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**Human-predator-prey conflicts: the impact of  
predation on prey species and models of  
a raptor-gamebird system**

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## **Abstract**

The role of predators and their management have become key developmental themes in applied ecology. Issues that involve predators of conservation concern killing economically valuable prey species are widespread, can be highly controversial, and pose urgent challenges worldwide. This thesis investigates current understanding of human-predator-prey conflicts and the impact of predators on their prey. A clearer picture of the current state of knowledge may offer directions for future research and the type of information that could be used to assess and manage these types of conflicts effectively.

This thesis begins with a review and analysis of human-predator-prey conflicts, involving livestock and game species, and shows that there is little scientific evidence of whether or not predators have ecological or economic impacts on these prey. Poor or inconsistent data collection across a range of case studies constrained attempts to identify ecological and social factors which may be related to depredation events and the success or failure of management. The subsequent chapter specifically reviews evidence of impacts of birds of prey on gamebirds in Scotland, and also reveals that there are fundamental gaps in current understanding of these predator-prey interactions.

In the following chapters I develop a series of models to improve understanding of the interaction between hen harriers and red grouse, one of the most controversial human-wildlife issues in the UK today. This work represents an important step in research in this field: it is the first time dynamical models of this system have been developed; it also provides a comparison between hypotheses for red grouse cycles. Furthermore, it is the first time a multi-species functional response has been used to model consumption of prey by a predator. The results of this work suggest that hen harriers and red grouse can coexist across a range of densities, and that the presence of alternative prey can reduce hen harrier consumption of grouse chicks. It also highlights how differences in model structure and complexity can lead to very different predictions about the impact of a predator on its prey.

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## General Introduction

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### The role of predation

The effects of predation are amongst the most pervasive in ecology (Ormerod 2002). Predation is one of the key factors governing patterns in natural systems, influencing the morphological and behavioural traits of prey species (e.g. cryptic plumage, chemical defence, prey flocking to evade predators), as well as the abundance and distribution of populations (Sih et al. 1998). At the ecosystem level, predation has major effects on species co-existence, food-webs and processes such as trophic cascades (Ormerod 2002). An example of a predator-induced trophic cascade is the grey wolf-moose-fir system on Isle Royale in North America: moose populations are influenced by the number of wolves, and fir trees show depressed growth rates for periods when wolves were rare and moose abundant (McLaren & Peterson 1994). With predation playing such a varied and important role in ecosystems, it is clear why predators have been a longstanding and traditional focus of basic ecological research.

Increasingly however, the role of predation and the status of predators have become central themes in applied ecology. Ormerod (2002) suggests that today, key developmental themes in predation research stem from management problems and applied issues. These issues include instances where: the conservation status of predators is at risk from human activities; predators are valuable as bio-control agents or natural enemies in ecosystem management; natural or introduced predators are viewed negatively because of their effects on other organisms (e.g. disease transmission or extinction of prey species); or, predators are controversial because they are perceived by different groups as being either desirable or undesirable, for

instance, where predators of conservation concern may also be responsible for impacts on valuable resources, such as game and livestock. In this thesis I will concentrate on the last of these issues, examining current understanding of human-predator-prey conflicts, evidence of impacts of predators on economically valuable prey species, and the type of information that might be used as a basis for management. I will also address, more specifically, one of the most controversial and high profile predator-prey conflicts in the UK: hen harrier predation on red grouse gamebirds.

### **Human-predator-prey conflicts**

Conflicts involving humans, predators and prey are ubiquitous and arise primarily because of competition for shared, limited resources. Two major areas of conflict involve depredation of livestock (e.g. wolves, lynx and coyotes killing cattle and sheep) and depredation of game species (e.g. raptors killing gamebirds), and tend to be highly contentious because the resources concerned are of economic value and the predators involved are often high profile and legally protected (Thirgood et al. 2000). The basic tenet of these conflicts is that predators reduce the density of prey that would otherwise be available to humans.

In recent decades the frequency and severity of human-predator-prey conflicts appears to have increased (Treves & Karanth 2003), mostly as a result of increasing and expanding human populations and activities, and the loss and degradation of natural habitats. In some areas, increases in predators populations, as a result of successful conservation programs and protective legislation, have increased or renewed past

conflicts (Mishra 1997; Breitenmoser et al. 1998; Boitani 2000; Messmer 2000; Treves et al. 2002).

Increasingly, social and political mobilisations in support of nature protection and animal welfare are leading to the re-evaluation of past strategies of managing conflicts, such as predator eradication schemes (Harbo & Dean 1983; Breitenmoser 1998; Fox 2001). Today, preventing and mitigating human-predator-prey conflicts must necessarily be based on an improved understanding of predator and prey ecology and public acceptance of wildlife management (Treves & Karanth 2003).

### **Impacts of predators on their prey**

Predators can affect prey populations in a number of ways. At the extreme, predation by generalist predators on small prey populations could result in extinction (Coté & Sutherland 1995). The consequences of introductions of rats and cats to offshore islands are an example of this. Because of their isolation, many island bird species have no natural defences and are thus highly vulnerable to introduced predators. Such predators have been responsible for at least 40% of the extinctions of endemic island birds (Groombridge 1992). In some cases, predators may benefit prey populations. For instance, there is considerable empirical evidence that predators select diseased prey (Schaller 1972; Hudson et al. 1992; Moore et al. 2002; Packer et al. 2002). In doing so, they may reduce the opportunity for further infection, the vulnerability of diseased individuals to predation, and increase the average health of the prey population (Packer et al. 2002). Maintaining top predators could indirectly benefit prey by limiting populations of smaller predators, that is, prevent meso-predator

release (Palomares et al.1995; Estes 1996). Predation has been proposed to explain cycles in some prey species (Watson & Moss 1979). In Canada and Alaska, where snowshoe hares are strongly cyclic, lynx and foxes are thought to drive the ruffed grouse cycle by switching to grouse when hares decline (Newton 1998). Predators may also regulate prey populations if their attack is density-dependent (i.e. when the percentage of the prey population killed by predators increases as prey population density rises) (Crawley 1992). Regulation is the process whereby a population shows a tendency to return to its equilibrium (Sinclair & Pech 1996). However, of primary concern in human-predator-prey conflicts, is whether and how predators can limit their prey, limitation being the process which sets the equilibrium level of populations (Sinclair & Pech 1996).

Many predation studies have been reviewed by Sih et al. (1985), Caro and Fitzgibbon (1992) and Crawley (1992). In a review of predation and limitation in bird numbers, Newton (1998) concluded that, with the exception of some gamebirds and ducks, predation appeared to play a minor role in the direct limitation of breeding numbers. Indeed, even where predators kill a large proportion of a particular prey each year, they do not necessarily reduce breeding numbers in the following year (Newton 1998). A primary reason for this lack of effect is that predation mortality may be compensatory: individuals killed by predators might otherwise have died from other causes of death, such as disease or weather. Removing one predator species may not necessarily lead to increased prey numbers as there may be a compensatory increase in numbers lost to another predator species (Redpath & Thirgood 1997). Similarly, for many species, a surplus of non-breeding individuals may be available to replace members of the breeding population that are killed.

However, managers of game species are concerned not only with maintaining breeding stocks, but also with maximising post-breeding populations. Predation, or any other form of mortality which lowers this population, may reduce the number of stock available for harvesting, and invariably will be perceived by hunting stakeholders as detrimental to these interests. In long-term studies of grey and red-legged partridge, Potts (1980; 1986) demonstrated that both breeding and post-breeding numbers increased considerably when predator numbers were reduced. In a review of predator-removal studies on 13 gamebird and waterfowl species, Newton (1998) reported that 69% showed an increase in post-breeding numbers. A long-term study by Redpath and Thirgood (1997) suggested that predation by hen harriers and peregrine on red grouse was largely additive, reducing both breeding density and the post-breeding surplus of grouse available for shooting.

Generalist predators can have considerable impact on their prey if they are sustained at high densities by one prey species but also take significant numbers of alternative prey (prey switching), because this results in indirect competition between the prey species (Holt & Lawton 1994). An increase in predation on one prey species as a result of an increase in another, is also an example of indirect competition and of an aggregative response. For instance, Kenward (1986) found that an increase in rabbit numbers at a Swedish study site attracted more goshawks and resulted in greater pheasant losses. In Fennoscandia studies have shown that vole populations do not cycle in situations where other prey are abundant, because predators are also abundant in these situations (Angelstam et al. 1984, 1985; Hanski et al. 1991). Redpath and Thirgood (1999) suggested that high densities of voles and meadow pipits could sustain high densities of raptors, which could suppress grouse cycles and hold

numbers at low levels. Hence, in any study of predation, it is important that the predator and the main prey are not considered in isolation, but examined in the context of alternative prey species (Redpath & Thirgood 1997). The potential for predators to limit prey species may also be influenced by other factors, such as habitat structure or interactions with other predators.

### **Detecting the impact of predators on their prey**

Whilst some predators are known to have detrimental effects on certain prey species, the effects can be difficult to characterise or quantify. Data on many aspects of predator-prey conflicts are often sparse, in marked contrast with the wealth of anecdotal or subjective opinion on these issues. Where scientific evidence is speculative or weak, public perceptions can become the focal point of debates about wildlife risks and management. Slovic et al. (1979) suggested that inadequate evidence is also likely to be interpreted in a way that reinforces existing perceptions. Public perceptions are hugely affected by local culture, tradition, and fears about the consequences of an event, such as economical pressures. These can lead to large and persistent biases, and ineffective or misdirected management. Hence, qualitative or subjective information should be treated with caution. However, it should not be ignored, because conflict resolution depends upon the cooperation of a large set of stakeholders.

The clearest way of assessing impacts is through manipulative experiments. In these, predators are either removed from an area or their numbers reduced, and prey numbers are monitored and compared with numbers in a control area where no

manipulation takes place. Ideally, to avoid ambiguity, treatments should be carried out simultaneously and switched between experimental and control areas. Good examples of this type of work have been carried out for predators of gamebirds in England (Potts 1986; Tapper et al. 1991), Sweden (Marcstrom et al. 1988), and North America (Greenwood 1986).

Where experimental manipulation of a system is not feasible, for instance where a predator species is protected, correlative information obtained by monitoring changes in prey populations in different areas, with different, natural levels of predation (Reynolds & Tapper 1996; Redpath & Thirgood 1997) or during natural changes in predator density (e.g. Lindstrom et al. 1994) can provide valuable insights (Caughley & Gunn 1996).

Valuable insights can also be obtained by modelling natural systems (Burgman et al. 1993). Mathematical models can be used to yield general ecological principles or for more practical applications (May 1974; Burgman et al. 1993; Gillman & Hail 1997), such as predicting the future abundance of populations or the impact of predation on a prey population (Kingsland 1985). Modelling predator-prey interactions requires an understanding of the way predator numbers and diet vary in relation to changes in prey density; these are a predator's numerical and functional responses (Solomon 1949). When combined, these responses predict the proportion of the prey population removed at different prey densities (Boutin 1995). In practice, the exact forms of these responses are difficult to determine, because fluctuations in the abundance of alternative prey often distort the relationship (Newton 1993). Consequently, few studies have quantified functional and numerical responses of predators. In terms of

human-predator-prey conflicts, the hen harrier-red grouse system is one of the best studied systems, for which a functional and aggregative response for hen harriers has been measured. Whilst an aggregative response does not represent a substitute for a numerical response, it does provide some measure of how predator numbers may respond to changes in prey density. The ecology and population dynamics of both hen harriers and red grouse have been the subject of intensive and extensive research over the past several decades, and long-term quantitative data makes it an ideal system to model.

### **Thesis aims and structure**

The aim of this thesis is to synthesise current understanding of human-predator-prey conflicts involving livestock and game species, and identify the type of information that may be useful for informing decision-makers and conservation policy in the future. I examine evidence of the impact of predators on economically valuable prey species, with particular emphasis on raptor-gamebirds conflicts, because these are among the most controversial and important human-wildlife issues in the UK today. I focus on the conflict involving hen harrier predation on red grouse, and develop a series of models of the predator-prey interaction. These models are among the first to quantify the impact of predation on grouse populations, and may be used to sharpen discussion on management of the system. They also serve to highlight how model structure may influence predictions.

In Chapter 1, I assemble a range of case studies on conflicts involving predators, and livestock and game species. I review reasons why conflicts may arise and the types of

management strategies which are currently in use. I then identify the important ecological and social variables associated with these conflicts and examine what factors are related to the success or failure of management.

Chapter 2 is a study commissioned by Scotland's Moorland Forum in response to concerns from the Scottish Gamekeepers Association about the impact of a range of raptor species on different gamebirds in Scotland. I look at evidence of impacts of raptors on gamebird numbers, the economic implications of these impacts and the importance of other factors of mortality on these interests. Areas for future research are also identified.

In chapter 3, I focus on the hen harrier-red grouse conflict and present a simple dynamical model of the system using a generic model for red grouse cycles. I show how the model's predictions about the impact of hen harrier predation on grouse dynamics depend on the way in which the functional response of hen harriers to grouse is modelled, and consider the implications for management.

In chapter 4, I investigate the impact of hen harrier predation on red grouse using two mechanistic models for grouse dynamics. This work provides the first comparison between the intrinsic and extrinsic hypotheses for red grouse cycles and investigates the potential interaction between predation and cycle mechanisms. I compare the results of the mechanistic models with those of the phenomenological model in chapter 3.

Chapter 5 examines the robustness of predictions made by the three deterministic models (chapter 3 & 4), by incorporating uncertainty into the hen harrier's functional and aggregative responses.

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## CHAPTER 1

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### Human-Predator-Prey Conflicts: Ecological Correlates, Prey Losses and Patterns of Management

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#### Abstract

*Conflicts between humans and predators are the product of socio-economic and political landscapes and are particularly controversial because the resources concerned have economic value and the predators involved are high profile and often legally protected. The current literature was reviewed to provide information on ecological and social factors common to human-predator-prey conflicts. This information was used to examine whether losses to predators and patterns of investment in husbandry could be linked to these factors. This work showed that livestock losses to predators were low and were negatively associated with net primary productivity and predator home range sizes, but were not affected by predator density, methods of husbandry or human population density. While there was no effect of husbandry on losses, variation in husbandry was explained by net primary productivity, predator density and percentage of stock killed by predators. Inconsistent and sparse data across conflicts may have limited the ability to identify important factors and resolve patterns, and suggests that there is no reliable or consistent framework for assessing and managing human-predator conflicts that involve game and livestock species. This work highlights the type of data that could be very informative to management if collected across a range of cases and habitats.*

**Keywords:** Predation; Livestock; Game; Conflict; Multi-species.

## **Introduction**

Conflicts between humans and predators are the product of socio-economic and political landscapes. They arise primarily because of competition between people and predators for shared, limited resources. The conflicts can be particularly controversial when the resources concerned have economic value and the predators involved are legally protected (Thirgood et al. 2000a). Many predators kill prey species that humans hunt, harvest or farm for consumption or recreation and occasionally they may even kill people (Caro & Fitzgibbon 1992; Thirgood et al. 2000b; Sillero-Zubiri & Laurenson 2001). While humans and predators have co-existed for millennia, the frequency of conflicts has grown in recent decades, largely because of the exponential increase in human populations and the resultant expansion of human activities (Woodroffe 2000; Conover 2002).

Despite major advances in understanding predator-prey dynamics and competitive interactions in the last 20 years (Krebs 2001), attempts to integrate this knowledge into the emerging field of human-wildlife conflict management have been slow (Conover 2002). Historical attempts to manage conflicts with predators, often in the context of agriculture and game resources, have centred on an array of decisions biased towards social and economic values of stakeholders which, in many cases, have led to a range of negative effects on predator populations (Weber & Rabinowitz 1996; Estes et al. 1998; Berger et al. 2001). However, as conservation issues increasingly occupy socio-political agendas and changing attitudes favour non-lethal approaches to wildlife management, it is clear that a shift is required, from decisions based primarily on competing economic interests, to those based on the evolving interplay between the ecological system and the socio-political system.

Most animals live in species-rich communities, yet most human-predator conflicts are described in terms of direct effects arising from simple 1-predator -1-prey interactions. The perception has been that a single predator directly reduces the density of prey available to humans and this can be prevented by removing predators from the system (Yodzis 2001). This simplistic and intrinsically symmetric view of the predator-prey system is a simplification of the trophic interactions in complex ecosystems. As predator conflicts do occur in real ecological communities, this oversight may partially underpin the failure of predator control and the rapid and widespread decline and extinction of many predator species. Because population interactions, including predator control, propagate over long and short pathways through a food web, it may thus be useful to examine qualitative and quantitative ecological descriptors of the communities in which predator conflicts have arisen.

The primary objective of this chapter is to explore published information on human-predator-prey conflicts involving livestock and game species, assess the important ecological and social variables associated with these conflicts, and identify patterns which may be related to the success or failure of management. The chapter begins with a brief review of human-predator-prey conflicts involving livestock and game species. Then, for each documented conflict, I summarize a set of commonly cited, basic ecological descriptors of the habitats and wildlife and affiliated socio-economic factors. These include geographic location and habitat descriptors, the corresponding diversity in and structure of the managed and extended food web, and the magnitude or potential for direct and indirect effects in the community at issue. These are supplemented by basic social factors such as human population density, income level and management regime in the conflict. For the set of conflicts where these data are

available, I examine statistically the relationship between the ecological descriptors, the social descriptors and the extent of predator based losses and management strategies.

## **Overview of Conflicts**

Human-wildlife conflicts that centre on livestock and game species are two of the most well known predator control problems worldwide. The conflicts tend to be long running and are of considerable economic importance in many parts of the world. They share the common characteristic of a well defined regime of management of land, human and animal resources. Moreover, their geographic locations ensure that examples exist from a wide range of ecosystem types.

### *Predator-livestock conflicts*

Livestock predation by mammalian carnivores is one of the most frequent sources of conflict between humans and wildlife throughout the world (Mech 1981; Cozza et al. 1996; Kaczensky 1996; Pedersen 1999; Mazzoli 2002). Perceived economic losses due to livestock depredation often lead to retaliatory responses by agro-pastoralists. These include carnivore persecution, opposition to wildlife sanctuaries close to farms, or resistance to the reintroduction of extirpated predators to protected areas. In many cases these responses hinder the conservation of threatened species, and increasingly, contravene the public and political aims of large carnivore management.

Livestock-carnivore conflicts are exemplified by wolf predation of sheep in North America and Europe, lynx *Lynx lynx* killing domestic sheep and semi-domestic reindeer *Rangifer tarandus* in Scandinavia, jaguars *Panthera onca* taking cattle in Venezuela and snow leopards *Panthera uncia* preying on livestock in the Himalayas (Oli et al. 1994; Mech et al. 2000; Linnell et al. 2001). Conflicts arise for several reasons. First, the large home ranges of carnivores draw them into recurrent resource-competition with humans, a problem exacerbated by habitat loss and fragmentation. Second, human exploitation of natural herbivores may reduce the availability of wild prey to predators and can increase the likelihood of attacks on livestock (Yalden 1993; Mishra 1997; Sillero-Zubiri & Laurenson 2001). When opportunities arise, carnivores specialised for ungulate predation may readily kill domesticated breeds, many of which may have lost their anti-predator behaviour (Polisar 2003). Linnell et al. (1999) suggest that artificial conditions, where high densities of easily caught prey are accessible, present a special situation for carnivores, potentially fostering surplus killing of livestock. Human negligence plays an important role in many predation incidents, where losses could be prevented by greater vigilance during grazing, preventing animals from straying, and returning herds to enclosures in daylight. In parts of Europe, changes in animal husbandry now mean that domestic livestock are rarely guarded and are thus more vulnerable to predation (Sillero-Zubiri & Laurenson 2001).

To a large extent, differences in national management approaches to such conflicts have their origins in the socio-economic circumstances of countries. Where carnivore eradication campaigns have been terminated, approaches to managing conflicts often entail a combination of selective removal of individuals (either translocated or killed),

financial compensation and improvements to livestock husbandry (Linnell et al. 1997; Boitani 2000; Swenson 2000; Ormerod 2002). For instance, in Sweden, where there is strong commitment to predator conservation, compensation schemes have been established for farmers, together with the selective removal of individual predators. In many developing countries a lack of involvement by government and private agencies in human-wildlife conflicts reflects, in part, priorities in other income sectors. Low compensation rates and bureaucratic attention directed at other issues may discourage farmers from applying for such schemes. Often the only perceived solution to predator problems is extermination (Oli et al. 1994; Mishra 1997; Sekhar 1998).

### *Predator-game conflicts*

Game hunting plays an important socio-economic role in many countries around the world, generating income and providing employment and recreation, particularly in rural areas. Predator control to benefit game populations and allow harvesting has been practised for almost 200 years and has severely reduced the abundance and distribution of many mammalian and avian predator species (Reynolds & Tapper 1996). Nowadays, predator control is subject to legal restrictions in many parts of the world and, as a consequence, many predator species have been recovering. However, this recovery has renewed past conflicts, particularly where hunters perceive protected predators as a threat to declining game and the income it generates. Consequently, illegal persecution of predators with the aim of improving hunting bags has become a persistent and significant conservation problem.

One of the clearest current examples of a predator-game conflict exists in the UK where many gamekeepers and hunters believe increasing populations of hen harriers *Circus cyaneus* and peregrines *Falco peregrinus* have contributed to the decline of red grouse *Lagopus lagopus scoticus* populations, and thus threaten the viability of hunting estates (Thirgood et al. 2000b). This is also the case for raptors, pheasants *Phasianus colchicus* and grey partridge *Perdix perdix* in France, England and Sweden (Kenward 2001; Bro et al. In prep.), and red kites *Milvus milvus* and European rabbits *Oryctolagus cuniculus* in Spain (Villafuerte et al. 1998). Mammalian carnivores such as red fox *Vulpes vulpes*, Eurasian lynx *Lynx lynx* and wolverines *Gulo gulo*, also come into conflict with European hunters (Palomares et al. 1995; Linnell et al. 2001). In North America, the protection and recolonisation of the grey wolf *Canis lupus* has raised concerns amongst hunters about the effects of predation on hunting quarry such as elk *Cervis elaphus*, white-tailed deer *Odocoileus virginianus* and moose *Alces alces* (Kunkel & Pletscher 1999). Hunting and conservation stakeholders generally agree that predators are not responsible for the long-term declines observed for many game species. Rather, the perception is that predators may contribute to population suppression or non-recovery in situations where game populations are already limited by other factors such as habitat deterioration, poor food supply, disease, and over hunting (Vinuela & Arroyo 2002).

