modelling, even when data are limited. Additionally, despite the restrictions imposed by the available data, it is still possible to make biologically relevant inferences with regards to the responses of hen harriers to shifts in the density of their alternate prey.

The biggest impact of community modelling was in the increase in uncertainty around the parameter estimates associated with the meadow pipit and field vole. Much of the uncertainty in the model is due to the over-parameterising of the model by using eight years of pipit data to estimate the five parameters associated with the passerine’s density, as opposed to being a result of the inclusion of the population dynamics of additional species in the state-space model. A similar increase in uncertainty would be observed in a single-species model if the number of parameters to estimate was increased so noticeably with such limited data.

As well as the increase in uncertainty, there were dramatic changes in the estimated values of the hen harrier parameters associated with the meadow pipits ($\alpha_0, \alpha_1, \beta_1$). The different estimates could be a result of either the poorly fitting process model, or of the increased uncertainty around the pipit density estimates. However, given that the hen harrier parameter associated with voles ($\beta_0$) only showed an increase in uncertainty, this would imply that the changes in parameter values are a consequence of the different pipit population dynamics between the partial supplementary feeding and community models, as opposed to a result of fitting a more complex model with greater inherent uncertainty.
Despite the changes in the parameters and the increased uncertainty, the estimated parameters pertaining to red grouse population dynamics were unchanged by the inclusion of models for the meadow pipit and field vole. The estimates of red grouse density in the community model exhibited the same cycles and responses to hen harriers and supplementary feeding as observed in the partial supplementary feeding model (Chapter 5). However, the addition of vole and pipit dynamics resulted in a difference in the grouse-harrier interactions between the two models. In the community model, hen harriers were estimated to have a larger impact on the red grouse through consumption of otherwise successfully reared chicks. The increase in harrier predation on grouse chicks is due to the lower pipit densities, which alter the raptors’ MSFR. Hen harriers’ greater consumption of grouse chicks is not apparent in the estimated grouse dynamics due to lower estimates of *T. tenuis* burdens, which allow for more grouse chicks to be successfully reared. Therefore, the same number of grouse chicks reach the autumn territorial contest in the two models, regardless of the increased predation.

The reduced pipit densities used in the harriers’ MSFR are a result of the estimates’ dependency on the prior for pipit carrying capacity, which was deliberately set at a low value. The inability of the parameters to update from the prior and the model estimates’ poor fit to the observed data are a consequence of an inadequate process model for pipit dynamics. The use of the logistic equation for the pipit process model was reliant on a number of assumptions. A more realistic model of pipit behaviour including the direct effect of harrier predation would better capture the passerine’s dynamics.

The lack of a readily apparent impact of the vole and pipit models on the estimated grouse dynamics makes it difficult to make inferences about the direct effects of hen harrier alternative prey densities on the red grouse. However, because the reduction of pipit densities resulted in hen harriers having a larger impact on red grouse chicks than previously estimated, management plans that attempt to control harrier numbers by reducing the density of meadow pipits are likely to have the opposite effect,
actually increasing the predation pressure on red grouse. This has important implications, since it means that the indirect exclusion of harriers from an area by habitat manipulation may not be possible.

My model does not allow for similar indirect inferences to be made about the effect of field voles on harrier numbers. Nevertheless, in the one year where vole density was estimated to be lower than the observed density, there was a drop in harrier movement into an area. Therefore, the possibility remains that harrier immigration into an area may be halted by removing field voles as a prey source. However, a 30% reduction in vole density and an almost two-thirds reduction in pipit density succeeded in lowering immigration by only one harrier pair. As a result, it is questionable as to whether this management action would actually be successful in achieving its aims. Additionally, it is unclear what the influence of fewer voles would be on the harriers’ consumption of red grouse chicks.

While the models for meadow pipits and field voles impact the grouse-harrier dynamics, they provide little biological insight into these species directly. The logistic model for the pipit process model is a poor fit, and would be better replaced by a model capable of capturing the apparent fluctuations of the species. This could be accounted for with the presence of additional data, which would allow for more detailed models better describing the pipits’ true dynamics. The same is true for the field vole; without additional data it is not possible to fit a process model for this microtine species, so I can only model the uncertainty I know must exist around the observation, as opposed to making any inferences about their population processes.