Presently, the most common game management practises include legal and illegal predator control, habitat modification and releases of farm-reared game. Proposed solutions to conflicts with predators include diversionary feeding, translocation, predator quotas and the encouragement of intraguild predation (Thirgood et al. 2000b). Although they are commonly identified as management options in the

conservation literature, there have been few experimental studies of their effectiveness. For instance, we know of only one case (see Redpath et al. 2001) where diversionary feeding has been tested. As such, effective, long-term solutions to predator-game conflicts remain elusive.

## Methods

We surveyed the management, conservation and ecology literature relevant to predator control, game and livestock management around the world. This involved an extensive search of web databases including the ISI Web of Science, European Environment Agency, Natural History Museum, Center for Sustainability and the Global Environment, Conservation International, USA Department of Agriculture, The World Bank Group, CIESIN and the United Nations Environment Programme.

For each study located, I attempted to document the following ecological data: latitude, biome, net primary productivity (NPP), plant community richness, predator home range size, predator density, predator-prey ratio, prey availability, % prey taken by predator, predator feeding behaviour (generalist/specialist), and the form of the predator's functional responses. Latitude, biome, NPP and plant community richness provided a large scale description of the study sites and habitats. Information on the predator and prey-predator ratio provided data on the specific predator and was used as a proxy for the structure and diversity of the food webs, as more detailed information was never reported.

I also documented human dimension data including: human population density, per capita Gross National Income (GNI), level of husbandry and predator conservation status. For NPP, human population density and GNI, regional means were taken from the following databases; SAGE, Atlas of the Biosphere, (2002); CIESIN, Gridded Population of the World (GPW) Version 2 (2000); The World Bank Group, World Bank Atlas (2001). For plant community richness ( $\alpha$ -diversity) I assigned mean

values by biome type given in Scheiner and Rey-Banayas (1994). The conservation status of predators was taken from the IUCN Redlist (2000) database. I obtained average male predator home range sizes from each case-study, using male home range sizes because confirmed livestock killers are commonly males (Linnell et al.1999). Husbandry regimes were divided into 5 categories: 1) no husbandry, 2) low intensity shepherding (<1/week), 3) fenced pasture, 4) high intensity shepherding (>1/week) and night enclosure, 5) fenced pasture, checking and enclosures. Predator control was present among all studies and was either indiscriminate (all predators hunted or trapped) or selective (only nuisance or target individuals removed). Percentage of prey taken was defined as the annual percentage of total livestock/game killed by a specific predator species in the study area.

The variables I chose are the most consistent set of common variables presented in the literature. Moreover, they are considered by many to be classical metrics of ecosystem description, are among the basic pieces of biological information collected on predators and are frequently identified as factors which may influence predator-prey interactions (Begon et al. 1996). For instance, small home range size may indicate high predator density and thus a high frequency of depredation. The opposite may also be true with large home ranges leading to persistent contact with certain patches of prey. Prey losses may be lower in areas with high primary productivity and community richness, where the diversity and abundance of prey is high (Meriggi & Lovari 1996). High human population density is likely to correlate with low predator density and thus fewer prey losses (Woodroffe 2000), and we might expect prey losses to decline where animal husbandry is intensive.

While many studies had some of this information, only 28 provided information on more than two of these factors. If they did not present more than two factors, they were not used in the database since they would not be useful in even the most basic analysis. Despite a large body of literature on human-predator conflicts, much of it fails to present ecological and socio-economic information specific to individual conflicts. Subsequently, I investigated the 28 studies with sufficient data for the relationship between the percentage of prey taken by predators and different explanatory variables using multiple regression with stepwise elimination of insignificant terms. An arcsine square root transformation was applied to the response variable, percentage of prey taken, to meet normality assumptions. I used forwards stepwise regression ( $\alpha$  to enter 0.25) beginning with a base model with NPP and home range in it to analyse percentage taken. I used backwards stepwise regression to identify which explanatory variables were related to the level of husbandry ( $\alpha$  to remove 0.1). All analyses were carried out using MINITAB Version 13.1.

## Results

### General Study Details

The total latitudinal range of case studies was 34°S-67°N with 8 tropical or subtropical (0-35°), 13 temperate (36-55°) and 7 boreal (56-67°) sites. Studies were conducted on all continents except Antarctica: North America (4), South America (2), Eurasia (17), Africa (4) and, Australia (1) (Table 1, see also Appendix 1.1). Predator-livestock conflicts dominated the literature, with a strong European bias. Several studies focused on lynx predation of sheep and reindeer. Most predator-game literature also came from Europe, with a strong emphasis on gamebirds. From 28 case studies we counted 19 different focal predator species (those perceived to be at the centre of the conflicts), 11 of which were included in the IUCN global redlist as either vulnerable, endangered or near-threatened. According to the IUCN redlist, major threats to the conservation status of these predators' are, persecution, declining prey base and habitat loss. Not included in the redlist are the grey wolf, brown bear *Ursus arctos* and hen harrier. However, all are listed in European Commission conservation directives as species requiring high priority conservation action by member states. Almost all the focal predators received some level of legal protection. However, persecution was observed in most cases. All focal predators were native with the exception of introduced red foxes in Australia.

**Table 1.**  
Summary of human-predator-prey case studies.

<i>Case study</i>	<i>Latitude</i>	<i>Predator species</i>	<i>Prey species</i>
<i>Predators-livestock</i>			
French Jura <sup>a</sup>	46 50N 5 80E	<b>Lynx</b> , dog.	Wild: Chamois, roe deer. Livestock: goats, sheep.
Swiss Alps <sup>b</sup>	46 40N 7 40E	<b>Lynx</b> , red fox, golden eagle.	Wild: roe deer, chamois, red deer, brown and white hare, marmot, black grouse, red squirrel, ibex. Livestock: sheep, goat.
Norway <sup>c</sup> Sweden <sup>c</sup>	61 30 N 11W 67 N	<b>Lynx</b> , snow fox red fox, wolf, wolverine, brown bear, golden eagle.	Wild: roe deer, mountain hare, red fox, black grouse, capercaillie, ptarmigan, hazel grouse. Livestock-sheep, semi-domestic reindeer.
Sweden <sup>d</sup> Norway <sup>d</sup>	67 N 17 40E 64 30 N	<b>Lynx</b> , wolf, brown bear, wolverine.	Wild: red fox, moose, mountain hare, capercaillie, black grouse, hazel grouse, willow grouse, ptarmigan. Livestock: semi-domestic reindeer.
CA, US <sup>e</sup>	39N 123 W	<b>Coyote</b> , golden eagle, mountain lion, black bear.	Wild: black-tailed deer, elk, brush rabbit, squirrel, dusky-footed wood rat, pocket gopher, California vole. Livestock: sheep.
Norway <sup>f</sup>	63N 10E	<b>Wolverine</b> , red fox.	Wild: moose, red deer, roe deer, hares, ptarmigan, rodents, wild reindeer. Livestock: sheep.
Minnesota, US <sup>g</sup>	46N 94W	<b>Wolf</b> , coyote.	Wild: elk, moose, bison, rabbit, small mammals. Livestock: cattle.
Wisconsin, US <sup>h</sup>	46N 92W	<b>Wolf</b> , coyote.	Wild: elk, moose, bison, rabbit, small mammals. Livestock: cattle.
Abruzzo, Italy <sup>i</sup>	42N 13 50E	<b>Wolf</b> , brown bear.	Wild: boar, roe deer, red deer, chamois, fallow deer. Livestock: cattle sheep, goat, horse.
Norway <sup>j</sup>	62N 12E	<b>Brown bear</b> , lynx, wolverine.	Wild: roe deer, moose, reindeer, hare, rodent, red fox, ptarmigan, black grouse. Livestock: sheep.

Southern Brazil <sup>k</sup>	26 50S 49W	<b>Mountain lion.</b>	Wild: roe deer, brocket deer, agoutis, capybara, paca, peccary, armadillo. Livestock: goat, sheep, cattle.
Kibber Reserve Trans-Himalaya, India <sup>l</sup>	32 05N 78 E	<b>Snow leopard, Tibetan wolf.</b>	Wild: blue sheep, ibex, red fox, pale weasel, stone marten, Himalayan mouse hare. Livestock: sheep, cattle, goat.
Annapurna Reserve, Nepal <sup>m</sup>	29N 83E	<b>Snow leopard.</b>	Wild: blue sheep, Himalayan marmot, Royles pika, stone marten, Tibetan snowcock, Himalayan snowcock. Livestock: yak, cattle, goat, horse, sheep.
Gokwe Zimbabwe <sup>n</sup>	18 10S 28 15E	<b>Baboon, lion, leopard, spotted hyena, bateleur, martial eagle.</b>	Plants, fruits, goats, sheep Wild: springbok, kudu reedbok, klipspringer, warthog, duiker, bushbuk, impala, zebra, roan, sable. Livestock: cattle, donkey, goats, sheep.
Nyamandlovu region, Zimbabwe <sup>o</sup>	19S 28E	<b>Painted hunting dog, hyena, feral dog, leopard.</b>	Wild: kudu, duiker, impala, eland, bushpig, warthog. Livestock: cattle.
Laikipia district Kenya <sup>p</sup>	1N 36E	<b>Leopards, lions, spotted hyena, cheetah.</b>	Wild: klipspringer, duiker, impala, rock hyrax, rodents. Livestock: sheep, cattle.
Llanos region Venezuela <sup>q</sup>	8N 70W	<b>Leopard, puma</b>	Wild: capybara, armadillo, spectacled caiman, fresh water turtle, tercay, collared peccary, white-lipped peccary, feral pig, white-tailed deer, Llanos sideneck. Livestock: cattle, horse, donkey, dog.
Bresse, France <sup>r</sup>	46-47N 5-6E	<b>Goshawk, fox, buzzard, dog, crow, mustelids.</b>	Wild: rodents, rabbits, voles, carrion. Livestock-poultry.
Golan Heights, Israel <sup>s</sup>	32N 35 50E	<b>Jackal, wolf, red fox, feral dog.</b>	Wild: gazelle, rodent, mustelids, lagomorphs, wild boar, rock hyrax, wild cat, jungle cat, griffon vulture.
Sth-Est Australia <sup>t</sup>	34S 148E	<b>Fox, feral pig.</b>	Wild: rabbit, quokka, bandicoot, insects rodents, carrion. Livestock: sheep.
<i>Predators-Game</i>			
Montana, US <sup>u</sup>	48N 115W	<b>Wolf, cougar, coyote, black bear.</b>	Wild: white-tailed deer, elk, moose bison, rabbit, small mammals. Game: white-tailed deer, elk, moose.
Pello, Finland <sup>v</sup>	66 52N 24 40E	<b>Red fox, stoat, raccoon dog, pine marten.</b>	Wild: black grouse, capercaillie, hazel grouse, willow grouse, small mammals. Game: black grouse.

Langholm, Sth Scotland <sup>w</sup>	55 30N 3W	<b>Hen harrier</b> , peregrine, red fox.	Wild: field vole, rabbit, meadow pipits, red grouse, rodents, skylark. Game: red grouse.
Dorset, Sth England <sup>x</sup>	50 70N 2-3W	<b>Buzzard</b> , red fox, tawny owl, sparrow hawk.	Wild: rabbit, passerine, carrion, small mammals, pigeon. Game: pheasant.
Spain <sup>y</sup>	39-43N 4-6W	<b>Red kite</b> , eagle owl, Bonelli's eagle, Golden eagle, Imperial eagle, Black vulture, wild cat, red fox, lynx, mongoose,	Wild: rabbit, carrion, reptiles, rodent, red legged partridge. Game: rabbit.
Central Nth France <sup>z</sup>	49-50N 2-4E	<b>Hen harrier</b> , red fox, crow, stone marten, magpie.	Wild: vole, rabbit, passerines, grey partridge. Game: grey partridge.

Bold lettering indicates the focal predator species in each case study.

<sup>a</sup> Stahl et al. (2001a), Stahl et al. (2001 b), Stahl et al. (2002); <sup>b</sup> Breitenmoser & Haller (1993); <sup>c</sup> Linnell et al. (2001), Odden et al. (2002); <sup>d</sup> Linnell et al. (2001), Pedersen et al. (1999); <sup>e</sup> Blewjas et al. (2002), Sacks & Neale (2002), Sacks et al. (1999), Conner et al. (1998); <sup>f</sup> Landa et al. (1999), Landa et al. (1997); <sup>g</sup> Treves et al. (2002), Mech et al. (2000); <sup>h</sup> Treves et al. (2002); <sup>i</sup> Cozza et al. (1996), Meriggi & Lovari (1996); <sup>j</sup> Dahle et al. (1998), Sagor et al. (1997); <sup>k</sup> Mazzoli et al. (2002); <sup>l</sup> Mishra (1997); <sup>m</sup> Oli et al. (1994), Jackson & Ahlborn (1989); <sup>n</sup> Butler (2000); <sup>o</sup> Rasmussen (1999); <sup>p</sup> Mizutani (1999); <sup>q</sup> Polisar et al. (2003), Hoogesteijn et al. (1993); <sup>r</sup> Stahl et al. (2002); <sup>s</sup> Yom Tov et al. (1995); <sup>t</sup> Greentree et al. (2000), Pech & Hood (1998); <sup>u</sup> Kunkel & Pletscher (1999); <sup>v</sup> Kaubala et al. (2000); <sup>w</sup> Redpath et al. (2002), Redpath & Thirgood (1997); <sup>x</sup> Kenward et al. (2001); <sup>y</sup> Villafuerte et al. (1998), Delibes & Hiraldo (1981); <sup>z</sup> Bro et al. (2003, unpubl.), Tombal (1982).

In each case study, the system was characterised by multiple predator and multiple prey species. All the focal predators were generalists, such that their diet consisted of a wide range of prey species. With the exception of lynx and semi-domestic reindeer (Norway), livestock and game were never the main prey. In all cases, livestock and game suffered predation from more than one species of predator. Many studies (57%) presented data on the timing of predation events, which usually coincided with predator and prey breeding periods. The percentage of total stock killed was the only consistent quantitative measure of the effect of predation, but only 3 out of 7 game studies provided this information.

### **Ecological correlates of conflicts**

This chapter found that predators were reported to kill 0.02-2.6% of livestock and up to 9% of game species annually. One third of the variance in the percentage of prey taken by predators was explained by NPP and predator home range (HR) (% Taken =  $0.25 - 0.00011 * HR - 0.31 * NPP$ ,  $r^2 = 33\%$ ). Predator density, latitude, husbandry level, human population density, species richness or biome were not included in the model. Our final model with only NPP and home range suggested a significant negative trend between percentage taken and home range ( $F_{1,14} = 5.8$ ,  $P=0.033$ ) and a negative trend with NPP ( $F_{1,14} = 3.78$ ,  $P=0.076$ ). Although NPP was only marginally significant, removing this term resulted in a non-significant coefficient for HR. The interaction between these two variables was non-significant. Variation in level of husbandry was significantly associated with NPP, predator density and the percentage of prey lost ( $F_{1,13} = 22.71$ ,  $P = 0.00$ ;  $F_{1,13} = 12.69$ ,  $P = 0.00$ ;  $F_{1,13} = 3.47$ ,  $P = 0.09$ ;  $r^2 = 77\%$ ). The level of husbandry increased with NPP and predator density, but decreased as

percentage of prey lost increased. Percentage of prey lost was marginally significant, however this term explained a significant amount of variation in the response variable.

## **Discussion**

One of the most common requests in the conservation management literature is for more information on the ecological details of a particular problem (Hoogesteijn et al. 1993; Linnell et al. 2001; Ormerod 2002). This is true across a wide range of conservation issues, from endangered and invasive species to predator control and classic natural resource management. In this study, I focused on identifying and analysing the quantity, quality and importance of ecological information relating to the control of predators of managed game species and livestock. This rather small subset of conservation problems nonetheless receives a large amount of attention because of the high profile of predators and the importance of livestock or game species to local economies.

Predators have been a long-standing and traditional focus of basic ecological research. Myriad studies have examined their population dynamics and behavioural ecology. Most research however, has been conducted in areas without livestock or game species, and consequently there is great variability in the type, quality and quantity of data relating to these problems. Hence, the data I was able to collate was very coarse and this made it difficult to determine quantitative relationships between ecological and social variables and the extent of predation. Thus, there may not be enough reliable data to detect patterns, even if they do exist. Furthermore, there appears to be no consistent approach to data collection and management in these conflicts. The lack of consistency is surprising, given the long history of human-predator conflicts. Then again, it is only recently that there has been a requirement to examine the ecological context of human-predator conflicts. In the past, little attention was paid to ecological

considerations because the primary goal of wildlife management was to fulfil social and economic requirements (Reynolds & Tapper 1996).

One of the most basic questions stakeholders need to ask about a particular conflict is, ‘are predators really a problem?’ and, if so, ‘will predator reductions improve the situation?’ Ecologists can help to answer this by quantifying the impact of predation. This must go beyond simply identifying the percentages lost. At a given point in time, the functional response represents the proportion of prey taken per predator, given prey availability. Over time, this consumption must be converted into total losses to the prey population and into predator numbers, the numerical response. These two “responses” and the intrinsic biology of the species define the predator-prey interaction. For any number of reasons, including the difficulty in collecting this type of data, we were only able to find information on percentages of prey lost to predators and almost no data on prey availability. Rarely were these data presented together and seldom in the context of the predator- prey interaction theory.

This study found that predators killed between 0.02 and 2.6% of livestock and up to 9% of game species annually and that around one third of the variation in this mortality was explained by predator home range and NPP. Losses decreased with both increasing NPP and predator home range. The multiple regression model indicated that NPP and home range have additive effects on losses, despite home range size generally decreasing with increasing NPP. We might tentatively conclude then that the effect of home range has something to do with either predator density or predator habitat requirements that are disassociated with primary productivity.

However, the coarse nature of the data and the number of ecological details subsumed by NPP and home range limit the ability to speculate further (e.g., Rosenzweig 1995).

This work failed to find a significant relationship between factors other than NPP and home range and percentage losses. Predator density is one missing variable that may be expected to explain variance given its inverse relationship to home range. However, it did not in these data. On one hand, we may be facing a statistical power issue given the low reporting rate of these pieces of information. Yet for the same sample sizes of other variables, we do get a significant effect. An alternative explanation may be that predator density may be a measure at a scale that is less significant to the data on losses than NPP and home range (while it is significant to the explanation of husbandry – see below). Another reason for the particular subset of variables may be the inconsistent method of data collection and reporting among these conflicts. Some countries (e.g., Norway and Sweden) have clearly established methodologies for validating predation losses. However, many studies relied on questionnaires, which provide subjective, and sometimes misleading, information. For instance, there is a recognised tendency for farmers to deliberately inflate losses, or fail to distinguish between proximate and ultimate causes (Conner et al. 1988; Wagner 1988; Oli et al. 1994; Treves et al. 2002; Polisar et al. 2003). Hence, information from this source must be viewed with caution.

In the literature we surveyed, prey availability was commonly identified as an important factor determining levels of conflict (Jorgenson & Redford 1993; Cozza et al. 1996; Meriggi & Lovari 1996; Dahle et al. 1998; Kunkel & Pletscher 1999; Mizutani 1999; Redpath & Thirgood 1999). Theoretically, alternative prey may either

dilute or exacerbate the effects of a predator on the primary prey (Wootton 1994). Kunkel and Pletscher (1999) suggested that the presence of deer may divert wolf predation from moose, allowing moose numbers to increase. Polisar et al. (2003) noted that high depredation on cattle by pumas (*Puma concolor*) occurred in areas where there was a low abundance of natural prey. Asseburg et al. (in review) also suggest that the availability of alternative prey may significantly reduce hen harrier consumption of red grouse. While these papers note the importance of prey availability, the numerical data necessary for inclusion in this analyses were rarely available. Furthermore, prey availability is influenced by habitat features (e.g., forest composition, topography, habitat interspersion), yet few studies provide more than a general description of study area.

Efforts to manage depredation invariably concentrate on attempts to control predator abundance, but the analysis showed that losses appear to be unrelated to predator density. Landa et al. (1999) found that livestock losses to wolverines were a function of prey availability, rather than the abundance of predators. On a ranch in Kenya, Mizutani (1999) found that high densities of leopards (*Panthera pardus*) have less of an impact on livestock than might be expected. Knowlton (1999) suggested coyote (*Canis latrans*) abundance is a poor predictor of sheep losses if livestock attacks involve only a few problem individuals. Conner et al. (1998) reported that kills of sheep by coyotes in California were not correlated with the number of coyotes, and Greentree et al. (2000) demonstrated that fox control had little effect on lamb production. Several studies (Bjorge & Gunson 1985; Reynolds et al. 1993; Sagor et al. 1997; Landa et al. 1999; Stahl et al. 2001; Blejwas et al. 2002) have shown that the removal of predators results in only a short-term reduction in prey losses, because the

same or other predator species rapidly re-establish themselves. Most of the focal predators in our case studies are considered to be endangered, at least on a regional basis, so that reducing their numbers is likely to conflict with other conservation management objectives.

Data from the reviewed studies suggest that whilst losses to predators are typically only a small percentage of livestock or game numbers, in some cases the economic consequences of these losses may be very significant in a local context. For instance, in villages in Nepal, loss of 2.6% of livestock holdings represented a loss of one quarter of the average annual per capita income (Oli et al. 1994). Yom-Tov et al. (1995) reached a similar conclusion about the costs of cattle predation by golden jackals (*Canis aureus*) in Israel. However, few studies present economic losses due to predation. Taking into account low levels of depredation and the fact that damage compensation is paid in many countries, conflicts may sometimes be considered a psychological rather than an economic problem (Breitenmoser et al. 1998).

Other causes of mortality such as disease, poor nutrition, injuries and poaching, can be far more serious than losses to predators. Mizutani (1999) found that livestock losses to carnivores on a ranch in Kenya were less than half those for disease. In Zimbabwe, Rasmussen (1999) found that poor management accounted for 43% of stock losses, disease 23% , and painted hunting dogs (*Lycaon pictus*) less than 2%. Crawley (1992) and Hudson et al. (1992) have suggested that predators may actually benefit prey populations by removing disproportionately large numbers of prey infected with parasites. Indeed, predation may mask poor dietary or health management of livestock (Cozza et al. 1996). The presence of predators sometimes

provides a convenient excuse for herdsmen to explain missing or stolen stock (Hoogesteijn et al. 1993; Rasmussen 1999). Yodzis (2001) suggests that attention invariably falls to predators because they are highly visible, and are frequently perceived as a nuisance.

Poor husbandry is often invoked to explain high levels of depredation (Linnell et al. 1996; Meriggi & Lovari 1996; Ciucci & Boitani 1998). However, the analyses found that the style of husbandry does not appear to affect losses due to predators in the studies we examined. Despite this, there is some variability in husbandry investment. The model showed that husbandry increases with increasing NPP and predator density. NPP's influence on husbandry levels may be linked to farming techniques (traditional vs. industrial), variation in quantity or quality of natural resources and variation in levels of industrial development and thus economic resources (e.g., Sharma & Singh 1997; Sivakumar & Valentin 1997; Cardoch et al 2002). It is understandable that where predator densities are high, stakeholders perceive an elevated risk to stock welfare and adapt protective measures accordingly (even though evidence suggests stock losses are not associated with predator density).

Predator conflicts are routinely described as a single, pairwise, predator-prey interaction, when in reality they are part of a complex ecological and economic community. The complex interactions arising from multi-species assemblages can have enormous practical implications for the effectiveness of different management systems (Yodzis 2000). Consequently, there has been a shift in emphasis in ecology and conservation from single-species to multi-species and ecosystem management in

recent years (Yodzis 1994; Palomares et al. 1995; Sih et al. 1998; Kunkel & Pletscher 1999; Yodzis 2000; Murdoch et al. 2002).

All of the conflicts I examined occur in multi-species communities. For instance, in Zimbabwe, cattle are killed by painted hunting dogs, hyenas (*Crocuta crocuta*) and leopards (Rasmussen 1999). In Spain, rabbits are a staple prey for at least 29 species of predators (Delibes & Hiraldo 1981). The focal predators were all generalists, and livestock and game were almost never the primary prey. Few studies, however, investigated any interaction other than that between the focal predator and focal prey. Moreover, they rarely provided any information on the attributes of the communities that are agreed on as important in the literature. Finally, the data available rarely provide insight into the functional and numerical responses of prey and predator, necessary for truly understanding the dynamics of these systems. As a result, little is known about how alternative prey and multiple predators affect predator-livestock/game systems.

There appears to be widespread agreement in the literature about the important factors which affect the extent and management of predation on livestock and game species. However, this chapter reveals that most studies of human-predator-prey conflicts rarely examine more than one particular factor. Consequently, this attempt to quantify important factors and general patterns between ecological and social variables and existing conflicts, was constrained. Clearly, ecological and social assessments of conflicts are still in their infancy, which explains why there is no consistent or reliable framework for managing depredation problems. This work presents an initial approach for examining and assessing conflicts in terms of ecological and social data

and highlights the type of data that could be very informative if collected across a range of cases and habitats.

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## Appendix 1.1

Ecological and human dimensions data for predator-prey case studies.

Case study	Latitude	Generalist /Specialist to prey	Ratio of predator (km <sup>2</sup> )	Predator home range (kg-C/m2/yr)	NPP *	Community Richness §	Human population density (km <sup>2</sup> )¶	GNI (US\$) ♂	IUCN predator status	Husbandry level status ¥	% prey taken	Predator functional response	Predator density (km <sup>2</sup> )
<i>Predator-livestock conflicts</i>													
Lynx & sheep <sup>a</sup>	46 50	G	0.22	364	0.4	38.99	50-100	high	V	3	0.26	-	0.01
Lynx & sheep <sup>b</sup>	46 40	G	0.27	293	0.4	38.99	50-100	high	V	1	-	-	0.01
Lynx & sheep <sup>c</sup>	61 30	G	0.45	1000	0.2	23.01	1-5	high	V	1	0.30	-	0.003
Lynx & sheep <sup>c</sup>	67 00	G	0.45	1000	0.2	23.01	1-5	high	V	3	0.02	-	0.003
Lynx & semi-domestic reindeer <sup>d</sup>	67 00	G	0.47	1000	0.2	23.01	1-5	high	V	2	1.0	-	0.003
Lynx & semi-domestic reindeer <sup>d</sup>	64 00	G	0.47	1000	0.2	23.01	1-5	high	V	1	2.3	-	0.003
Coyote & sheep <sup>e</sup>	39 00	G	0.60	-	0.5	38.99	5-25	high	NL	5	2.5	-	0.6
Wolverine & sheep <sup>f</sup>	63 00	G	0.22	800	0.2	23.01	5-25	high	V	1	0.6	-	0.003
Wolf & cattle <sup>g</sup>	46 00	G	0.33	-	0.5	38.99	5-25	high	NL	5	-	-	0.02
Wolf & cattle <sup>h</sup>	46 00	G	0.33	136	0.5	38.99	5-25	high	NL	5	0.07	-	-
Brown bear & Sheep <sup>i</sup>	62 00	G	0.43	1450	0.2	23.01	1-5	high	NL	1	0.13	-	-
Wolf & sheep <sup>j</sup>	42 00	G	0.25	130	0.4	38.99	50-100	high	NL	4	-	-	-
Mountain lion & sheep/goats <sup>k</sup>	26 50	G	0.25	-	0.4	37.33	50-100	upper-mid	NT	4	-	-	0.07
Snow leopard & cattle <sup>l</sup>	32 05	G	0.20	-	0.3	33.14	5-25	low	E	4	-	-	-
Snow leopard & cattle <sup>m</sup>	29 00	G	0.20	25.5	0.4	33.14	5-25	low	E	4	2.6	-	-
Baboon & goats <sup>n</sup>	18 10	G	0.46	10	0.4	33.14	25-50	low	NL	4	2.6	-	-
Lions & cattle <sup>n</sup>	18 10	G	0.46	200	0.4	33.14	25-50	low	V	4	1.7	-	-

Appendix (continued).

Case study	Latitude	Generalist /Specialist	Ratio of predator to prey	Predator home range (km <sup>2</sup> )	NPP* (kg-C/m <sup>2</sup> /yr)	Community Richness §	Human population density (km <sup>2</sup> ) ¶	GNI (US\$) □	IUCN predator status ¥	Husbandry level ¢	Husbandry % prey taken	Predator functional response	Predator density (km <sup>2</sup> )
Leopard & sheep <sup>n</sup>	18 10	G	0.46	15	0.4	33.14	25-50	low	E	4	0.6	-	-
Painted hunting dog & cattle <sup>o</sup>	19 00	G	0.50	660	0.4	33.14	25-50	low	E	4	0.17	-	0.019
Leopard & cattle <sup>p</sup>	01 00	G	0.10	52.8	0.6	33.14	25-50	low	E	4	0.20	-	-
Jaguar & cattle <sup>q</sup>	18 10	G	0.15	33.4	0.6	37.33	5-25	upper-mid	NT	2	1.3	-	-
Fox & poultry <sup>r</sup>	46 50	G	1.20	-	0.4	23.69	5-25	high	NL	4	0.48	-	2.5
Jackal & cattle <sup>s</sup>	32 00	G	0.36	-	0.2	33.14	250-500	low-mid	NL	4	1.7	-	1.69
Fox & sheep <sup>t</sup>	34 00	G	0.40	6	0.3	23.69	1-5	high	NL	3	-	-	0.07
<i>Predator-game conflicts</i>													
Cougar & deer <sup>u</sup>	48 00	G	0.67	-	0.3	38.99	5-25	high	NT	1	9.09	-	0.01
Wolf & deer <sup>v</sup>	48 00	G	0.67	-	0.3	38.99	5-25	high	NL	1	6.07	-	-
Fox & grouse <sup>v</sup>	66 52	G	0.57	0.7	0.2	23.01	1-5	high	NL	1	-	-	0.21
Hen harrier & red grouse <sup>w</sup>	55 30	G	0.50	-	0.3	23.69	5-25	high	NL	1	-	Type III	0.21
Buzzard & pheasant <sup>x</sup>	50 70	G	0.57	-	0.3	23.69	50-100	high	NL	2	4.3	-	0.15
Red kite & rabbit <sup>y</sup>	41 00	G	1.75	-	0.3	33.14	25-50	high	NL	1	-	-	0.3
Hen harrier & grey partridge <sup>z</sup>	49 50	G	0.44	-	0.4	23.69	50-100	high	NL	1	-	-	-

\* SAGE, Atlas of the Biosphere, (2002) (available at: <http://www.sage.wisc.edu/atlas/>).

§ Mean community richness by biome type. Source: Scheiner, S.M. and Rey-Benayas, J.M. (1994).

¶ CIESIN, Gridded Population of the World (GPW) Version 2 (2000) (available at <http://sedac.ciesin.org/plue/gpw/>).

□ The World Bank Group, World Bank Atlas 2001, Income per person (1999) (available at <http://nebulaworldbank.org/Website/index.htm#>).

¥ IUCN Red List of Threatened Species (2000) (available at <http://www.redlist.org/search/search-basic.html>).

¢ (1) No husbandry, (2) Low intensity shepherding, (3) Fenced pasture, (4) High intensity shepherding, (5) Fenced pasture, checking & enclosures.

<sup>a</sup> Stahl et al. (2002); Stahl et al. (2001a), Stahl et al. (2001b); <sup>b</sup> Breitenmoser & Haller (1993); <sup>c</sup> Linnell et al. (2001), Odden et al. (2002); <sup>d</sup> Linnell et al. (2001), Pedersen et al. (1999); <sup>e</sup> Blewjas et al. (2002), Sacks & Neale (2002), Sacks et al. (1999), Conner et al. (1998); <sup>f</sup> Landa et al. (1999), Landa et al. (1997); <sup>g</sup> Treves et al. (2002), Mech et al. (2000); <sup>h</sup> Treves et al. (2002); <sup>i</sup> Cozza et al. (1996), Merrigi & Lovari (1996); <sup>j</sup> Dahle et al. (1998), Sagor et al. (1997); <sup>k</sup> Mazzoli et al. (2002); <sup>l</sup> Mishra (1997); <sup>m</sup> Oli et al. (1994), Jackson & Ahlborn (1989); <sup>n</sup> Butler (2000); <sup>o</sup> Rasmussen (1999); <sup>p</sup> Mizutani (1999); <sup>q</sup> Polisar et al. (2003), Hoogesteijn et al. (1993); <sup>r</sup> Stahl et al. (2002); <sup>s</sup> Yom Tov et al. (1995); <sup>t</sup> Greentree et al. (2000), Pech & Hood (1998); <sup>u</sup> Kunkel & Pletscher (1999); <sup>v</sup> Kaubala et al. (2000); <sup>w</sup> Redpath et al. (2002), Redpath & Thirgood (1997); <sup>x</sup> Kenward et al. (2001); <sup>y</sup> Villafuerte et al. (1998), Delibes & Hiraldo (1981); <sup>z</sup> Bro et al. (2003, unpubl.), Tombal (1982).

## CHAPTER 2

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### **Evidence of impacts of birds of prey on gamebirds in Scotland: a report to Scotland's Moorland Forum.**

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#### **Abstract**

*Over the last century, there have been substantial declines in most wild populations of gamebirds in Scotland. Although predation by raptors is not considered to be a main cause of these declines, there is widespread debate and concern amongst game hunting and conservation stakeholders that raptors may be a major factor limiting gamebird numbers and shooting activities. In this chapter, I undertake a study commissioned by Scotland's Moorland Forum to review evidence for impacts of raptors on gamebird numbers and productivity, economic implications and relative impacts of other factors on these interests in Scotland. Of the studies available, some were based on questionnaires and many collected information on the diets of birds of prey as components of ornithological studies, or investigated the ecology and population dynamics of species, rather than addressing raptor-gamebird issues. There have been few attempts to quantify the impact of raptors on capercaillie, black grouse, red-legged partridge and pheasant in Scotland. The most comprehensive assessments exist for hen harriers predation on red grouse, and sparrowhawk predation on grey partridge. These studies suggest that the impact of predation is greatest when gamebird populations are already low as a result of other factors. There was very little information on the economic consequences of raptor predation. This work highlights areas where future research might be directed and the type of information that could be used to quantify impacts, and improve management advice.*

## Introduction

There has been a substantial amount of interest from land managers, conservationists, scientists, members of the public and the media on the impacts of birds of prey on gamebirds, fisheries and other wildlife interests in the UK. A number of key publications have partly addressed these issues (e.g. Redpath & Thirgood 1997; Thirgood et al. 2000; UK Raptor Working Group 2000; Thompson et al. 2003). However, to date, none of these studies has specifically addressed these issues for Scotland.

This study came about as the result of Petition 449 on predatory birds submitted by the Scottish Gamekeepers Association (SGA) to the Scottish Parliament, which was placed before the Environment and Rural Development Committee for consideration. The petition called for an independent investigation into the impacts of predatory birds on gamebirds, waders, songbirds and fisheries. The Committee asked the Minister for the Environment and Rural Development to request Scotland's Moorland Forum to commission appropriate research to consider the petition. The Centre for Conservation Science, in collaboration with the British Trust for Ornithology, was commissioned to undertake the study. This chapter is derived from Section 2 of the report, and assesses evidence of

1. the effects of birds of prey on the abundance and productivity of gamebird populations;
2. the relative impacts of other factors on gamebird abundance and productivity;
3. the economic implications of raptor predation on gamebirds and game hunting activities.

The study begins by listing raptor and gamebird species of concern in Scotland, and criteria for the literature search. For contextual purposes, I also provide an overview of the importance of the game hunting industry in Scotland, and the conflict that has arisen from raptor predation on gamebirds. I then present evidence for impacts of different raptor species on a range of gamebird species and discuss the findings.

## **Raptor and gamebird species of concern in Scotland**

### ***Birds of prey***

Hen harrier *Circus cyaneus*

Peregrine *Falco peregrinus*

Common Buzzard *Buteo buteo*

Golden eagle *Aquila chrysaetos*

Sparrowhawk *Accipiter nisus*

Goshawk *Accipiter gentiles*

Red kite *Milvus milvus*

Tawny owl *Strix aluco*

### ***Gamebirds***

Pheasant *Phasianus colchicus*

Red-legged partridge *Alectoris rufa*

Red grouse *Lagopus lagopus scoticus*

Capercaillie *Tetrao urogallus*

Grey partridge *Perdix perdix*

Black grouse *Tetrao tetrix*

## **Literature search**

I surveyed the management, conservation and ecology literature relevant to gamebirds, birds of prey and predator control in Britain and Europe. This involved an extensive search of web databases including the ISI Web of Science, together with a number of organisational websites: Game Conservancy Trust (GCT); Royal Society for the Protection of Birds (RSPB); British Trust for Ornithology (BTO); Centre for Ecology and Hydrology (CEH); British Association for Shooting and Conservation (BASC); Scottish Gamekeepers Association (SGA); Scottish Natural Heritage (SNH); Department for Environment, Food and Rural Affairs (DETR); Countryside Alliance (CA); and, the National Gamekeepers Organisation (NGO). “Grey” literature and other unpublished material were obtained from these websites and from representatives of these organisations, who were also involved in the formal consultation part of the review. For each study, I attempted to document the following information: predator and prey species; study location and period; nature of the evidence; impact of predation on gamebird numbers and productivity; economic impact; and relative impact compared to other factors. I also noted any limitations on the usefulness of existing studies for assessing impacts of raptor predation.

## **Importance of gamebird hunting in the UK**

Gamebird hunting plays an important socio-economic role in the UK, providing employment, recreation and income for landowners and many rural communities. Management for gamebirds also benefits conservation by maintaining and creating habitats (e.g. woodland planting and coppicing, maintaining hedgerows, maintaining heather moorland by burning, planting cover crops) that support a range of bird species and other taxa in areas that might otherwise be converted to forestry or farming (Hudson 1984; GCT 1999). In Britain, gamekeepers have responsibility for nearly 6 million acres of wildlife habitat, 30% of which has a conservation or landscape designation (BASC 1995). A number of shooting estates are also involved in 'green' tourist activities, such as bird watching (University of Strathclyde 2001).

In the UK, game hunters make up 1.2% of the population (Martinez et al. 2002) with an estimated average annual expenditure of £1500 per hunter (Cobham Resource Consultants 1997). Recent figures suggest a substantial increase in the number of hunters over the last decade, with foreign visitors, particularly North Americans, accounting for the greatest increase in demand (University of Strathclyde 2001). In Scotland, tourism figures suggest that expenditure on shooting/stalking/hunting holidays is second only to hiking and rambling holidays (Cobham Resource Consultants 1997).

Each year in the UK, around 20 million pheasants and 2 million red-legged partridge are released for sport, together with small releases of grey partridge (Tapper 1999, Arroyo & Beja 2002). Hudson (1992) estimated that almost half a million red grouse

are shot annually. There is an average of 22 days shooting per year (few shoots have over 50 days a season), and an estimated 3600 shoots with one or more keeper (UK Raptor Working Group 2000; BASC 2004). Average seasonal bags for shoots are around 3000 pheasants and 1800 partridge. Three quarters of game shot in Britain is sold to game dealers and 12% is sold by shoots, direct to the public. Tax revenue from shooting activities is thought to be considerable. For instance, in Scotland around two million pheasants are shot each year and the SGA (SGA website) suggests that the government receives “probably £5 in VAT for every pheasant from birth to death”.

Studies assessing the economic importance of gamebird hunting are scarce; a few reports have commented on the importance of gaming activities in general (deer stalking, fisheries and gamebirds). Two major studies on grouse shooting in Scotland have evaluated capital generated and implications for local economies (see McGilvray, J. 1995 and University of Strathclyde 2001). The most recent study found that, in 2000, 4500 people were employed in grouse-related activities, the equivalent of 940 full time jobs, supporting a total wage income of £14.8 million and contributing £17 million in GDP. Investment in grouse management has also increased with 33% of shooting estates investing more than 50% of revenues on improving grouse moors in 2000, compared with only 6.3% in 1994 (University of Strathclyde 2001).

## **Birds of prey and gamebirds: the conflict**

In Scotland, gamebirds have been managed for shooting since at least the 19<sup>th</sup> century. The primary aim of game management is to increase the number of birds available to be shot in a given area during the shooting season. A combination of approaches is used to achieve this:

1. Increase the size and/or productivity of populations through habitat management, provision of food and shelter, predator control and management of disease and parasites;
2. Minimise non-hunting losses of adult gamebirds through predator control and habitat management to control dispersal; and
3. Supplement wild populations with released birds through captive rearing.

(Robertson & Rosenberg 1988).

Over the last century there have been substantial declines in most wild populations of gamebirds and shooting bags in Britain. Today, in Britain, around 25 million gamebirds are hunted annually, with galliforms, mainly pheasant, red grouse and partridge, comprising 70% of all hunting bags (Martinez et al. 2002). Estimates suggest that the number of red grouse *Lagopus lagopus scoticus* shot has fallen by 50% over the last century (Hudson 1992). Once widespread across Britain, the black grouse *Tetrao tetrix* is now mostly confined to Scotland and parts of northern England and Wales. Hancock et al. (1999) suggested a 90-93% decrease in numbers shot since the 1900s. Between 1870-1930 around two million grey partridge *Perdix perdix* were killed annually (Tapper 1999). Since the 1950's bags have fallen by over 80%, as has the species overall abundance, such that it has become an important management

concern in Europe. The status of the non-native red-legged partridge *Alectoris rufa*, is difficult to assess because of large scale releases. However, Tapper (1999) suggests there has been a marked decline in numbers since 1985. The capercaillie *Tetrao urogallus*, became extinct in Britain in the 18<sup>th</sup> century but was reintroduced in the mid 19<sup>th</sup> century. The population was estimated at 20,000-50,000 birds in the 1970s, but recent surveys estimate numbers of around 2,000 individuals, entirely restricted to Scotland (RSPB unpublished survey). The pheasant *Phasianus colchicus*, is widespread across Britain, absent only from large areas of northwest Scotland. Around 12 million pheasants are shot each year, however, it is estimated that only around 10% of the harvest consists of wild birds (Tapper 1999).

There are a number of possible causes of declines in gamebird populations and shooting bags including: changes in farming, habitat loss or deterioration, disease, overshooting, reductions in the number of gamekeepers and predation. Whilst raptors are not considered to be the cause of long-term declines, a large part of the hunting sector perceives predation by raptors to be a major factor limiting gamebird numbers and shooting bags. As well as direct killing of gamebirds, game managers have expressed concerns about indirect effects such as stress, disease or dispersal arising from raptor activity, as well as disruption of shoot days (Harradine et al. 1997; Allen & Feare 2003).