The modelling of the community dynamics of the hen harrier and their prey provides useful insights into the species interactions, with only small increases in cost. The need for additional data on all the species involved in the system is the largest cost to fitting the community model. However, there is little additional computational expense, since there was no increase in run time from the partial supplementary feeding to the community model. Given the ability to obtain useful biological insights in spite of the data limitations in the grouse-harrier system and limited additional costs, there is no major impediment to community modelling becoming part of the
ecologists standard toolbox. The framework can only improve as field studies are designed with community modelling in mind and the amount of data available, for any species, increases. Until that point, the method will be limited by the amount of data available, especially if ecologists wish to avoid strong assumptions or dependence on prior distributions.
Chapter 7

Conclusions

In Chapter 2 I present state-space modelling, placing its use within an ecological context. I discuss the many advantages of the modelling approach, from the direct inclusion of uncertainty to the modularisation of the state process. The model framework can include the population dynamics of multiple species, but this aspect of state-space modelling had yet to be explored. I used the relationship between the hen harrier (*Circus cyaneus*) and the red grouse (*Lagopus lagopus scoticus*) as a case study to explore multi-species modelling in a state-space context. I started by developing single-species models for the two birds in Chapters 3 and 4, assuring myself that the models were capable of capturing the species’ dynamics. I then combined the two single-species models in Chapter 5, implementing multi-species state-space models for the first time. Finally, in Chapter 6 I further extended the multi-species interactions to include uncertainty around the estimates for the harriers’ alternate prey species, the meadow pipit (*Anthus pratensis*) and field vole (*Microtus agrestis*), addressing some of the questions with regards to the limits of the multi-species modelling approach.

The limits associated with multi-species state-space modelling are much the same as for single-species models: time and data. The complexity of models incorporating multiple species requires careful thought to ensure that the species are interacting on the correct spatial and temporal scale. The intricacy of such models increases the computational time needed to run the models. My models serve as an example, since
the simplest, the single-species hen harrier model (Chapter 3), takes only minutes to run. However, as the models grow more complex, the run time increases, taking hours for the grouse-only model and days for the interaction models to run the same number of iterations. Yet, there was a threshold to the run time, since the community model did not take noticeably longer to run than the two-species models. As well as requiring more time, multi-species models necessitate data on all the species of interest in the ecological community. Due to the attention paid to the grouse-harrier interactions over the years, information was available for all four species. However, even with a 25 year time series for the red grouse and eight years of data on the hen harrier, meadow pipit and field vole, there were still limitations in the amount of information available. This is due, in part, to the fact that the studies from which the data came were not designed to address the questions I proposed. Therefore, certain information, such as data on the parasite *Trichostrongylus tenuis* and aggressiveness in cock grouse, was missing all together. Other information was simply more limited, keeping me from being able to build a process model for field voles without using as many parameters as data points.

The twin problems of time and data are addressed in different ways. The run time for complex models will decrease with the increasing computational power of personal computers. Additionally, while I employed the free software WinBUGS for my model fitting, it is known to be slow to update the MCMC chain. It is possible to decrease the run time of the models by coding model-specific algorithms. However, depending on the skill of the individual, this may not provide an overall decrease in the time spent on the models. As for data limitations, this can be addressed in future field studies. Knowing that it is possible to fit multi-species models of ecological communities should result in studies being designed to investigate the relationships between different species of interest. This purpose-specific data will provide more information than data meant to answer different questions from other studies. No matter the species under consideration, the issues behind time and data limitations must be addressed.

As well as addressing the physical ability of state-space modelling to incorporate state process models for more than one species, I sought to address some of the
ecological questions surrounding the grouse-harrier debate. From the single-species harrier model in Chapter 3, I saw a high dependence on vole density with regards to harrier movement. This was surprising, yet serves to explain why harriers are found in young conifer plantations, which would not initially seem to be their natural habitat. In Chapter 4 I used the single-species grouse model to investigate the possible causes of the red grouse cycles; the territorial (intrinsic), parasite (extrinsic) or combined (both intrinsic and extrinsic) hypotheses. I found evidence to support the idea that it is a combination of the intrinsic and extrinsic hypotheses that drive the red grouse cycles, since this was the only model able to produce red grouse cycles under biologically realistic parameter values. This has implications for the management of grouse for shooting, since addressing just one of the mechanisms is unlikely to succeed in halting the cycles.