Game managers have long considered raptors to be damaging to their quarry and in the past control of avian and mammalian predator species was practised to benefit game populations. This resulted in many species being exterminated from large parts of Britain (Reynolds & Tapper 1996), and an artificial reduction in predation pressure

by raptors (Newton 1979). Since the introduction of legislation prohibiting the killing of birds of prey, the withdrawal of organochlorine pesticides, and conservation efforts to restore biodiversity, populations of some raptors have been recovering and reoccupying areas from which they had been extirpated (e.g. Watson 1997; UK Raptor Working Group 2000). Whilst this recovery has been seen as a conservation success, it has also renewed past conflicts with game managers. As a consequence, illegal persecution of birds of prey, with the aim of improving hunting bags, has become a persistent and significant conservation problem. Some hunting stakeholders consider the impact of raptors so great that there have been calls for changes in the law to allow the licensed removal of problem individual raptors (Harradine et al. 1997; UK Raptor Working Group 2000). However, this option is unacceptable to conservation stakeholders, given the uncertain conservation status of many raptor species in Britain and the relative importance of the UK's raptor populations within the European context (Greenwood et al 2003). Furthermore, although gamebirds occur in the diets of most raptors species in Britain (Cotgreave 1995), there is widespread disagreement amongst stakeholders about the extent of the impact of raptor predation on populations. In the next section I review the evidence for impacts of birds of prey on gamebirds in Scotland, reporting also on relevant studies in other parts of Britain and Europe.

## **Evidence for impacts of birds of prey on gamebird populations**

Here, I present the results of a literature search for evidence on the impacts of different raptors species on a range of gamebird species. Where possible, information on impacts on gamebird numbers and productivity, as well as economic implications, are summarised. For each species of gamebird the importance of other factors of mortality is also indicated. Relevant studies discussed here are summarised in Tables 1-5 of Appendix 2.1.

### **Grey Partridge *Perdix perdix* (see Table 1)**

The grey partridge is a widespread and economically valuable gamebird adapted to small grain cereal farming (Tapper et al. 1996). A combination of land enclosure, increased cultivation and intensive predator control in the 18<sup>th</sup> and 19<sup>th</sup> centuries made it one of Europe's most numerous gamebirds (Tapper et al. 1996). However, since the 1960's, the grey partridge has undergone a 7% per annum decline in the UK (BTO website; Potts 2002), and an 18.7 % reduction in breeding range between the 1970's and 1990's (Gibbons et al. 1993). Nowadays, in most areas, grey partridge are seldom shot; although there remain a few estates, most of which are in lowland eastern Britain, where wild birds and small scale annual releases are managed for sport (Tapper 1999). The grey partridge is currently listed under SPEC (Species of European Conservation Concern) category 3 (i.e. unfavourable conservation status in Europe, Hagemeyer & Blair 1997) and is included in the UK red data book. It is also the focus of a UK Species Biodiversity Action Plan .

The ecology and population dynamics of the grey partridge have been the subject of intensive research over the past 50 years. Consequently, causes of the population decline are well understood: high chick mortality caused by reduced insect abundance following the introduction of herbicides in the 1950s (Southwood & Cross 1969). Numerous studies have confirmed this relationship, but predation by foxes and corvids has also been identified as having a large effect on autumn and spring stocks. In studies of partridge on the Sussex Downs, Potts (1980; 1986) found that predation on breeding birds was density dependent in populations where there was no predator control by gamekeepers. A simulation model based on this study suggested that, when nest predation is low, the partridge population increases to a much higher level than when predation is high (Potts & Aebischer 1991). Tapper et al. (1996) demonstrated, experimentally, that a seasonal reduction in the number of predators significantly improved the breeding success of partridges, resulting in both improved breeding density and higher August stocks sufficient to sustain shooting. Potts and Aebischer (1991) also noted that “the experience of generations of gamekeepers indicated a considerable increase of partridge numbers with a decrease of predator numbers”.

These, and other studies, have shown that predation is a significant problem for populations of grey partridge, if they are to be conserved for shooting. The results provide a strong argument that predator control is an effective conservation tool for the species. However, these studies also showed that the primary predators of grey partridge are foxes *Vulpes vulpes* and corvids, in particular the carrion crow *Corvus corone* and the magpie *Pica pica*. There are few studies of the effect of raptors on grey partridge, and there have long been calls for research in this area (see Potts 1986; GCT 1999; Tapper 1999).

Our search of the literature found two studies linking grey partridge kills to predation by sparrowhawks *Accipiter nisus*. Newton & Marquiss (1982), in a long-term study of diet, predation and breeding in sparrowhawks in Scotland, found that partridge made up 0.08% of all prey items during spring-summer. The most recent and comprehensive study of raptor predation on grey partridge found that sparrowhawks were frequently seen attacking or feeding on grey partridge (Watson 2004). The study looked at both the impact of raptors and shooting on spring stocks of partridge. Watson (2004) showed that most losses to raptors occurred in winter, and a deterministic model predicted that the level of loss could result in a 39% reduction in spring stocks, compared with a 23% loss from shooting. It appeared that raptor predation and shooting losses were largely additive. Further, the impact of raptor predation was greatest when partridge densities were reduced to low levels by shooting and habitat loss.

Hen harriers *Circus cyaneus* and marsh harriers *Circus aeruginosus* have been identified as important predators of grey partridge in France. Bro et al. (2001) suggested that together, they can cause up to 29% of female mortality during breeding. In Hungary, records suggest that a 50% decline in adult annual survival rates coincided with a four-fold increase in the abundance of raptors, mainly buzzards and marsh harriers (Lajta project cited in Tapper 1999). Swann and Etheridge (1995) found that grey partridge comprised 1.9% of bird prey in buzzard nests in Scotland. In East Anglia, grey partridge made up 2.2% of prey remains for Montagu's harriers (Underhill-Day (1993)). Watson (2004) found that hen harriers, buzzards and peregrines had little effect on partridge populations in southern England. Recent radio-tracking work on the survival of reared and wild grey partridge at two sites in

Scotland (Parish & Sotherton, unpublished data) found that these birds experienced 39% (n=126) and 82% (n=78) mortality respectively over a period of about twelve months after release: it was estimated that raptors took 5.6% (n=7) and 28% (n=22) of all birds radio-tracked at these sites. During this study, both buzzards and sparrowhawks were seen attacking (but not killing) partridges but it is unknown which raptor species contributed most to mortality (Parish pers. comm.).

### **Other threats and challenges**

*Pesticides:* a primary cause of mortality is chick starvation, usually due to shortages of insect food brought about by the use of herbicides and pesticides. This was the main cause of decline in the partridge population during the 20<sup>th</sup> century and continues to be a threat to their future survival (Southwood & Cross 1969; Potts 1973; Potts & Vickerman 1974; Green 1984; Rands 1985; Sotherton & Robertson 1990).

*Habitat loss:* hedge removal and field enlargement has resulted in the loss of grassy nesting cover and increased exposure to a variety of predators (Potts 1980). Loss of field margins affects the supply of chick food (Bro et al. 2000). Nests in cropped fields are vulnerable to farming disturbance and mowing (Potts 1980; Bro 2001).

*Other predators:* in many cases, as a consequence of the decline of the partridge, gamekeepers switched attention from protecting nests from predators to other activities, or were made redundant. Where predator control has been maintained, stocks appear to have declined less than where there is no control (Tapper 1996; Potts 2002). It is well established that the main nest predators of partridge are foxes and

corvids. Weasels, stoats, rats and feral cats also take hens and eggs (Tapper 1996). In a study in France, Bro et al. (2000) estimated that foxes and small mammal predators were responsible for 64% of partridge mortality.

*Disease:* Tompkins et al. (2002) suggested that the transmission of shared parasites from ring-necked pheasants, specifically the caecal nematode *Heterakis gallinarum* may be a cause of decline of the grey partridge in the UK. It may also be a factor preventing the recovery of the remaining wild grey partridge populations. The nematode *Syngamus trachea* is an indicator of poor nutrition and, in the past, has been a major source of chick mortality (Potts 1980). However, in recent decades the parasite has become less prevalent. Sinusitis is a significant respiratory disease in partridge, causing coughing and mouth breathing. Protozoan enteric disease is a problem for managers rearing partridge, but little is known about the organism which causes it, resistance or sources of infection (Tapper 1999).

*Shooting:* Potts (1980) and Bro et al. (2000) have suggested that driven shooting may be unsustainable at low partridge densities. Watson (2004) found that shooting accounted for 32% of partridge deaths at a site in Sussex and 7% across 20 sites in England. He also suggested that shooting could extinguish stocks when productivity is low.

**Red-legged partridge *Alectoris rufa*** (see Table 1)

The red-legged partridge was introduced into the UK in the 18<sup>th</sup> century but did not reach its current distribution until the 1930s. Captive rearing and releases of red-legged partridge commenced in the 1960s as a means of maintaining a partridge shoot, despite the decline of the grey partridge. Current UK releases are estimated at around 2 million birds per year (Tapper 1999; BASC 2004). The current status of the wild population is difficult to assess because of the large scale of releases. However, data from the Game Conservancy Trust (Tapper 1999) suggests that there has been a marked decline since 1985, following the trend of recent declines observed in France, Italy, Spain and Portugal. Wild stocks of British birds are thought to lie between 90,000 and 250,000 pairs (Stone et al. 1997), equivalent to approximately 700,000 individual post-breeding birds (Gibbons et al. 1993). It is thought that numbers could increase to around 335,000 pairs following suitable habitat management and improved or intensified gamekeeping (Tapper 1999).

The red-legged partridge has been less susceptible than the grey partridge to the effects of a reduction in cereal crop insects because its chicks consume more seed and vegetable matter. However, it appears to be more affected by predation during the nesting period. Potts (1980) and Rands (1988) have suggested that the higher levels of nest predation observed for red-legged partridge may occur because they are less well adapted to existing nesting habitat than the native grey partridge.

Scientific studies on the impact of raptor predation on populations of red-legged partridge are scarce. Furthermore, information on the relative importance of predation with respect to other mortality factors does not exist. Sixty-one percent of 996 UK

game managers questioned by Harradine et al (1997) reported problems caused by raptors in the previous year, and a total of 1566 “incidents” were recorded. Incidents were defined as being specific occasions on which, for example, a raptor had attacked pheasants at a release pen. These were regarded as minimum numbers as some respondents classed continual raptor attacks at release pens as single incidents. Sparrowhawks were reported in 36% of incidents involving gamebirds, 8% of which involved partridge. Gamekeepers estimated that average losses of partridge to sparrowhawks were around 7.5% per annum. In the same survey, *Buteo buteo* were implicated in 20% of incidents, 6% were associated with partridges. The authors acknowledged that gamekeepers may have differing views on what constitutes problems caused by raptors, and different interpretations of evidence for these problems, and attempted to reduce this problem by careful survey design.

A number of studies have recorded partridge in the diets of raptor species and the effect of raptors on nest success, but none distinguished between the two species. Underhill-Day (1985) found red-legged partridge in 0.5% of English marsh harrier pellets and 1.0% of prey remains. In Spain, Yanes et al. (1998) found that predation on red-legged partridge nest attempts, mostly by foxes and magpies, was between 15.2 and 74.3%.

### **Other threats and challenges**

*Disease:* Millan et al. (2004) found a high prevalence and intensity of helminths in some farmed partridge, despite the routine use of anti-helminthics. Released partridge

may therefore have a negative effect on wild populations by exposing them to new parasites .

*Climate change:* The wild red-legged partridge is poorly adapted to cold, wet conditions and is thus restricted to lowland areas. Predicted increases in the frequency and distribution of these types of conditions may negatively affect breeding success and survival of the species in the future (Hill et al. 1999).

### **Pheasant *Phasianus colchicus*** (see Table 2)

The pheasant is non-native to Britain, but is thought to have been resident since the 15<sup>th</sup> century (Hill & Robertson 1988). Over the last century it has become an increasingly important quarry species and now comprises around 55% of lowland game bags (Tapper 1999). There is considerable economic investment in rearing and releasing birds during the summer, to augment numbers available for shooting during winter. Each year around 20 million pheasants are released, and around 12 million are shot (Potts 1990; Tapper 1999). Wild bred birds are thought to comprise only about 10% of the annual harvest (Tapper 1999).

Many released birds are lost to causes other than hunting each year, only a small proportion survives until the following spring. Until recently, little was known about the timing and causes of these losses. However, Turner & Sage (2003) documented the mortality of released pheasants in southern England. The study used six release pen sites and radio-tagged 25-30 birds in each pen (pens contained up to 2000

pheasants). Birds were located and their fate recorded several times each week, over the pre-shooting period and during the shooting season. The results showed that 25% died before the shooting season began, mostly due to predation by foxes. A further 13% were predated or scavenged during the shooting season. 37.5% of pheasants were shot and 10 % died from disease and accidental death. Only a few birds were killed by raptors. Nevertheless, a high frequency of raptor sightings at or around release pens, and reports of related problems from gamekeepers across the UK have led some authors (Harradine et al. 1997; Allen et al. 2000; Allen & Feare 2003) to express concern about the potential effect of raptor predation on released pheasants.

The presence of large numbers of young, naïve birds in and around pens in late summer provides a highly concentrated source of prey that several raptor species may be well suited to exploit (Thompson et al. 1997; UK Raptor Working Group 2000). Pheasant release pens are commonly situated in woodland habitat, thus, species that prefer to hunt in these areas, such as sparrowhawks, goshawks, buzzards and tawny owls *Strix aluco*, are those most likely to encounter pheasants in or around pens (Allen & Feare 2003). A number of other factors, including timing of releases and age of released birds, may influence the exposure of released birds to raptor predation (Allen & Feare 2003). Pheasant chicks grow rapidly and soon attain a size that is too large for most raptors to handle easily (Allen & Feare 2003).

Almost all game keepers questioned by Harradine et al. (1997) reported incidents of raptor predation at pheasant release pens. Overall, losses to raptors were reported to be under 5% and commonly less than 1%, but occasionally over 10% of released birds were reported to be killed. Over 70% of incidents reported were attributed to

sparrowhawks, buzzards and tawny owls, and average losses to these species were 1.94%, 3.17% and 1.79% respectively (Harradine et al. 1997). Allen et al. (2000) estimated levels of predation during the release period from an examination of pheasant carcasses. Losses to raptors were found to be low, mostly less than 1% with no losses over 5%. In contrast, losses of up to 18% were reported within pens, with foxes and disease the greatest cause of mortality. The average cost of a driven bird is around £20 (Allen et al. 2000), so even small percentage losses can be financially serious. Allen et al. (2000) suggested that the total cost of all losses after release could be up to 100 times greater than the cost of losses to birds of prey during the period immediately after release. This study found no evidence of indirect losses (due to the effects of stress, vulnerability to disease and dispersal) due to the presence of high densities of raptors around release sites, although it is possible that these effects might become apparent under exceptional levels of predation.

Kenward et al. (2001) estimated that 4.3% of the deaths of pheasant released at a study site in Dorset could be attributed to buzzards, 0.7% to tawny owls, 0.6% to sparrowhawks and 3.2% to foxes. These represented only a small proportion of total losses and, in the majority of cases, probably had a negligible impact on the subsequent hunting bag. Birds made up 47% of prey items, of which 9% were pheasant, consumed by buzzards at Langholm in Scotland (Graham et al. 1995). In similar studies at Moray and Glen Urquhart, pheasants comprised 28% of all bird remains in buzzard nests (Swann & Etheridge 1995). Pheasants made up 0.6% of all prey items recorded in the spring and summer diet of sparrowhawks in Annan, Scotland (Newton & Marquiss 1982). The remains of pheasants have also been found

in the nests of buzzards in Wales (Sim 2003), red kites (Walters Davies & Davis 1973; Wildman et al. 1998) and golden eagles (Marquiss et al. 1985).

There is widespread concern among game keepers about the potential effects of recent increases in goshawk numbers in Britain on gamebird numbers. There is little information about the impact of this species on gamebirds, although an early study by Kenward (1981) found a low incidence of adult pheasants in the diet of goshawks, which was attributed to a high availability of alternative prey.

### **Other threats and challenges**

*Management:* hand-reared birds have lower breeding success and survival than wild counterparts (Hill & Robertson 1988; Robertson & Dowell 1990). This may be due to genetic factors; lack of parental influence, reduced resistance to infection, difficulties utilising a natural diet, stress during rearing, and loss of wildness. Dowell (1990) found that pheasants reared without the presence of adult birds showed reduced predator avoidance.

*Habitat:* loss of low ground and shrub cover reduces availability of chick food and shelter in winter, which may increase the risk of detection by predators (Hill & Robertson 1988). Predation on young pheasants has been found to increase when there is less than 60% ground cover at release sites (Lloyd 1976). Allen et al. (2000) also found that lower predation levels, in and around release pens, were associated with higher foliage density at 1.5 metres above ground level. Habitat structure may also affect predation on pheasants, by influencing the availability of alternative prey.

*Disease:* disease transmission can be higher in reared birds than in wild populations, because they are confined at high densities. Released birds can act as parasite vectors or reservoirs of disease for wild birds (Tompkins et al. 1999). *Rotavirus* infection has been diagnosed with increasing frequency since the 1970s, and can affect young birds through diarrhoea and rapid death. Surviving birds usually have poor growth rates (Tapper 1999). High levels of disease in some pheasant populations are reported to contribute to high goshawk predation levels in Sweden (Goransson 1975 cited in Kenward 1977).

*Tick infestation:* in some parts of Britain, pheasants are infested by the sheep tick *Ixodes ricinus* during spring and summer (Hoodless et al. 2003). This ectoparasite can have both direct and indirect effects on gamebird fitness. Documented direct effects include, anaemia, irritation resulting in increased preening and decreased anti-predator vigilance, and reduced visual perception when ticks aggregate around the eye area. Indirect impacts may result from transmission of bacteria and viruses. Hoodless et al. (2002) showed that high tick burdens can have a negative impact on wattle development, harem acquisition, male territoriality, and female survival and productivity.

*Other predators:* fox predation is a major cause of pheasant mortality (Robertson 1988; Turner & Sage 2003). The vulnerability of newly released birds may be due to poor predator recognition and avoidance, and the fact that birds often remain in large flocks, close to release pens. Aggregation of prey is known to increase the foraging success of predators (Tinbergen et al. 1967).

**Capercaillie *Tetrao urogallus*** (see Table 3)

Capercaillie became extinct in Britain in the 18<sup>th</sup> century following extensive felling of pinewood habitats and a period of cool wet summers. They were reintroduced into Scotland in the 19<sup>th</sup> century by landowners interested in shooting. Even though forests were small and fragmented, capercaillie bred successfully and increased in numbers, spreading through east and central Scotland. Since the 1970s the population has declined from approximately 20,000 birds to an estimated 2,000 (Kortland, unpublished data), and extinction is possible within 15 years (Kortland 2002). The capercaillie is listed in the UK Red Data Book as a species of high conservation concern and is the focus of a UK Biodiversity Action Plan. Within Scotland, a national conservation strategy, involving a network of Special Protection Areas (SPAs), has been established in an attempt to halt further declines.

When they were more common, capercaillie were shot either as trophies or on organised drives, but bags were never large. Since the recent reductions in numbers, landowners have imposed a moratorium on shooting, and since 1982 the rights for capercaillie shooting have not been let on Forestry Commission land (Batten et al. 1990). However, this does not appear to have had any effect on the decline (Tapper 1999).

The main demographic cause of the decline has been low breeding success (Moss et al. 2001), exacerbated by deaths of adult birds flying into fences (Baines & Summers 1997; Moss et al. 2001). At two sites in Scotland, Catt et al. (1994) estimated that collisions with fences accounted for 32% of annual mortality. Weather can affect the timing and rate of plant growth in spring and the availability of arthropods to chicks

in early summer. Tetraonids appear to respond to variations in the onset of spring growth by laying poorer quality eggs when springs are later. This has important implications for the future of these birds, as Scotland's precipitation is expected to increase by 8% between 1990-2050 (Hill et al. 1999).

Other factors that may have contributed to declines are: habitat destruction through changed silviculture practises (e.g. underplanting of non-native softwoods); overshooting in the 1950s and 1960s, when capercaillie were regarded as a pest by foresters and farmers and both birds and eggs were destroyed (Batten et al. 1990); reductions in chick-rearing habitat through red deer browsing; and increased predation by foxes and corvids (Moss et al. 2000).

In coniferous habitats in Fennoscandia, capercaillie is an important part of the summer diet of golden eagles (Tjernberg 1981). In Scotland, they occur in the diet of buzzards (0.02% of bird remains in buzzard nests) (Swann & Etheridge 1995) and golden eagles (Marquiss et al. 1985). Baines et al. (2004) studied the relationship between capercaillie breeding success and predator abundance in Scotland and found that foxes, pine martens and crows had a significant negative effect on productivity, but raptors had a lesser effect. There have apparently been no other studies documenting the effect of raptor predation on capercaillie in Scotland.

**Black grouse *Tetrao tetrix*** (see Table 4)

Until the last century, black grouse were widespread across Britain from Cornwall and Devon northwards, and were especially numerous in parts of the Pennines and the Southern Uplands of Scotland. However, populations declined in the 1930's, and crashed in the 1940's (Ratcliffe 1990). Gamebag records indicate a decline of approximately 90% in the number of birds shot since the early 1900's in northern England and Scotland. Since 1989 the number of males recorded on leks in spring has halved (Baines & Hudson 1995), and recent population estimates put the number of displaying males at around 7000 (Hughes et al. 1998). The species range has also contracted since the 1960's, particularly in the south and west (Gibbons et al. 1993). Nowadays, black grouse are restricted to parts of Wales, northern England and Scotland, and are shot on only 25% of estates (Baines & Hudson 1995). Similar declines have occurred across Europe, with the number of young reared per hen decreasing by 60% since the 1950s (Baines 1991). The decline in black grouse is so serious that the species was included in the UK Red List of Birds of conservation concern. It is a priority species under the UK Biodiversity Action Plan, which aims to stabilise numbers and prevent further fragmentation of the species range.

Large-scale habitat loss and deterioration, principally through agricultural expansion, intensification, and afforestation in upland Britain (Cramp & Simmons 1980; Yalden 1986), and grazing pressure in the Scottish Highlands, have been associated with the decline of black grouse populations. Deer and stock fences have also been implicated as a cause of high mortality (Hughes et al. 1998). Predation has been widely recognised as an important proximate cause of adult mortality in black grouse (Angelstam 1984; Picozzi & Hepburn 1984) and a main cause of nest failure (Bernard

1982), although its effect on chick mortality is poorly understood (Hughes et al. 1998). Foxes, mustelids and corvids tend to be the main predators of nests and chicks, while foxes and raptors kill adults (Angelstam 1984; Picozzi & Hepburn 1984; Willebrand & Marcstrom 1988). Few studies in Britain have addressed the role of raptor predation on this species. However, Picozzi (1986, unpublished report) described predation by raptors as the most frequent cause of death in first-year birds in north-east Scotland. Warren and Baines (2002) used radio transmitters to study the dispersal, survival and causes of death of 70 individual black grouse in the North Pennines in England. First-year survival was lower than that of adult birds, owing to predation in autumn and winter by stoats and raptors. Of 26 corpses that allowed an assessment of death, 39% were killed by raptors, probably peregrines, and 30% by stoats.

Several studies in Fennoscandia have shown a negative relationship between black grouse abundance and/or breeding success, and predator abundance. In Sweden, black grouse breeding success and density increased when foxes and pine martens were controlled (Marcstrom et al. 1988). Summers et al. (2004) found that control of crows and foxes at sites in England led to increases in black grouse productivity (Summers et al. 2004). Buzzards, peregrines and goshawks have been identified as potentially important predators of black grouse in mainland Europe, but little is known about their impact on this species in Scotland.

### **Red Grouse *Lagopus lagopus scoticus* (see Table 5)**

Since the mid 1800s grouse shooting has been one of the major land uses and most important sources of income for many estates in Scotland. Heather moorland comprises about 25% of the uplands and about 50% of this is managed for grouse (Hudson 1992). A recent study by the University of Strathclyde (2001) found that, in 2000, grouse hunting generated over 940 jobs in Scotland, supporting a total wage income of £14.8 million and contributing £17 million to GDP. Successful management of the grouse-shooting industry depends upon high population densities of grouse. Hudson (1992) suggested that the costs of grouse management would not be covered unless grouse density exceeded 60 birds km<sup>-2</sup>.

During the last century the number of red grouse shot in the UK declined by 50% (Hudson 1992). Particularly severe long-term declines occurred after the Second World War, and after the 1970s in Scotland and Wales, although grouse numbers remained relatively stable on many north English moors (Tapper 1999). Research suggests that in the last decade there have been no further declines in autumn grouse densities, and there has been a considerable increase in shooting activity since 1995 (GCT website; University of Strathclyde 2001). Current estimates suggest a British breeding red grouse stock of 250,000 pairs (Stone et al. 1997). Based on count data from 2003, there are approximately 129,700 pairs in Scotland (GCT unpublished data).

The cause of long-term declines appears to be multifactorial: large scale habitat loss (overgrazing and afforestation have led to a 20% reduction in heather moorland) (Thompson et al. 1995); widespread degradation of the remaining heather moorland;

disease (e.g. louping ill and the nematode worm *Trichostrongylus tenuis*) (Hudson 1992); changes in management (85% decline in the number of gamekeepers across Scotland) (Hudson 1992); and increases in the numbers of predators. Concerns surrounding the possible effects of predation have focused on raptors. In areas where red grouse are available they form part of the diet of golden eagle, goshawk, hen harrier, peregrine and buzzard (Linden & Wikman 1983; Mearns 1983; Watson et al. 1993; Graham et al. 1995; RSPB website).

Jenkins et al. (1964) found that non-territorial grouse were most likely to be killed by predators in a high density grouse population at Glen Esk, although peregrines took very few of these birds. Picozzi (1978) estimated that hen harriers removed only 7.4% of grouse chicks from a Scottish moor with high grouse densities. Hudson (1992) concluded that 34% of grouse found dead on moors in England had been killed by raptors, whereas the figure for Scotland was 48%. Peregrines were thought to be responsible for 74% and 64% respectively of this predation. Hudson (1992) suggested that on low density moors, over-winter losses fell more heavily on territorial birds. Further work by Redpath (1991) supported the hypothesis that low density grouse moors were likely to experience higher levels of predation. Comparisons between matched pairs of moors demonstrated that moors with hen harriers produced 17% fewer grouse than moors without harriers, although no causal link was demonstrated.

Hudson et al. (1997) investigated the cause of mortality for 729 red grouse corpses on ten sites of managed moorland in Scotland and England. 52% of deaths in Scotland were assigned to raptor kills and 42% in England. Of the deaths attributed to raptors, the authors felt able to distinguish between medium/large raptors and small raptors on

194 occasions: 78% were classed as medium/large raptor kills. Peregrines and harriers were the main raptor species sighted during fieldwork, but it was not possible to attribute deaths to particular raptor species. The authors tried to avoid miss-assigning cause of death by noting locations of corpses relative to tracks or fences. Where there were signs of more than one predator, they considered that mammals were more likely to scavenge than raptors. In another study conducted on a 17km<sup>2</sup> area of moorland managed for red grouse between 1999 and 2001, 29 of 55 radio-tagged grouse were taken by predators, with 8 of these attributed to raptors (Smith & Howarth unpublished data). Using data on prey remains and pluckings from 14 studies across Britain, Ratcliffe (1993) calculated that red grouse comprised 40% by weight of all prey taken by peregrine during the breeding season, and estimated that the annual mortality due to predation was 1.6-5.3% .

The most comprehensive study to date, conducted at six study sites in Scotland, including Langholm estate, suggested that hen harriers and peregrines were capable of limiting grouse populations at low densities and reducing shooting bags (Redpath & Thirgood 1997). However, peregrines were unlikely to limit grouse numbers in the absence of other predators. Harrier densities were found to be influenced by the availability of alternative prey (e.g. meadow pipits and field voles) and not by grouse. The study found that raptor predation in spring removed, on average, 30% of the potential breeding stock of grouse, and 37% of grouse chicks in summer. Most adult and chick losses were thought to be additive to other forms of mortality. Together, they were estimate to reduce post breeding numbers of grouse by 50%. Overwinter mortality was estimated as 30% but it was not possible to determine what proportion of these grouse would have survived in the absence of raptors (Thirgood et al. 2000).

A simple model combining the estimated reduction in breeding productivity with observed density dependence in winter losses, predicted that grouse breeding numbers would have increased by 1.9 times and post breeding numbers by 2.5 times over 2 years in the absence of predators (Thirgood et al. 2000). A more recent model (Redpath and Thirgood 2003), incorporating information about the hen harrier functional response, suggested that grouse could coexist with harriers at densities suitable for driven shooting (i.e.  $\geq 60$  grouse  $\text{km}^{-2}$ ) provided harrier density did not exceed  $\leq 0.3 \text{km}^{-2}$ . Although, this depended on the breeding success of grouse prior to predation. The authors suggested that reducing predation rates by providing supplementary food could increase the likelihood that grouse reach required minimum densities.

Other work currently underway is modelling the influence of multiple prey species, on harrier consumption rates of grouse chicks. Asseburg et al. (in press) suggest that a high availability of meadow pipits and field voles may reduce predation on grouse chicks. They propose that models that do not explicitly account for the effects of alternative prey may overestimate the impact of predation on a particular prey species.

In response to concerns about the effects of raptors on red grouse shoots in northern England, English Nature conducted an assessment of raptor presence and disturbance on a large number of driven grouse shoots (Robson & Carter 1999; 2001). Over two years, a total of 170 drives at eleven sites were monitored: 17 drives (2%) were disturbed by raptors in 1999, and 9 drives (7%) in 2000 (Robson & Carter 1999; 2001). Species implicated in these disturbances were peregrine, hen harrier, buzzard and raven.

## **Other threats and challenges**

*Other predators:* foxes and corvids are important predators of red grouse (Hudson 1992; Redpath & Thirgood 1997; Leckie et al. 1998). High densities of a suite of predators can have significant effects on grouse dynamics when grouse densities are already low as a result of other factors (Redpath & Thirgood 1997).

*Habitat:* the highest densities of grouse occur when heather cover is 40-80%. Declines in quality and quantity of heather moorland are considered the principal reason for reductions in driven grouse shooting (Barnes 1987). Aerial photographs indicate that 48% of heather at Langholm moor was lost between 1948-1988. Loss of heather habitat is largely due to overgrazing in winter by sheep and deer, conversion to forestry, and reduced levels of managed heather burning which stimulates new growth. Grazing pressure on upland shrub communities can also reduce invertebrate biomass, which may be detrimental to chick survival (Park et al. 2001).

*Disease:* parasites can have a large effect on grouse densities. Grouse on some moors are seriously affected by louping-ill, a viral disease transmitted between host animals by sheep ticks, which can reduce chick survival by up to 80% (Hudson 1992). The nematode worm *Trichostrongylus tenuis*, which causes the disease strongylosis, is widespread in grouse populations. High levels of infection can reduce grouse breeding success and cause direct mortality. Studies using worm-killing drugs (Dobson and Hudson 1994) have shown that this parasite can cause the cyclic fluctuations in grouse numbers observed on moors in this region. Infected individuals in these populations may be more vulnerable to mammalian predation.

## **Discussion**

Long-term declines in gamebird numbers and shooting bags in Scotland have been attributed to a number of factors. Although it is generally agreed that raptor predation is not a main cause of these declines, there is widespread concern and debate amongst hunting and conservation stakeholders about the role of raptors in determining gamebird dynamics and the effects of this on hunting activities. Here, I summarise the scientific evidence underpinning these concerns, comment on the limitations of existing studies, and recommend areas where future research should be directed.

The literature search revealed that relatively few studies have assessed the impact of raptor predation on gamebirds in Scotland or elsewhere, a finding borne out by a number of other studies (e.g. Newton 1992; Martinez et al. 2002; Allen & Feare 2003; Graham et al. in press; Valkama et al. in prep). Quantitative assessments of impact are scarce, and assessments of impacts were often based on game managers opinions. Two reports that used the latter approach (Harradine et al. 1997; Allen et al. 2000) concurred that losses of released pheasants and red-legged partridge were generally under 5%, and only occasionally over 10%. Information of this kind can highlight areas or species of concern. However, it is subjective by nature, may be prone to bias, and can sometimes lead to misleading conclusions.

Many studies of the effects of raptor predation on gamebird populations, measured the survivorship of gamebird species but were unable to determine the precise fate of missing individuals. Others collected information on raptor diets as part of ornithological studies, rather than addressing gamebird issues (Allen & Feare 2003).

Dietary data can be obtained from direct observations of kills, gut contents and prey remains, and can provide information on what species are consumed by raptors and their relative importance in their diet. Where the abundances of predator and prey species are known, dietary data may also facilitate estimates of the proportion of the prey population taken by predators. However, the simple presence of a species in a raptor's diet does not imply that the raptor will have an impact on prey dynamics, and a high proportion of a certain prey type in the diet does not necessarily equate to a high impact on prey numbers. The proportion of a raptor's diet that is made up of gamebirds is of less concern to game managers than the number of game birds that are taken and the time of year losses occur.

It is well documented that avian dietary studies are prone to bias if some prey remains are more conspicuous than others, or if predators are more likely to be sampled when they are eating a particular prey (Kenward 1977). Furthermore, diet composition may be strongly influenced by time of year and environmental conditions (Cotgreave 1995).

The dietary studies reviewed here show that gamebirds, especially young birds, occur in the diets of most Scottish raptors, but they usually only constitute a small component (Allen & Feare 2003). Some studies estimated the proportion of raptor diet which is comprised of gamebirds. However, few related this to gamebird population size and even fewer estimated how this might affect the pre-harvest population or breeding numbers (Valkama & Korpimaki 2002). A number of dietary studies failed to differentiate between prey species, using general categories, such as 'other birds' or 'tetraonids' instead. Similarly, kills by different raptors were often not

distinguished, making it difficult to identify which species were most important. Interpreting causes of death from gamebird remains found at nests or in pellets can be problematic because these may have been scavenged rather than taken as live game.

Experimental removals of gamebird predators have generally shown that reducing populations of predator species allow a considerable improvement in gamebird production (Reynolds et al. 1988). However the experimental studies reviewed here concentrated on mammals (foxes and mustelids) and corvids, because legal considerations prevent experiments of this type involving raptors. The interpretation of predator removal studies can be complicated by confounding factors, such as changes in management. In addition, the ecological and environmental characteristics of control and experimental areas may not be well matched. If experimental and control areas are in close proximity, this may reduce the effectiveness of predator removal. Removing single predator species may have little or no effect if there is a compensatory increase in predation by other species (Korpimaki & Norrdahl 1998). In these circumstances, simple “before and after” comparisons cannot provide reliable evidence of the effects of removal. These studies are likely to be most reliable when experimental designs allow for spatial and temporal replication and treatment reversal (Cote & Sutherland 1995)

Correlations between time series of predator and prey numbers were reported in a number of studies. For instance, Bro et al. (2001) found that partridge spring densities were negatively associated with harrier abundance, and population growth rate decreased when harrier abundance increased. Similarly, Thirgood et al. (2000) found that red grouse density increased over time on moors with low harrier numbers, but

remained stable on sites where harrier abundance was high. Whilst time series analyses of this kind can provide strong evidence for a causal relationship, additional information on trends in potentially confounding factors (such as habitat loss) is required before this evidence can be considered conclusive.

The impact of raptor predation on gamebirds depends largely on the way in which raptors respond to changes in prey density (Redpath & Thirgood 1999). They can respond by changing individual predation rates (the functional response) or by changing their density (the numerical response) (Soloman 1949). Studying predator and prey simultaneously is demanding, in terms of time, money, and level of information recorded. Consequently, information about the functional and numerical responses of raptors is scarce. One notable exception is hen harriers. In a long-term study of the hen harrier-red grouse system in Scotland, Redpath & Thirgood (1997) found that small changes in grouse chick density could lead to marked changes in harrier predation rates. The study suggested that predation by harriers could potentially reduce the ability of very low density grouse populations to increase, thus suppressing grouse cycles and reducing shooting bags, if harriers' were maintained at high density by abundant alternative prey. Redpath & Thirgood (2003) suggested that driven shooting of red grouse might be compatible with relatively low harrier densities, and that supplementary feeding could be used to reduce predation on grouse. A recent model supports the theory that a high availability of alternative prey can reduce harrier predation on grouse and allow the two species to coexist (Asseburg et al. in review). Incorporating this information into future models of the harrier-grouse system should improve both the realism and reliability of existing models, and our understanding of the way in which raptors and their prey can interact.

A comprehensive study (Watson 2004) on the effect of raptor predation on grey partridge in England concluded that sparrowhawks were only likely to have a negative effect on partridge populations when partridges had been reduced to very low densities by habitat degradation and overshooting.

Evidence for impacts of raptors on capercaillie, red-legged partridge, black grouse and pheasants is scarce. Most of the literature concerning these species has dealt with other causes of mortality, for example, disease, habitat loss, or other predator species. Given widespread concerns about the impact of raptors on these species, as well as the difficulties in managing such systems, there is a clear need to undertake further empirical and quantitative research on the functional and numerical responses of raptors preying on these species, and to develop predictive models for individual raptor-gamebird interactions. Further research is also required to distinguish between additive and compensatory losses to raptors, since it cannot be assumed that all gamebirds that survive raptor predation are available for shooting.

There has been very little assessment of the economic implications of gamebird losses to raptors. Financial losses have been calculated in very simple terms for pheasants, although work is currently underway at the Centre for Ecology and Hydrology to determine the economic impacts of raptor predation on red grouse in Scotland. In many cases, losses may be trivial on a national scale but very significant locally. There may also be considerable differences between the financial consequences of losses of young and adult gamebirds. In some parts of Europe, farmers are compensated for livestock/game losses to predators. This may be one approach to resolving raptor-gamebird conflicts in Scotland in the future. However, it would

require reliable estimates of the economic losses due to raptor predation, including indirect losses, such as, jobs or tourism. Finally, future studies of the impact of raptor predation on gamebirds should also evaluate, quantitatively, the impacts of other mortality factors. This will enable managers to prioritise and direct management efforts as effectively as possible.

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## Appendix 2.1

Table 1: Studies of raptor predation on Grey & Red-legged partridge

Raptor species	Study area	Nature of evidence/data	Results relating to:		Reference
			Numbers/productivity	Relative impact compared to other impacts	
<b>Sparrowhawk Buzzard</b>	Sussex, Dorset, Lincolnshire 20 sites 2001-2004	Effect of raptor predation on <b>grey partridge</b> . Losses to raptors calculated using partridge counts, bag data & raptors kill rates from carcasses. 150 partridges radio-tagged	18% radiotagged birds (150) lost to raptors  Most losses to raptors in late winter  12% overwinter losses to raptors . In hypothetical absence of shooting, losses to raptors 17%  Model suggests that when population numbers are low, raptor predation could result in a 39% reduction in average spring pair density	Shooting responsible for 23% reduction in spring stocks  Raptors, sparrowhawks in particular can accelerate declines when populations are reduced to low levels by habitat loss & overshooting  Shooting & raptor predation largely additive  Grey partridge unimportant in diet of buzzards, peregrines, hen harriers	Watson 2004

<p><b>Sparrow hawk</b></p>	<p>Britain 1996</p>	<p><b>Red-legged partridge.</b> Gamekeeper questionnaire-problems with raptors &amp; managing gamebirds 996 respondents (31% of sample)</p>	<p>7.54% Red-legged partridge losses</p>		<p>Questionnaire survey: potential biases from respondents Not peer reviewed Potential mis-assignment of kills to raptors Actual losses may be under or over-estimated due to reports of 'several' raptors rather than actual numbers involved.</p>	<p>Harradine et al. 1997 (BASC survey)</p>
<p><b>Buzzard</b></p>	<p>Northern Scotland 1977-89</p>	<p><b>Grey partridge</b> Buzzard dietary analysis: pellets; prey remains. 2 buzzard populations Mean sample size 15 buzzards yr<sup>-1</sup></p>	<p>Grey partridge in 1.9% of remains of birds in buzzard nests</p>	<p>Effect on grouse populations negligible.</p>	<p>Study focused on breeding success of buzzards Potential bias toward identifying conspicuous items in diet. Difficult to identify numbers of individuals in prey remains</p>	<p>Swann &amp; Etheridge 1995</p>

<p><b>Montagu's harrier</b></p>	<p>East Anglia, England 1983-84</p>	<p>Dietary analysis: pellets, prey remains, plucking sites Prey identification using 4 harrier pairs. Feeding rates observed on 10 harrier nests</p>	<p>Partridge comprised 2.2% prey remains</p>		<p>Gamebirds not reared in study area</p> <p>Small sample size of harriers</p> <p>Only some items identified toward end of study.</p> <p>Partridge species not specified</p> <p>Study focused on feeding rates &amp; breeding in harriers</p> <p>Potential bias toward identifying conspicuous items in diet.</p> <p>Difficult to identify numbers of individuals in prey remains</p>	<p>Underhill-Day 1993</p>
<p><b>Marsh harrier</b></p>	<p>East Anglia, England 1983-84</p>	<p><b>Red-legged &amp; grey partridge</b> Harrier dietary analysis: pellets, prey remains. 3 pairs yr<sup>-1</sup> in study area.</p>	<p>Red-legged partridge comprised 0.5% pellets, 1.0% prey remains Grey partridge comprised 0.7% prey remains</p>		<p>Potential bias toward identifying conspicuous items in diet.</p> <p>Difficult to identify numbers of individuals in prey remains</p> <p>Small sample size</p>	<p>Underhill-Day 1985</p>

<p><b>Sparrow hawk</b></p>	<p>Annan, Scotland. 10 year study</p>	<p><b>Grey partridge</b> Sparrowhawk dietary data: prey remains, plucking posts ~100 sparrowhawk pairs in study areas each year</p>	<p>Grey partridge 0.08% of all prey items during spring-summer</p>		<p>No record of sparrow hawk or partridge numbers in study area, so not possible to estimate proportion of birds taken</p> <p>Potential biases in identifying prey remains</p>	<p>Newton &amp; Marquiss 1982</p>
<p><b>Hen harrier Marsh harrier</b></p>	<p>North-central France 10 study areas 3 years</p>	<p><b>Grey partridge</b> Radio-tag &amp; monitoring cause of decline in female adult survival. 3-30 pairs 100 ha<sup>-1</sup> Comparative analysis between contrasting study areas</p>	<p>Hen &amp; marsh harriers cause up to 29% female mortality during breeding</p> <p>Predation rate increased with harrier abundance &amp; was negatively correlated with partridge density</p>	<p>Direct negative impact of farming on mortality low (6%)</p> <p>Foxes &amp; small mammals (64%)</p> <p>Collision with cars &amp; diseases 8%</p>	<p>Results are correlative &amp; do not demonstrate causal relationship btw harrier recovery &amp; partridge decline</p> <p>Study of harrier diet independent of partridge mortality data &amp; did not quantify partridge abundance</p> <p>No quantitative historical data on changes in demographic estimates &amp; environmental factors</p>	<p>Bro et al. 2001</p>

Table 2: Studies of raptor predation on Pheasant

Raptor species	Study area	Nature of evidence/data	Results relating to:			Limitations of study	Reference
			Numbers/productivity	Economy	Relative impact compared to other impacts		
<b>Buzzard</b>	Welsh marshes 1983 & 1986	Breeding success of buzzards. Dietary data: prey remains at nests	5.1% of prey remains			Study focused on life history traits of buzzards	Sim et al. 2001
<b>Buzzard</b>	Dorset, Southern England 1990-95	Raptor predation investigated at 28 pheasant release pens using: prey remains, observations at 40 buzzard nesting sites, gamekeeper records 136 radio-tagged buzzards	~ 21000 pheasants released, 4.3% deaths attributed to buzzards. Weak relationship between severity of predation and proximity of buzzard nests	Estimated loss to buzzards considered small since shoots generally harvest $\leq$ 50% released birds	0.7% deaths to tawny owls 0.6% to sparrow hawks, 3.2% to foxes	Potential bias in attributing pheasant deaths	Kenward et al. 2001
<b>Buzzard</b>	Britain 1996	Gamekeeper questionnaire survey : problems with raptors & managing gamebirds	Buzzards kill 3.2% of released pheasants. On 8 occasions buzzards accounted for 10% or more of kills.		Total losses 18% :foxes & disease thought to be main cause Sparrow hawk 1.94% losses to raptors	Questionnaire: potential biases from respondents Potential mis-assignment of kills to raptors.	Harradine et al. 1997 (BASC survey)