Once I combined the two single-species models into one multi-species interaction model for the hen harrier and red grouse in Chapter 5, I was able to make inferences about the impact of hen harrier predation on red grouse cycles. I found evidence that the hen harriers do, in fact suppress grouse cycles, and thus their density. While unsurprising, it is useful to have a theoretical model supporting the empirical data. I also investigated the impact of diversionary feeding on red grouse chick survival. I found that providing harrier nests with supplementary food was unsuccessful at significantly increasing grouse densities. While there was a slight increase in grouse density, mildly more pronounced in the spring than in the fall, the diversionary feeding of hen harriers failed to increase grouse densities to those predicted in the complete absence of the bird. However, there is some reason to believe that other factors were impacting grouse chick densities during the time period of the study (Redpath et al., 2001b), so it is possible that my model attributes too large a negative effect to the hen harrier.

Finally, in Chapter 6, the inclusion of meadow pipit and field vole dynamics to create a community state-space model allowed me to make some inferences with regards to the possible effect of habitat manipulation on the impact of harrier predation on red grouse chicks. My model suggests that, while reducing meadow pipit density will
decrease harrier survival, it will also increase the raptors’ impact on grouse chicks. Similar inferences could not be drawn about shifts in vole density, although there are some indications that decreased vole density would lead to less harrier immigration into an area. The impact of reduced vole density on grouse chick consumption was unclear, so this aspect of the model would benefit from further investigation if it is to be beneficial to the management of grouse moors.

Despite the limitations associated with the data, the models proved to be able to provide useful inferences about the predator-prey interactions of the hen harrier and the red grouse, meadow pipit and field vole. The models presented in this thesis allow inferences to be made about the behaviour of the species and how they interact with one another. This provides useful tools for management, as well as hypotheses that can be tested in the field. In turn, the new field studies will provide additional data, improving the future use of the models. Statistically, the cost of modelling multi-species and community dynamics was the need for data to inform the models, the increase run time of the models, and the increased uncertainty surrounding the parameter and state estimates. However, the approach is applicable to many areas of ecological modelling and should not be discounted due to fears of being too complex or difficult to fit.

There are a number of possible extensions to the work presented in this thesis. With regards to the hen harrier and red grouse, records of bag data for Langholm moor extend back into the 1940’s, but were not considered as a source of data in this thesis due to time limitations. If these records could be incorporated, it may be possible to avoid the issues involving the prior sensitivity of the initial states for spring and autumn grouse density (see Chap. 4), as well as reduce the level of uncertainty around the density estimates themselves. Furthermore, an model detailing the interactions between parasites and aggression could be developed as a possible mechanism for the cause of the cycles in red grouse. While the fitting of such a model would require data to be available on both *T. tenuis* burdens and aggressiveness in red grouse, progress on the conceptual model could be made in advance of such data becoming available. Additionally, more comprehensive models for the meadow pipits and field
voles could make better use of the available data. The models fit in Chapter 6 were chosen to display the ability of state-space modelling to account for community dynamics, as opposed to being the best possible fit to the data. This leaves room for further research, especially as data becomes available from new research taking place on Langholm moor. There is no reason to limit extensions to the work presented in this thesis to the hen harrier and red grouse. The ability of state-space modelling to account for multi-species interactions would be better supported by applying the model framework to other communities of interest for which suitable data exists. Some systems worth exploring may be the snowshoe hares (Lepus americanus) and lynx (Lynx lynx) in Canada, or wolves (Canis lupis) and elk (Cervus canadensis) in the United States. Fisheries science is likely to be another field in which appropriate data sets may be available for investigation.

This thesis had three main objectives, all of which were met over the course of my research. First, I sought to achieve the technical aim of building and fitting multi-species state-space models. This was achieved in Chapters 5 and 6, where I successfully fit two- and four-species state-space models to the available data. Secondly, I wished to investigate the behaviours of both the single-species and multi-species systems of interest. In Chapters 3 and 4, I looked at the individual behaviours of hen harriers and red grouse, respectively, examining the population dynamics of the species in isolation. In Chapters 5 and 6 I investigated predator-prey and community interactions, looking at the behaviour of the system as a whole, rather than as individual species. My third and final aim, given the models and an understanding of the system’s behaviour, was the applied goal of answering questions about grouse-harrier management. Chapters 3 - 6 all addressed some part of this issue, from single-species aspects, such as ways to halt grouse cycles at high densities, to a more community based approach, which suggests that supplementary feeding alone is not enough to mitigate the grouse-harrier conflict. Taken together, the achievement of these goals proves the applicability and accessible nature of the multi-species state-space framework.
Bibliography


and indirect effects of predation by hen harriers *Circus cyaneus* on trend in breeding birds on a Scottish grouse moor. *Ibis* **150** *(S1)*, 27–36.