<b>Buzzard</b>	Langholm, Scotland 1993	Buzzard dietary data- pellets & prey remains. 19 buzzard pairs sampled	Red grouse constituted 11% of all prey remains & 24% of all bird remains Pheasant 9% of all bird remains		Tawny owl 1.79% losses to raptors	Actual losses may be under or over-estimated due to reports of 'several' raptors rather than actual numbers involved. Potential bias toward identifying conspicuous items in diet. Difficult to identify numbers of individuals in prey remains Uncertainty about selectivity of prey taken to nests	Graham et al. 1995
<b>Buzzard</b>	Northern Scotland 1977-89	Dietary analysis: pellets, prey remains. 2 buzzard populations Mean sample size 15 buzzards yr <sup>-1</sup>	Pheasant in 60/210 remains of birds in buzzard nests	Effect on grouse populations negligible.		Study focused on breeding success & diet of buzzards Potential bias toward identifying conspicuous items in diet. Difficult to identify numbers of individuals in prey remains	Swann & Etheridge 1995
<b>Buzzard Sparrowhawk Tawny owl</b>	14 estates Britain	Carcass descriptions. Observation of	Losses to raptors mostly <1%, never over 5%	5% loss for an average pen of 1000 adult birds equates	Total losses 18% -pens with highest losses attributed to foxes &	Difficult to distinguish predator species responsible for kills,	Allen et al. 2000 (ADAS)



<b>Tawny owl</b>	Britain 1996	Gamekeeper questionnaire survey- raptors & managing gamebirds	1.79% pheasant losses	Total losses 18% -foxes and disease thought to be main cause  Buzzard 3.2% losses to raptors  Sparrowhawk 1.94% losses to raptors	Questionnaire: potential biases from respondents  Potential mis-assignment of kills to raptors Actual losses may be under or over-estimated due to reports of 'several' raptors rather than actual numbers involved.	Harradine et al. 1997 (BASC survey)
<b>Montagu's harrier</b>	East Anglia, England 1983-84	Dietary analysis: pellets, prey remains, plucking sites Prey identification using 4 harrier pairs. Feeding rates observed on 10 harrier nests	Pheasant comprised 8.9% pellets, 15.2% prey remains		Study focused on feeding rates & breeding in harriers  Gamebirds not reared in study area  Small sample size of raptors  Potential bias toward identifying conspicuous items in diet.  Difficult to identify numbers of individuals in prey remains	Underhill-Day 1993

Table 3: Studies of raptor predation on Capercaillie

Raptor species	Study area	Nature of evidence/data	Results relating to:			Reference	
			Numbers/productivity	Economy	Relative impact compared to other impacts		
Golden eagle Buzzard Sparrowhawk Kestrel Goshawk	Scotland 7-14 forest areas. 1991-2001	Investigated whether differences in breeding success between forests were explained by predator abundance.	Breeding success negatively related to combined influence of crows, foxes and to lesser extent raptors.		Breeding success was negatively related to index of predator abundance.  Killing foxes increased capercaillie abundance  Fox and crows have a bigger impact on capercaillie than pine martens  Gamekeeper density only weakly related to crow and fox indices, therefore did not contribute to explaining breeding success	Baines et al. 2004	
<b>Buzzard</b>	Scotland 1977-1989	Buzzard breeding success and diet	0.02% of bird remains in buzzard nests			Dietary study, no information on effects on capercaillie populations	Swann & Etheridge 1995

<b>Golden eagle</b>	Southern Scotland 1974-1980	Breeding success & diet: pellets, prey remains	Large birds- galliforms included in diet.			No detailed data on proportions of different gamebirds in diet	Marquiss et al. 1985
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Table 4: Studies of raptor predation on Black grouse

Raptor species	Study site	Nature of evidence/data	Results relating to:			Limitations of study	Reference
			Numbers/productivity	Economy	Relative impact compared to other impacts		
<b>Peregrine</b>	Northern England 1998-2000	Radio-tagged grouse (70 birds): dispersal, survival rates & causes of death recorded	39% of 26 corpses killed by raptors (probably peregrine)		Other causes of death: Foxes (7%), Stoats (30%) Disease (12%), collision fences & wires (12%)	Focus on dispersal & survival rates of grouse.  No information on raptor numbers or different species  No information on potential effects of radio-tags  Study did not detail where corpses were found	Warren & Baines 2002
<b>Buzzard</b>	Sweden 1985-93	Dietary data-prey remains & pellets Average of 14 nests observed each year	Grouse chicks comprise 4.2% diet Buzzards switch to grouse when vole densities decrease			Study focuses on the 'alternative prey hypothesis' for buzzards. No information about impact of predation on grouse.	Reif et al. 2001

<b>Buzzard</b>	Northern Scotland 1977-89	Buzzard breeding success & dietary analysis: pellets, prey remains	Black grouse 1.4% of remains of birds in buzzard nests	Effect on grouse population negligible.		Study focused on breeding success of buzzards Potential bias toward identifying conspicuous items in diet.	Swann & Etheridge 1995
<b>Peregrine</b>	Southern Scotland 1975-80	Dietary data (during breeding season): prey remains, pellets, plucking posts 367-56 peregrine territories visited each season	Black grouse comprise 1.1% diet by weight		74 bird species identified in diet Domestic pigeon most important prey species (49.4% of food)	No information on predator/prey abundances or proportion of losses	Mearns 1983
<b>Raptors</b>	Scotland 1983-	Breeding success of black grouse, causes of declines	35% (11/31) radio-tagged birds killed by predators: mainly birds of prey & foxes			Raptor species not identified. Study focused on black grouse ecology. Not peer reviewed	Picozzi & Hepburn 1984

Table 5: Studies of raptor predation on Red grouse

Raptor species	Study site	Nature of evidence/data	Results relating to:		Limitations of study	Reference
			Numbers/productivity	Economy		
Hen harrier	Data from Langholm moor and 5 other sites in Scotland (Redpath & Thirgood 1997)	Model of the impact of harrier predation on red grouse populations	Model suggests that breeding densities of harrier ( $\leq 0.3 \text{ km}^{-2}$ ) can co-exist with driven grouse shooting depending on breeding success of grouse prior to predation  Supplementary feeding of harriers may enable grouse to reach higher densities		Simple, deterministic non-cyclic model of red grouse  No information about harrier numerical response  Not peer reviewed	Redpath & Thirgood 2003

<p><b>Hen harrier Peregrine</b></p>	<p>6 sites in Scotland including Langholm estate, 1992-98</p>	<p>Grouse &amp; harrier densities, grouse losses estimated from counts, carcasses, radio-tracking. Simple model for harrier predation on grouse  Functional &amp; numerical responses</p>	<p>Raptors not associated with long-term declines in bags  Low density grouse population appear more susceptible to limitation through raptor predation than high density populations  Raptors removed 30% of potential breeding stock each spring  Hen harriers removed 37% grouse chicks in summer  Losses to harriers &amp; peregrines reduce autumn grouse densities by ~50%  Predation by peregrines alone unlikely to limit grouse populations  Red grouse comprise 15% of peregrine diet  Model predicted: in absence of raptors for 2 years grouse density in spring would be 1.9 times greater and 3.9 times greater in autumn</p>	<p>Impact of hen harrier predation greater than peregrines  Excessive grazing has reduced area of heather for grouse-considered major cause of long term decline in bags.</p>	<p>Detailed population studies on grouse conducted only at Langholm.  Data on numerical &amp; functional responses of harriers &amp; peregrine taken from different moors. Habitat differences between study areas may influence predation rates.  Few data at high grouse densities Additional data used from a study by Picozzi (1978) to measure functional response of harriers  Changes in harrier numbers in response to prey numbers represent an aggregative rather than numerical response  Simple non-cyclic deterministic model used to predict losses.</p>	<p>Thirgood et al. 2000  Redpath &amp; Thirgood 1999  Redpath &amp; Thirgood 1997</p>
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<p><b>Raptors</b></p>	<p>Scotland 10 years</p>	<p>Demographic data &amp; grouse corpses collected from 10 areas of managed moorland (6 in Scotland). Areas searched monthly. 125 corpses recovered in England, 604 in Scotland</p>	<p>Proportion of chicks taken by harriers highest at low chick densities (~67 chicks km<sup>-2</sup>) Functional responses: Harriers Type III Peregrine Type II Peregrine &amp; harrier do not respond numerically to grouse density 52% of kills attributed to raptors Suggested that predation could lead to lower breeding densities of grouse for Scottish populations, than for English populations</p>		<p>37% kills by mammals 11% other violent causes</p>	<p>Study did not demonstrate that low grouse densities resulted from raptor predation. Confounding factors: habitat loss, territorial behaviour of grouse. Some areas not checked regularly due to weather or to avoid breeding grouse</p>	<p>Hudson et al. 1997</p>
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<b>Buzzard</b>	Langholm, southern uplands of Scotland 1993	Buzzard dietary data-pellets & prey remains. 19 buzzard pairs sampled	Red grouse constituted 11% of all prey remains & 24% of all bird remains			Potential bias toward identifying conspicuous items in diet. Difficult to identify numbers of individuals in prey remains Uncertainty about selectivity of prey taken to nests	Graham et al. 1995
<b>Buzzard</b>	Northern Scotland 1977-89	Buzzard breeding success & dietary analysis: pellets, prey remains	Red grouse 15.7% of remains of birds in buzzard nests	Effect on grouse populations negligible.		Study focused on breeding success of buzzards Potential bias toward identifying conspicuous items in diet. Difficult to identify numbers of individuals in prey remains	Swann & Etheridge 1995
<b>Peregrine</b>	Table of 14 studies across Britain	Dietary data, prey remains, pluckings	Red grouse comprise 40% by weight of all prey taken by peregrines Ratcliffe estimated predation by peregrines could be 1.6-5.3% of grouse populations each year			Table of 14 studies documenting prey taken by peregrines Predation estimate based on several assumptions about average peregrine brood size, food requirements, grouse breeding success and numbers	Ratcliffe (1993)

<b>Golden eagle</b>	9 regions in Scotland 1982-85	Dietary analysis from pellets summer & winter, some prey remains Sampled 104 eagle pairs in winter, 217 pairs in summer (across 9 regions)	Tetraonids comprise 40% of diet in East Highlands. Small component of diet elsewhere	Sheep, lagomorphs, deer & miscellaneous prey major component of diet in most areas.	Dietary study Biases in data due to under representation of larger prey. Not possible to identify species in pellets consistently Small number of brief visits to large number of pairs	Watson et al. 1993
<b>Hen harrier</b>	Scotland 1987-88	Grouse breeding success- 6 paired moors with & without harriers Observation of hunting harriers & prey remains at nests	Grouse on control moors produced 17% more young than on moors with harriers Harriers removed a minimum of 24% of grouse chicks in 6 weeks after hatching Grouse chicks accounted for 32% of 299 prey items at harrier nests. Grouse populations at low density most vulnerable to high chick losses.		Bias in dietary analysis	Redpath 1991
<b>Golden eagle</b>	Scotland 1974-80	Dietary data- pellets, prey remains	Red grouse comprise ~26% of pellets collected in spring	Proportion of grouse in diet has declined with increasing afforestation as eagles forage at	Study focuses on golden eagle breeding success diet and distribution, no information on impacts on grouse	Marquiss et al. 1985

<b>Goshawk</b> <b>Hazel grouse</b>	Finland 1975-77	Prey availability & predator diet	No numerical response to grouse, marked functional response but uncertainty about shape.  Hazel grouse comprise between 4-34% diet  Estimated average predation rate on grouse ~12% breeding season.	higher altitudes above treeline	Study in Finland, no hazel grouse in UK  Functional response included data from other studies	Linden & Wikman 1983
<b>Peregrine</b>	Southern Scotland 1975-80	Dietary data (during breeding season): prey remains, pellets, plucking posts  367-56 peregrine territories visited each season	Red grouse comprise 3.7% diet	Domestic pigeon most important prey species (49.4% of food)	No information on predator/prey abundances or proportion of losses	Mearns 1983
<b>Peregrine</b>	Southern Scotland 1978-79	Winter dietary data: pellets and prey remains  Peregrines occupied 15 of 37 sites	Grouse comprise 5.4% of prey items from pluckings Grouse comprise 11.8% prey items from pellets		No information on predator/prey abundances or proportion of losses	Mearns 1982

<b>Hen harrier</b>	Northeast Scotland 1970-74	Harrier dispersion, breeding. 1 study area Dietary data- prey remains at nests	Estimated 7.4% reduction in chick numbers Red grouse chicks comprised 34% of diet			Bias with dietary data High density grouse moor, no comparison with low density moor	Picozzi 1978
<b>Red Kite</b>	Wales 1967-70	Dietary analysis: pellets, prey remains, plucking posts, direct observation 39 nest sites	Red grouse in 1/758 pellets and remains in 4 /39 nests	Effect on grouse populations negligible.	Preference for invertebrates, corvids (juveniles) & mammals in diet Carrion important Scavenging mostly in winter	Dietary study No data on kite densities, or prey densities	Walters Davies & Davis 1973
<b>Hen harrier</b>	Angus, Scotland 1956-61	Importance of predation on grouse from prey remains	Predation unimportant in limiting grouse numbers or shooting bags		Foxes & raptors killed similar proportions of grouse	Vigorous predator control employed at study site, no comparison with a moor without predator control.	Jenkins et al. 1964

## CHAPTER 3

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### **A phenomenological model of the impact of hen harrier predation on red grouse dynamics: comparing single- and multi-species functional responses.**

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#### **Abstract**

*Depredation of economically valuable prey species is a common cause of human-wildlife conflict around the world. In the UK one of the most contentious issues concerns the conflict between the conservation of hen harriers and commercial hunting of red grouse. Long-term studies in Scotland have suggested that hen harriers can limit grouse populations at low densities. However, there have been few attempts to model this interaction. Here, we used a phenomenological model for red grouse dynamics and modelled the effects of harrier predation using both a single-species and a multi-species functional response, we also accounted for the hen harriers' aggregative response to variations in prey density. The single-species model predicted that low densities of harriers could suppress grouse cycles, eventually leading to a crash in the population. Conversely, the multi-species model predicted that there is potential for driven grouse shooting and high densities of breeding harriers to co-exist if a high abundance of alternative prey is available. Our results suggest that alternative prey can strongly influence harrier consumption of grouse chicks. Hence, ignoring the effects of alternative prey could give a misleading impression of a predator's effects on its prey.*

## Introduction

Raptor predation on populations of gamebirds is a re-emerging conflict across Europe and has resulted in the widespread persecution of raptors with significant consequences for the population status of several species (Thirgood et al. 2000a; Viñuela & Arroyo 2002). Despite legal restrictions and a growing conservation ethic, persecution of raptors by hunters or gamekeepers continues since they are perceived to reduce gamebird harvests. Yet, few detailed studies of the impact of raptors on gamebird populations have been made (Newton 1992; Valkama et al. 2004; see Chapter 2). Some of the most comprehensive studies concern the hen harrier *Circus cyaneus* and the red grouse *Lagopus lagopus scoticus* system in Britain. Evidence suggests that predation by harriers may be a major factor limiting grouse populations and reducing shooting bags (Redpath 1991; Redpath & Thirgood 1999).

### *Hen harriers and red grouse: the stakeholder conflict*

The hen harrier is a rare bird of prey in the UK and, while formerly it was widespread throughout a diversity of habitats, today it is mainly restricted to the moorlands of Scotland where it feeds on red grouse chicks. The grouse-shooting industry plays an important socio-economic role in the UK. Successful management of the grouse-shooting industry depends on high population densities of grouse. Since the mid-seventies, there has been a long-term decline in grouse shooting bags in Scotland. This has been attributed primarily to habitat loss and to increased predation from foxes (Hudson 1992). However, long-term studies and measures of the functional response of hen harriers to grouse have led to the conclusion that they can limit grouse populations at low density, suppressing population cycles and reducing

shooting bags (Redpath & Thirgood 1999; Thirgood & Redpath. 2000; Thirgood et al. 2000). The perception amongst hunter stakeholders is that raptor predation is the single most important factor reducing grouse harvests, and this has resulted in widespread persecution, despite legal protection (Etheridge et al. 1997).

From a gamekeeper's viewpoint, persecution of hen harriers on grouse moors is not unreasonable (although it is illegal) because it is perceived as ensuring the viability of the shooting estate for which he or she is responsible. The viability of shooting estates is also important to conservationists because these areas help to conserve upland habitats that support a range of rare bird species and which might otherwise be converted to forestry or sheep farming (Hudson 1984). However, gamebird hunting may become unacceptable to the general public if the only way it can be sustained is by the persecution of rare birds of prey (Etheridge et al. 1997).

Several potential solutions to the harrier predation problem have been proposed including raptor translocation, raptor quotas, intraguild predation, habitat management and supplementary feeding (Thirgood et al. 2000). However, few have been rigorously tested. Managers are currently focusing on the effectiveness of supplementary feeding, however, before management strategies can be assessed it is crucial to first understand what impact hen harriers can have on grouse dynamics and numbers.

*Assessing the impact of predation: functional and numerical responses*

The impact of predation on prey populations depends largely on whether and how predators respond to changes in prey density (Redpath & Thirgood 1999). They can respond by changing their own density (the numerical response (NR)), or by changing the rate at which they consume prey (the functional response (FR)) (Solomon 1949). Functional and numerical responses, are among the most influential concepts in predator-prey theory (Boutin 1995), and the shapes of FR and NR curves have important consequences for predator-prey dynamics. An understanding of the consequences of their shape can inform long-term strategic management of problem species.

Conventionally, FR's have been divided into three types. A linear (sometimes called Type I) FR has a constant slope, which results in a constant proportion of the prey population being taken per predator at all prey densities. In a hyperbolic (or Type II) FR a decreasing proportion of the prey population is taken per predator as prey density increases. A predator with a hyperbolic FR can, in principle, drive a prey population to extinction if that population falls to low levels, for example, as a result of stochastic events. A sigmoidal (or Type III) FR implies that foraging is inefficient at low prey densities, resulting in density dependent prey mortality at low prey densities and inversely density dependent mortality at high densities (Crawley 1992). Sigmoid FR's are used to model 'switching' behaviour, where the predator increases its consumption of alternative prey species when the density of their preferred prey is low. Switching can have a stabilising effect on predator-prey dynamics (Oaten & Murdoch 1975).

A range of FR types has been observed in avian predators. In some specialist species a linear FR has been recorded within the observed ranges of prey abundance (Korpimaki & Norrdahl 1989, 1991), and some generalist predators appear to exhibit a hyperbolic FR (Wikman & Linden 1981; Nielsen 1999; Redpath & Thirgood 1999). Usually, however, generalist predators are thought to have sigmoidal FR's (Oaten & Murdoch 1975; Dale et al. 1994). For hen harriers preying on red grouse chicks, evidence suggests that the FR is indeed sigmoidal so that, at low to intermediate densities, small changes in grouse chick density can result in marked changes in predation rates (Redpath & Thirgood 1999).

An important limitation of these studies is that the FR curves are described in terms of changes in the abundance of a single prey species, with the assumption that the densities of other prey species remain constant. Information on changes in the density of alternative prey is not reported in most studies (Boutin 1995). Generalist predators eat a variety of prey items, and their response to one particular prey species may be influenced by the availability of alternative prey, this influence may dilute or exacerbate the effects of a predator on the focal prey species. For example, Kunkel and Pletscher (1999) suggested that the presence of deer may divert wolf predation from moose, allowing moose numbers to increase. Mizutani (1999) found that abundant wildlife reduces predation by leopards on livestock. Polisar et al. (2003) noted that jaguar predation on cattle was highest in areas where there was a low abundance of natural prey. There is also evidence that a high supply of natural prey may produce a numerical response in predators, resulting in 'apparent competition' (Fuller 1990; Yom-Tov et al. 1995). That is, when two prey species share a common predator, an increase in one prey species may lead to an increase in their shared

predator, causing a subsequent decline in the other prey species (Holt 1977). This may even lead to competitive exclusion of one prey (Holt et al. 1994; Bonsall & Hassell 1997).

One promising way to understand better how generalist predators adjust their diet in response to prey abundances is to document their multi-species functional response (MSFR), that is, their response to changes in the abundance of all prey species (Yodzis 1998). Asseburg et al. (in review) recently fitted an MSFR to availability and consumption data from three primary prey species of the hen harrier (red grouse, meadow pipits *Anthus pratensis* and field voles *Microtus agrestis*). Their model suggested that the presence of alternative prey could significantly reduce harrier consumption of red grouse.

An MSFR provides a more realistic representation of the way in which a generalist predator may respond to changes in prey density than a traditional single-species FR (SSFR). Consequently, it may offer a more robust foundation for assessing the impact of management action taken towards generalist predation on prey populations. In this chapter, I model the impact of harrier predation on a red grouse population, using both a SSFR and the MSFR of Asseburg et al. (in review). I first explore whether and how red grouse density, cycle amplitude and periodicity change when the availability of alternative prey is manipulated. I then consider the implications for managers of the system. This work represents one of the first attempts to model the impact of hen harrier predation on red grouse dynamics using the predator's functional response, and lays the foundations for a predictive framework that can be used to assess the

impact of predation on grouse populations, and evaluate different management strategies.

I used a simple, deterministic, discrete time modelling approach to model grouse dynamics. Difference equations are more realistic than their continuous analogue for grouse because reproduction occurs at a distinct time each year. I did not explicitly model the dynamics of hen harriers because there is no measure of their NR. Rather, I predicted variations in harrier density using their aggregative response (AR) to changes in the density of alternative prey. ARs represent a preference by consumers for patches in which the density of food is high and thus the expected rate of food consumption is highest (Begon et al. 1996). AR's should not be confused with NR's, which result from births and deaths and typically occur on a much slower time scale (Turchin 2004).

## Methods

### Red grouse population model

Around 60% of red grouse populations in the UK show cyclical behaviour (Haydon et al. 2002), but there is considerable variation in the periodicity of these cycles, with significant evidence of cyclic behaviour in the 2-15 year range (Haydon et al. 2002). In Scotland, grouse populations frequently exhibit 4-8 year cycles (Dobson & Hudson 1992). For parsimony, I do not explicitly model the mechanisms that have been proposed to cause grouse cycles (Dobson & Hudson 1992; Moss & Watson 2001; Berryman 2003; Turchin 2004) in this chapter. Instead, I rely on a generic delayed-density dependent model to mimic the dynamics that characterise red grouse populations. The model I employ is an adaptation of a density dependent function first described by Hassell et al. (1975).

$$N_{t+1} = N_t (1 + c) (1 + dN_{t-1})^{-k} \quad (1)$$

where  $N$  represents the density of red grouse  $\text{km}^{-2}$ . The quantity  $c$  is the average number of female chicks produced by a pair of grouse, and therefore,  $(1+c)$  is what May (1981) calls the ‘multiplicative growth factor per generation’ (i.e.,  $\lambda$ ). The strength of density dependence is denoted by  $k$ , and  $d$  sets the carrying capacity.

The parameters for density dependence and carrying capacity are set to values which give cycles with a period of approximately 6 years ( $c=3.3$ ,  $k=1.9$ ,  $d=0.0191$ ), and limit the amplitude of fluctuations to within plausible ranges (Minimum = 33, maximum =

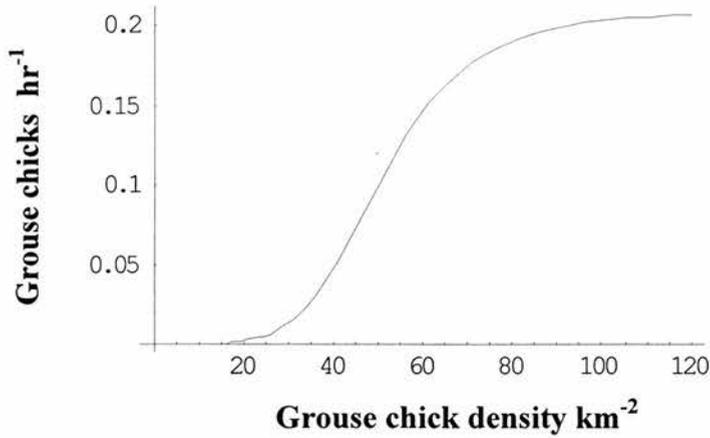
99 grouse km<sup>-2</sup>). In the field, red grouse populations are known to be quasi-cyclic (Potts et al. 1984; Haydon et al. 2002), fluctuating variably, with peaks in abundance occurring somewhat irregularly both within and between populations (Potts et al. 1984; Hudson 1992). I did not attempt to mimic this behaviour, but used biologically plausible estimates of grouse density and fecundity, and assumed that demographic rates remained constant over time. The aim was to create a plausible, if oversimplified, scenario which could be used to examine the outcome of adding predation to a grouse population undergoing cyclic dynamics, and to probe the potential consequences of different management strategies.

### **Functional response of hen harriers**

Redpath and Thirgood (1999) fitted the following sigmoidal FR to data on the relationship between the number of red grouse chicks brought back to hen harrier nest ( $f_g$ ) per hour and the density of grouse chicks ( $n_g$ ) at the beginning of the harrier breeding season.

$$f_g = cn_g^\theta (d^\theta + n_g^\theta)^{-1} \quad (2)$$

where  $c$  is the maximum killing rate and  $d$  is the half-saturation constant (i.e. grouse density at which 50% of the maximum consumption occurs).  $\theta$  is an exponent that regulates the nonlinear relationship between numbers of prey consumed and grouse density. Figure 1 shows the curve they fitted to their data.



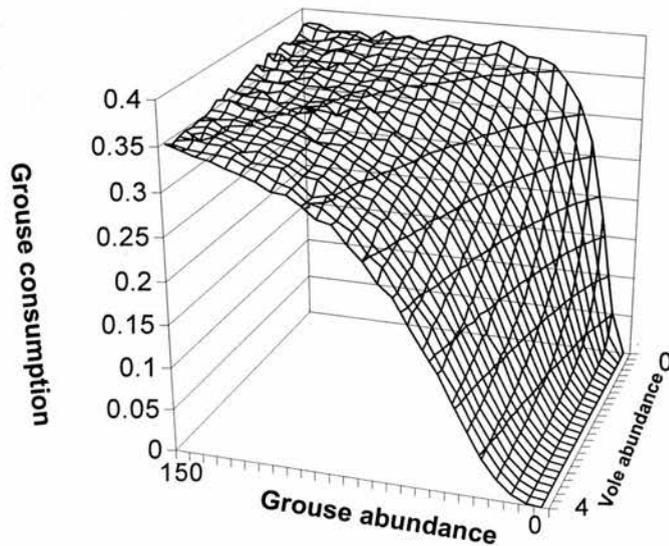
**Figure 1.** Rate at which grouse chicks are brought to harrier nests in relation to the density of grouse chicks. The fitted curve is:  $f_g=0.21n_g^{5.1}/(51^{5.1}+n_g^{5.1})$  (Reproduced from Redpath & Thirgood, 1999).

Extending this work, Asseburg et al. (in review) incorporated information on the numbers of alternative prey (meadow pipits and field voles) consumed by hen harriers, and their densities, to fit an MSFR of the form

$$f_i = \frac{a_i n_i^{m_i}}{1 + \sum_j b_j n_j^{m_j}} \quad (3)$$

where  $f_i$  is consumption of prey  $i$  per hour, and  $n_i$  denotes the abundance of prey  $i$ . The quantity  $a_i$  represents the attack rate of the predator on species  $i$ . The ratio  $a_i/b_i$  gives the maximum possible rate of consumption for prey  $i$ .  $m$  is an index which relates the way the predator attack rate changes with prey density, the effect is to change the

curvature of the functional response (Asseburg et al. in review). The MSFR can be reduced to a SSFR by setting alternative prey abundances to zero. Figure 2 illustrates how the contours of the MSFR change with the abundance of alternative prey.



**Figure 2.** Hen harrier consumption of red grouse in response to changes in grouse density and vole density (both in individuals  $\text{km}^{-2}$ ). The FR to grouse appears sigmoidal at different levels of vole abundance. As vole density increases, the contours of consumption move toward higher levels of grouse density (Asseburg & Smout, unpublished).

The MSFR describes the response of individual predators, it does not account for any intraspecific competition or interference between harriers. However, male harriers, unlike many other British raptors, are not strongly territorial, and appear to be relatively tolerant of each other (Newton 1979; Redpath 1991; Redpath & Thirgood 1999). Nor does it account for prey depletion, nest site variation or harrier mating

system, all of which may influence predation rates. The MSFR was fitted using Monte Carlo Markov Chain methods (see Asseburg et al. in review). For the deterministic model I used the means of 200 random draws from the posterior distributions for each of the MSFR parameters (Table 1) (data provided by C. Asseburg).

**Table 1.** Mean parameter values for the MSFR.

$a_g$	$a_v$	$a_{mp}$	$m_g$	$m_v$	$m_{mp}$	$t_g$	$t_v$	$t_{mp}$	$b_g$	$b_v$	$b_{mp}$
0.0007	3.757	1.821	2.505	1.134	1.199	2.694	2.249	1.699	0.002	8.451	3.095

The FR is for prey consumed per harrier, per hour. Given that harriers hunt for 15 hours day<sup>-1</sup>, and feed their chicks for around 60 days year<sup>-1</sup> (Redpath & Thirgood 2003), harrier consumption was rescaled to a yearly rate (equivalent to 900 hrs of foraging) and multiplied by the density of harriers km<sup>-2</sup> ( $H$ ) to estimate the number of grouse removed km<sup>-2</sup> year<sup>-1</sup>. I incorporated predation into the grouse model by subtracting the off-take estimated from the FR from the total grouse population.

$$N_{t+1} = [(N_t(1+c) - Hqf_g)(1 + dN_{t-1})^{-k}] \quad (4)$$

where  $q$  is a scaling constant for the time harriers spend hunting each year.

### **Aggregative response of hen harriers**

Hen harriers tend to aggregate in regions with high densities of meadow pipits and field voles (Redpath & Thirgood 1999; Redpath et al. 2002), resulting in a local increase in predator numbers. I used the following linear equation fitted to abundance data (Redpath & Thirgood, unpublished data) collected between 1992-1998 from 6 different moorlands to describe this AR:

$$H = 0.00263 n_{mp} + 0.000124 n_v \quad (5)$$

where  $n_{mp}$  is meadow pipit density and  $n_v$  refers to voles. The relationship explains 75% of the variation in the data. I rescaled abundances of meadow pipits and voles from their original units of counts  $\text{km}^{-1}$  transect and captures per 100 trap nights respectively, to numbers  $\text{km}^{-2}$ , to match the units used for the FR. Meadow pipit abundance explains far more of the variance in hen harrier density than field vole numbers, and so I concentrated on this aspect of the relationship. I looked at the effect of increasing harrier densities on grouse dynamics by running simulations for a range of meadow pipit densities (e.g., 10, 50, 90, 130  $\text{km}^{-2}$ ). I also investigated what happened when the number of harriers remained constant while the abundance of alternative prey changed.

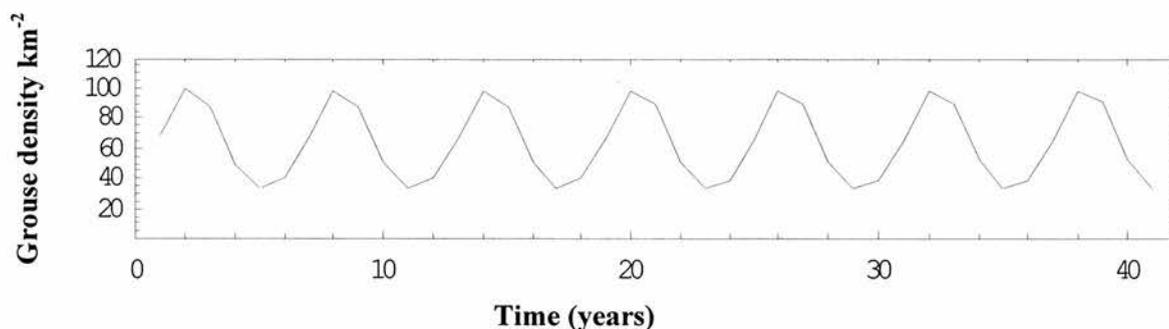
Model simulations were carried out using Mathematica 4.1. I ran the models over 2000 timesteps with an initial adult grouse density of  $40\text{km}^{-2}$  in the first year and  $30\text{km}^{-2}$  in the second year, and used the last 40 years to measure cycle amplitude, periodicity and mean density. Cycle amplitude was estimated as the ratio of maximum

to minimum density, and period from the dominant frequency in a spectral density diagram. (See Appendix 3.1 for model code).

## Results

### Red grouse model

Equation (1) describes a population with cyclic dynamics (Fig. 3). In the absence of predation, cycle period is approximately 6 years, population size ranges between 33-99 grouse  $\text{km}^{-2}$  with an average density of 63 birds  $\text{km}^{-2}$  and amplitude of 3.



**Figure 3.** Red grouse population density  $\text{km}^{-2}$  in the absence of hen harriers. Initial grouse density was  $40 \text{ km}^{-2}$ .

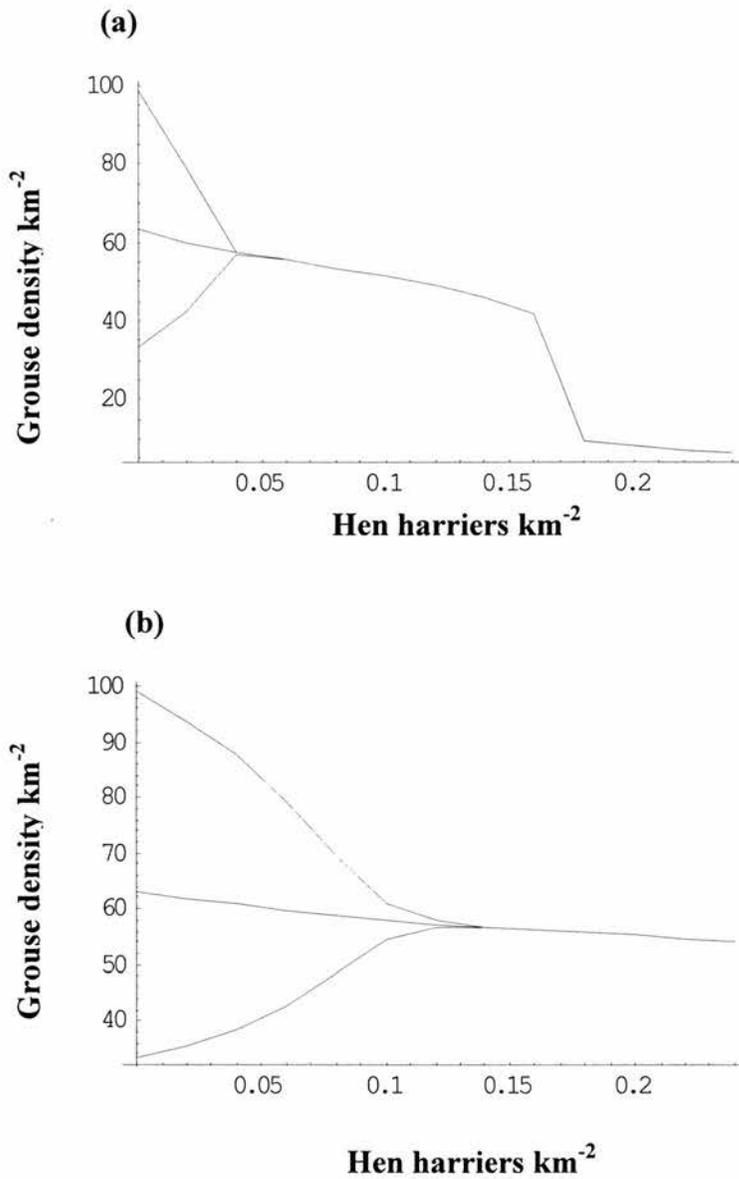
### *Predation model using a single-species functional response*

I generated a simple one predator-one prey system by incorporating the harriers' SSFR into the model. Figure 4(a) shows the relationship between harrier density and minimum, maximum and mean grouse densities. This relationship was non-linear: as hen harrier density increased, grouse cycle amplitude dampened rapidly, converging to a stable point equilibrium of  $55 \text{ grouse km}^{-2}$  at a harrier density of  $0.06 \text{ km}^{-2}$ . As harrier density increased above this level, equilibrium grouse density gradually

declined until harrier numbers exceeded  $0.16 \text{ km}^{-2}$ , whereupon the population crashed to  $9 \text{ grouse km}^{-2}$ .

*Predation model using a multi-species functional response*

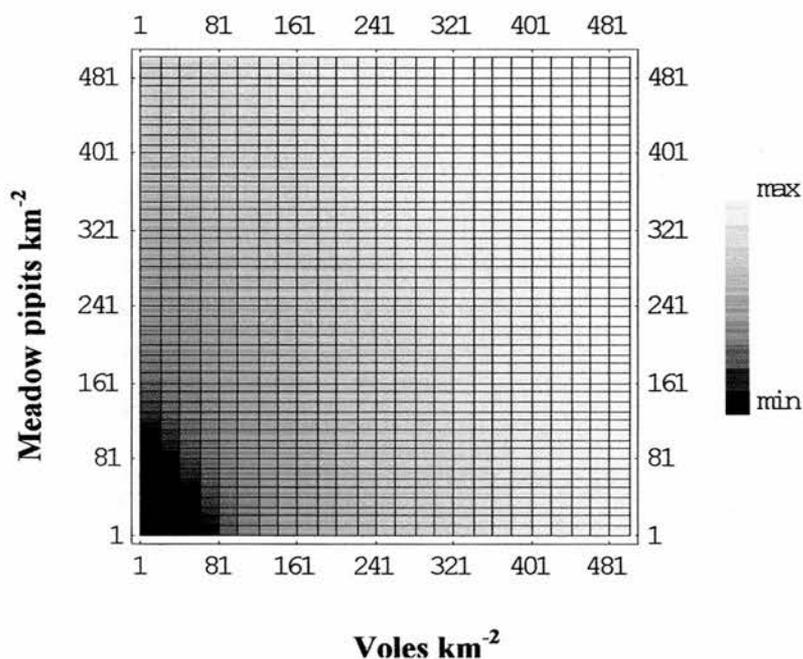
Incorporating a MSFR into the model resulted in a 1-predator 3-prey system. Figure 4(b) illustrates how the dampening effect of predation seen in Figure 4(a) diminished when a constant, and relatively low, number of alternative prey were present ( $100 \text{ voles km}^{-2}$  and  $60 \text{ meadow pipits km}^{-2}$ ). Cycle amplitude converged to a stable point equilibrium of  $56 \text{ grouse km}^{-2}$  at a harrier density of  $0.14 \text{ km}^{-2}$  and declined further to  $50 \text{ grouse km}^{-2}$  when harrier density reached  $0.4 \text{ km}^{-2}$



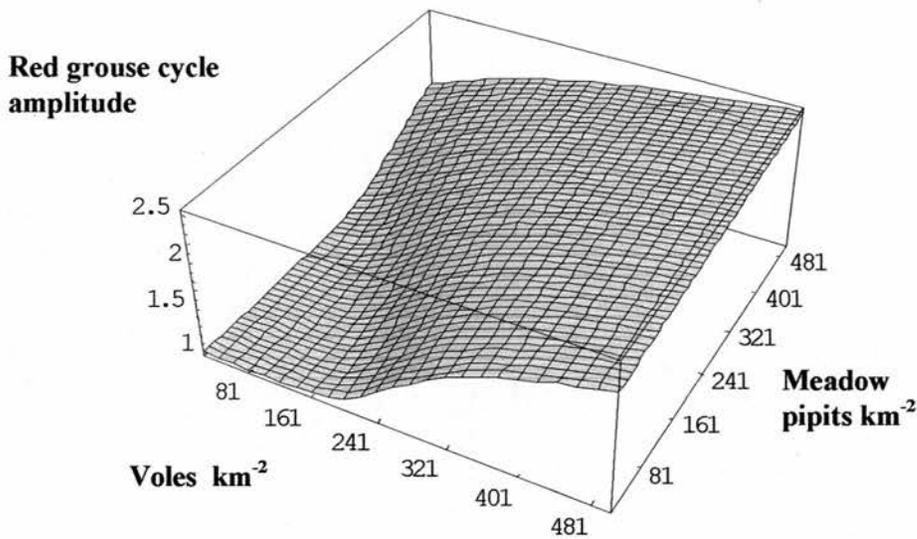
**Figure 4.** Variation in minimum, maximum, and mean grouse densities ( $\text{km}^{-2}$ ) with increasing harrier density. (a) Using a SSFR, (b) Using a MSFR with a constant density of alternative prey ( $100 \text{ voles km}^{-2}$ ,  $60 \text{ meadow pipits km}^{-2}$ ).

When harrier density was held constant at  $0.14 \text{ km}^{-2}$  and the density of alternative prey was increased, mean grouse density (Fig. 5) and cycle amplitude increased (Fig. 6). Across the range of alternative prey densities mean grouse density increased by

26% and amplitude more than doubled, indicating that grouse cycles return when high densities of both meadow pipits and voles are present. Increasing the density of meadow pipits when vole density was kept low had little effect on cycle amplitude, but increasing the density of voles when pipit densities were low had a strong effect. Increasing alternative prey densities beyond the ranges shown in Figures 5 and 6 had little additional effect on either metric. The effect of alternative prey on cycle periodicity was trivial.



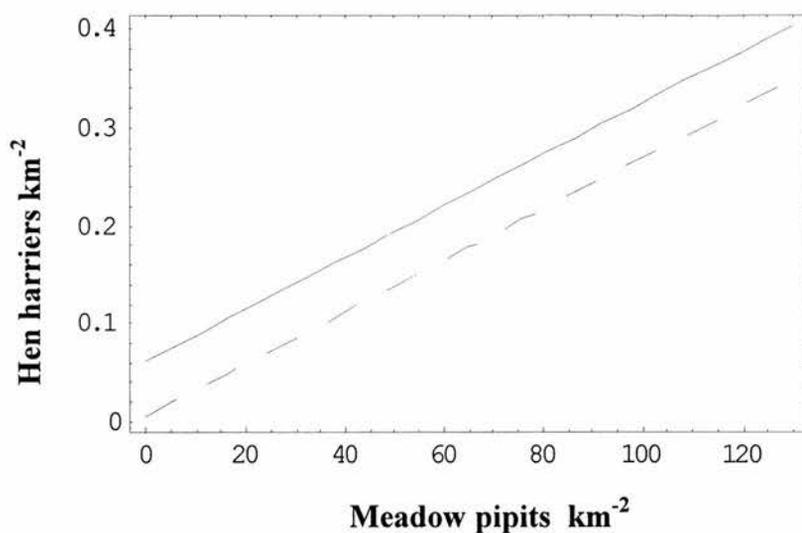
**Figure 5.** Density plot showing the relationship between mean grouse density (range is 45-61 grouse km<sup>-2</sup>) and the densities of meadow pipits and field voles with a population of hen harriers at a density of 0.14 km<sup>-2</sup>.



**Figure 6.** Relationship between grouse cycle amplitude and the density of alternative prey when harrier density is  $0.14 \text{ km}^{-2}$ .

*Incorporating the hen harriers aggregative response*

The analysis presented above was based on the assumption that harrier densities is unaffected by the density of alternative prey. In reality, harriers show an AR to alternative prey density. I used equation (5) to investigate the effect of this relationship on grouse dynamics. The predicted relationship between harrier and alternative prey densities is illustrated in Figure 7. Here, vole numbers were held constant at either high or low values. A ten-fold increase in vole abundance had a small effect on harrier density, whilst small increases in meadow pipit density yielded a far stronger influence.



**Figure 7.** Harrier density in relation to meadow pipit abundance when voles are constant at  $50 \text{ km}^{-2}$  (dashed line) and  $500 \text{ km}^{-2}$  (solid line).

Table 2 summarises how grouse population density changed as harrier density increased in response to changes in alternative prey densities. In the worst case scenario, when there were  $0.34 \text{ harriers km}^{-2}$  and no voles, mean grouse density was reduced by 25% and cycle amplitude from 3 to 1. However, when voles were abundant mean density declined by only 9.5%, although, amplitude remained low at 1.1.

**Table 2.** Mean, minimum and maximum grouse density for a range of alternative prey and harrier densities.

Meadow pipits $\text{km}^{-2}$	0			10			50			90			130		
Voles $\text{km}^{-2}$	0	50	500	0	50	500	0	50	500	0	50	500	0	50	500
Hen harriers $\text{km}^{-2}$	0	0.006	0.06	0.02	0.03	0.08	0.13	0.14	0.19	0.24	0.25	0.3	0.34	0.35	0.4
Grouse density $\text{km}^{-2}$															
Mean	63	62	62	58	59	61	52	55	60	49	52	58	47	51	57
Minimum	33	34	35	47	41	36	52	55	41	49	52	48	47	51	55
Maximum	99	97	95	71	81	92	52	55	81	49	52	69	47	51	60

## Discussion

The impact of predation on prey populations has been a topic of scientific debate for decades, and currently lies at the heart of a number of human-wildlife conflicts involving raptors and gamebirds throughout Europe. Although raptors are often persecuted because they are predators of socio-economically valuable game species, there is little empirical information about their impact on prey populations (Newton 1992; Valkama et al. 2004) and, consequently, there is no framework for effectively managing such systems.

Understanding a predator's FR and NR is important for assessing its potential to limit prey populations. However, few studies have quantified predators' FRs or NRs; and those that have frequently considered single prey species only (Schmitz 1995; Valkama et al. 2004). For generalist predators, such as the hen harrier, the rate of predation on a certain prey species may be strongly influenced by the availability of alternative prey. In theory, switching behaviour can alleviate predation pressure on any one prey type and promote persistence of both prey and predator populations (Maynard Smith 1974; Andersson & Erlinge 1977; Van Baalen et al. 2001).

The hen harrier-red grouse system has been extensively studied over the past decade and a SSFR, an AR and an MSFR have been quantified for harriers. However, to date, our understanding of the impact of harriers on grouse populations has been based on a comparison of grouse breeding success and different harrier densities. Modelling has focused on simple, non-cyclic grouse dynamics without any consideration of the effects of alternative prey on harrier consumption of grouse chicks. Here, I developed a simple cyclic model for grouse dynamics and incorporated both the MSFR and AR of harriers

to three prey species and compared the results to those of a simple 1 predator-1 prey model.

Theoretical studies suggest that generalist predators may be able to stabilize fluctuations in their prey if predator densities are unrelated to prey densities, and if their FR results in some density dependent predation (Hanski et al. 1991). Hen harriers do not respond numerically to red grouse and Redpath and Thirgood (1999) have argued that harrier predation could dampen grouse cycles and “trap” grouse at a low density equilibrium. Overall, the results of this study supported these predictions, although the extent of the impact of predation varied between models.

The results from our first model, which used a SSFR for harrier consumption, suggested that harriers could have a severe impact on grouse populations, stabilizing cycles at relatively low predator densities and causing the population to crash at intermediate predator densities.

In the second model we incorporated a MSFR, accounting for voles and meadow pipits in the harriers’ diet. With constant and relatively low densities of alternative prey, grouse cycles were stabilized, but at much higher densities of harriers than suggested by the model with an SSFR. Further, the multi-species model did not predict a crash in the grouse population, even at high harrier densities. When harrier density was held constant (which in a management context is akin to implementing a raptor quota) and the density of alternative prey increased, grouse cycles returned and mean grouse density increased.

In the third model, I added an AR to account for the relationship between alternative prey densities and harrier density. The density of harriers on a moor is set, essentially, by the abundance of meadow pipits. However, voles have a stronger indirect influence on harrier consumption of grouse. Redpath (1991) suggested that increasing alternative prey densities may increase harrier densities, culminating in an overall increase in mortality of red grouse chicks. This effect was demonstrated by Kenward (1986) who found that an increase in rabbit numbers attracted more goshawks *Accipiter gentiles* and resulted in greater pheasant *Phasianus colchicus* losses. Similarly, our model predicted that when harrier density increased in response to increasing pipit density grouse cycles stabilised and the equilibrium density declined. However, when voles were abundant, cycles persisted, even at high harrier densities. This result supports the findings of Marcstrom et al. (1988) who studied predation on tetraonid populations in Sweden, and concluded that large vole populations reduced predation on breeding grouse. Similarly, Reif et al. (2001) found that the proportion of grouse consumed by buzzards *Buteo buteo* in Finland was negatively related to the abundance of voles.

The conventional aim of management for grouse moors is to maximize the number of grouse available for shooting. Hudson (1992) determined that driven grouse shooting would only be financially viable when densities exceed 60 birds km<sup>-2</sup>. For the given set of parameter values, the first and second models suggested that mean grouse density would decline below this threshold once harrier density exceeded 0.02 km<sup>-2</sup> and 0.06 km<sup>-2</sup>, respectively. However, grouse persisted at densities of around 60 birds km<sup>-2</sup> with harrier densities as high 0.2 km<sup>-2</sup>, provided there were high densities voles. This far exceeds the level recommended by Potts (1998) (0.04 breeding harriers km<sup>-2</sup>) to fulfill the needs of both harrier conservation and grouse management.

The results presented here demonstrate that ignoring the effects of alternative prey can give a misleading impression of a predator's effects on its prey, which could result in ineffective management practises. For instance, basing management strategies on predictions of the first model with an SSFR could lead to calls to reduce harrier numbers in order to increase grouse density, and may exacerbate the ongoing problem of illegal persecution of harriers. However, a model incorporating both the MSFR and NR suggests that grouse shooting can coexist with high densities, and that management should focus on maintaining high densities of alternative prey, particularly voles, possibly via habitat manipulation or by supplementary feeding using voles rather than meadow pipits.

These results support the growing realization that a single-species approach to managing biodiversity is inadequate (Yodzis 1994; Estes 1996; Mangel 1996) and that, contrary to widespread perceptions, there is potential for driven grouse shooting and high densities of breeding harriers to co-exist. My approach to model building in this chapter has been 'strategic' (May 1973): I have sacrificed precision in an effort to gain general insights and principles. Even though the models do not correspond in detail to any single real community, they provide a simple framework for investigating the impact of harrier predation on grouse dynamics, and how model structure may influence predictions. The phenomenological nature of the models means that they may serve as a template for making predictions about other, similar systems.

In the next chapter, I use a mechanistic modeling approach, postulating the ecological nature of state variables that drive red grouse dynamics. In doing so, I aim to improve the realism of the models and gain insight about the interaction between predation and the mechanisms that cause grouse cycles.

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### **Appendix 3.1. Mathematica code for phenomenological harrier-grouse model**

```

fMeanPop[rmp_, nv_, tmax_] :=
Module[{a = 0.0191, b = 1.9, c = 3.3
, k = 900, (*h=0.14*), h = rmp*0.00263 + nv*0.0001241,
th = 5.1, ag = 0.0007025, amp = 1.82139, av = 3.7569,
tg = 2.6944, tmp = 1.6995, tv = 2.24958, mg = 2.505,
rmp = 1.19986, mv = 1.134, bg, bmp, bv, pdel, pt},
bmp = amp*tmp;
bv = av*tv;
bg = ag*tg;

pdel =
NestList[
{#[[2]],
(#[[2]] + c*#[[2]] -
h*k*(ag*(c*#[[2]])^mg) /
(1 + bg*(c*#[[2]])^mg + bmp*rmp^rmp +
bv*nv^mv)) * (1 + a*#[[1]])^(-b)} &,
{40, 30}, tmax];
pt = Transpose[pdel][[1]];
pt = Table[pt[[i]], {i, 900, tmax}];

Return[pt]
(*Return[Mean[pt]]*)
(*Return[Max[pt]/Min[pt]]*)

(*sp=Abs[Fourier[pt]];
sp[[1]]=0;
per=N[(tmax-900)/Position[sp,Max[sp]][[1,1]]];
Return[per];*)

];

```

## CHAPTER 4

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### **The impact of hen harrier predation on red grouse dynamics: two mechanistic models.**

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#### **Abstract**

*Current research on red grouse cycles focuses on two hypotheses: one involving intrinsic factors; and the other, interactions with macroparasites. Here, for the first time, I used both models to investigate the impact of hen harrier predation on red grouse dynamics. The aim was to gather insight into the interaction between predation and the state variables that have been proposed to drive grouse cycles, and to improve the realism of past models of the predator-prey system. I was also interested in whether the predictions of phenomenological and mechanistic models were similar. The results show that there is good qualitative and quantitative agreement between the host-parasite model and the simple phenomenological model: hen harriers can stabilise grouse cycles, but, with a high abundance of alternative prey, driven grouse shooting is still viable across a range of harrier densities. The extent of the impact of predation differed between mechanistic models: the intrinsic model predicted a minimal effect, whereas the impact was stronger under the host-parasite model. Under all models, single-species and multi-species functional responses generated different predictions about the impact of a predator on its prey. The interaction between predation and red grouse cycle mechanisms was indirect.*

## Introduction

The illegal killing of raptors on moorland areas across the UK is considered to be one of the principal threats to UK populations of hen harriers (*Circus cyaneus*), peregrine falcons (*Falco peregrinus*) and golden eagles (*Aquila chrysaetos*) (Watson 1997). In many cases, despite legal protection, raptors are killed because of the perception that they can reduce the size of red grouse (*Lagopus lagopus scoticus*) harvests. The hen harrier is thought to be the most persecuted bird in the UK (Bibby & Etheridge 1993; Etheridge et al. 1997; RSPB 2002), and is on the country's red list of species of high conservation concern (BCCP 1996) due to its historic decline and unfavourable conservation status in Europe (Tucker & Heath 1994). Severe persecution restricted hen harriers to the Orkneys and Western Isles by the end of the 19<sup>th</sup> century. The slow recovery observed throughout the 20<sup>th</sup> century now seems to have reached stagnation with persecution on grouse moors believed to be the major factor holding the number of breeding birds well below its estimated historical level (Potts 1997). A study by Etheridge et al. (1997) suggested that, in the absence of illegal killing, the population of hen harriers in Scotland would increase, initially by 13% per year.

Despite widespread speculation and debate concerning the effects and management of harrier predation on grouse populations over the last few decades, models quantifying the impact have been slow to emerge. Early work by Thirgood et al. (2000a) involved a simple non-cyclic model where the reproductive rate of red grouse was varied in the presence and absence of raptors. The model predicted that raptor predation could reduce mean autumn grouse densities by up to 50%. Redpath and Thirgood (2003) subsequently attempted a more quantitative approach by incorporating a single species functional response (SSFR) of hen harriers to grouse density into the non-

cyclic model. The model suggested that driven shooting could co-exist with breeding harriers over a range of grouse and harrier densities, although very high harrier densities could prevent grouse numbers from reaching the minimum threshold for shooting (Redpath & Thirgood 2003). In Chapter 3, I developed a phenomenological model for cyclic grouse dynamics and incorporated the hen harriers' MSFR and AR in order to investigate the effects of alternative prey on hen harrier consumption and abundance. The results suggested that high densities of alternative prey could substantially reduced the impact of predation and indicated that there is potential for driven grouse shooting over a wide range of harrier densities.

Here, I build on earlier work by modelling the impact of hen harrier predation using two different mechanistic models for grouse dynamics. In so doing, I aim to gather insight into the interactions between predation and the state variables that have been proposed to drive grouse cycles, as well as improve the realism of past models for the harrier-grouse system. Again, I compare model predictions using a SSFR and a MSFR, and also examine whether the predictions of phenomenological and mechanistic models are qualitatively and quantitatively similar. This work provides the first comparison between the intrinsic and extrinsic hypotheses for red grouse cycles.

## **Mechanisms for red grouse cycles**

The red grouse *Lagopus lagopus scoticus* is a socio-economically valuable gamebird of heather moorlands, whose populations are managed to promote high densities for sports-shooting (Miller 1980). Populations of red grouse show cyclic fluctuations in numbers, a phenomenon that has concerned gamekeepers and hunters, and fascinated ecologists, for well over a century (Hudson et al. 2002). Several mechanisms, including food, predators and hunting have been ruled out as explanations for grouse cycles (Hudson et al. 1992; Moss & Watson 2001; Turchin 2004). The debate remains fixed on two hypotheses, both of which have gained some measure of theoretical and empirical support: the interaction between grouse density and macroparasite infection; and the role of intrinsic factors, such as territoriality and aggressiveness.

The parasite hypothesis proposes that grouse cycles are generated by parasite-induced reductions in host fecundity and survival, interacting with the degree of parasite aggregation and stochastic effects (Dobson & Hudson 1992; Hudson 1992; Hudson et al. 1992; Hudson et al. 1998). According to the aggressive territorial hypothesis, population cycles are caused by delayed density-dependent changes in the aggressiveness and spacing behaviour of male red grouse (Mountford et al. 1990; Moss et al. 1996; Matthiopoulos et al. 1998, 2000, 2002, 2003; Mougeot et al. 2003).

Support for these competing hypotheses has fluctuated over time. The case for disease-induced cycles received widespread support following studies which described the presence of large numbers of nematode worms in grouse (Cobbold 1873; Dougall 1875; Lovat 1911). Focus later shifted to the role of spacing behaviour in the population dynamics of grouse, and by the 1970's there was general consensus

that competition determined population densities, and that variations in parasite prevalence were a consequence of social exclusion (Jenkins et al. 1963).

In 1978 Anderson and May published a theoretical framework which allowed the dynamics of the host-parasite relationship to be captured accurately. They identified the potentially destabilising role of parasite infection and described how this could generate oscillations in host abundance. Dobson and Hudson (1992) used this framework to develop an empirically based model of the grouse-nematode parasite system, which, when parameterised, captured the correct structure of density dependence in grouse populations in Northern England. Experimental studies with anti-helminthic drugs lent strong support to this hypothesis because they resulted in increased host fecundity (Hudson 1986; Hudson et al. 2002) and reduced cycle amplitude (Hudson et al. 1998).

Elsewhere, investigations into the role of intrinsic factors lead to the proposal of a mechanism based on differential behaviour towards kin and non-kin (Mountford et al. 1990; Watson et al. 1994; Matthiopoulos et al. 1998). However, a lack of experimental evidence contributed to the view that social and intrinsic mechanisms were unlikely to generate regular cycles (Stenseth & Ims 1980). Recently, however, an experimental investigation of aggressive and territorial behaviour of male red grouse on English and Scottish moorlands demonstrated that intrinsic processes can have fundamental effects on population dynamics. Mougeot et al. (2003) showed that increasing the aggressiveness of territorial cocks using testosterone implants, reduced recruitment and breeding density of red grouse in the following year and changed population trajectories from increasing to declining.

## The host-parasite hypothesis

The nematode *Trichostrongylus tenuis* is a specialist enemy of red grouse which inhabits the caeca of adult birds. Nematode eggs pass from the host and develop into an infective larval stage. The infective larvae then migrate to the growing tips of the principle plant food plant of grouse, heather *Calluna vulgaris*, and infection occurs when the larvae are ingested by feeding grouse. Once inside the bird, the larvae move toward the caeca and may enter a period of arrested development (hypobiosis) (Hudson et al. 1992). Time delays caused by hypobiosis, together with changes in the growth rate of the grouse population, explain variations in grouse cycle period (Dobson & Hudson 1992). However, the main cause of oscillations is the interaction between the parasite and host fecundity. Cycles occur when the ratio of parasite-induced reduction in host fecundity to parasite-induced reduction in host survival is greater than the degree of parasite aggregation within the host population (Hudson et al. 2002).

### *Model structure*

To model the dynamics of the red grouse-nematode parasite system, Dobson and Hudson (1992) employed the theoretical framework developed by Anderson and May (1978), but with a slightly different parameterisation and the addition of direct density dependence in the host population to capture the role of territorial behaviour. The model consists of three coupled differential equations describing changes in the number of hosts ( $N$ ), free-living larvae ( $D$ ), and adult parasites ( $T$ ).

$$\frac{dN}{dt} = (a - b)N - wN^2 - (\alpha + \delta)T \quad (1)$$

$$\frac{dD}{dt} = \frac{\lambda TN}{N + N_o} - (\mu_D + b + \theta)D - \alpha \frac{TD}{N} \quad (2)$$

$$\frac{dT}{dt} = \theta D - (\mu_T + b + \alpha)T - \alpha \frac{T^2}{N} \left( \frac{k+1}{k} \right) \quad (3)$$

The parameters used in these equations are defined in Table 1. They correspond to the birth and death rates of the host and parasite at each stage of their life cycles. The term  $wN^2$  in equation (1) results in self-limitation in the grouse population. The model assumes that the free-living stages are short-lived compared with the dynamics of the adult worms, arrested larvae or hosts. Transmission probability is determined by the parameter  $N_o = \gamma/\beta$ . The proportion of free-living larvae that successfully establish in hosts is  $N/(N + N_o)$ .

**Table 1.** Population parameters for *T. tenuis* and red grouse.

Symbol	Parameter	Estimated value
$a$	Grouse fecundity	2.24 year <sup>-1</sup>
$b$	Grouse mortality	1.055 year <sup>-1</sup>
$\lambda$	Parasite fecundity	8.5 year <sup>-1</sup>
$\mu_T$	Adult worm mortality	1.24 year <sup>-1</sup>
$\mu_D$	Arrested larvae mortality	0.6 year <sup>-1</sup>
$\gamma$	Mortality of free-living parasite stages	9 year <sup>-1</sup>
$\theta$	Rate at which arrested larvae develop into worms	50
$\alpha$	Parasite pathogenicity	$2.27 \times 10^{-4}$ worm <sup>-1</sup> year <sup>-1</sup>
$\delta$	Parasite reduction in host fecundity	$5.031 \times 10^{-4}$ worm <sup>-1</sup> year <sup>-1</sup>
$k$	Aggregation of parasites in hosts	0.5
$\beta$	Transmission rate	0.1 larvae <sup>-1</sup> host <sup>-1</sup> year <sup>-1</sup>
$N_0$	Transmission constant	$\gamma/\beta$
$w$	Density dependent reduction in grouse breeding success	0.0023 grouse <sup>-1</sup> year <sup>-1</sup>

Derivation of parameter estimates is discussed in Hudson et al. (1992) and Dobson and Hudson (1992). Values here have been chosen from within the ranges given by Dobson and Hudson (1994).

### The aggressive, territorial hypothesis

The proposed impact of territorial behaviour on long-term population dynamics emerges from the interaction between aggressiveness and population density (Watson & Jenkins 1968; Watson 1985; Moss, Parr & Lambin 1994). Red grouse are territorial birds and population change is driven primarily by the recruitment of young to the territorial population (Watson & Jenkins 1968). During the autumn, cocks take up territories whose size is related to the overall level of aggressiveness in the population. Aggressiveness is affected by the density of young and old cocks taking part in the territorial contest. In a population with many aggressive competitors,

young birds stand a low chance of establishing territories. This is thought to cause a population decline that is only reversed when density drops low enough for aggressiveness and territorial requirements to lessen (Mougeot et al. 2003).

### *Model structure*

I used a model developed by Matthiopoulos et al. (2003). This involves a discrete-time approach because fecundity, mortality and recruitment occur at different times in the red grouse life cycle. The model comprises two coupled difference equations with two state variables: the number of males in the territorial population ( $G$ ) and the aggressiveness of territorial cocks ( $A$ ).

$$G_{t+1} = G_t (s + d_t / (1 + jA_t G_t (1 + d_t))) \quad (4)$$

$$A_{t+1} = A_t (1 - L + (U + L) L G_{t+1}^c / G_e^c U + L G_{t+1}^c) \quad (5)$$

The model tracks male numbers because it is assumed that only territorial birds reproduce, and the number of territories is determined by the interactions between males only. Hens gain territories by associating with cocks and therefore cock numbers determine hen numbers (Moss et al. 1996; Matthiopoulos et al. 2003). To find total population density,  $G$  must be multiplied by two, assuming birds are monogamous.  $s$  is the yearly survival rate of adult cocks, and  $d$  is breeding success. The term in the denominator of equation (4) describes recruitment, (i.e. the proportion of young cocks born in the spring of year  $t$  that are recruited into the population in autumn  $t$ ).  $G_t(1+d_t)$  is the density of cocks competing for territories in autumn of year

$t$ , and  $j$  is an arbitrary constant determined by the characteristics of the environment (see Matthiopoulos et al. 2003).

Under the given set of parameter values (Table 2), the model produces grouse cycles with a period of 8 years, close to that of the phenomenological model described in Chapter 2.  $U$  and  $L$  in equation (5) represent the maximum and minimum by which aggressiveness can increase or decrease within a year.  $C$  is a control parameter affecting the slope of the function around  $G_e$ , the equilibrium density of territorial cocks. Survival and breeding success were determined from field studies (Hudson 1986; Moss & Watson 1991; Dobson & Hudson 1994; Moss et al. 1996). The values of the remaining parameters were chosen arbitrarily from within the ranges used by Matthiopoulos et al. (2003); these only influence maximum population size and not the qualitative dynamics of the system.

**Table 2.** Parameter values used in territorial grouse model.

Symbol	Parameter	Value
$s$	Survival rate	0.5
$d$	Breeding success	1.3
$U$	Max annual increase in aggressiveness	1.73
$L$	Min annual increase in aggressiveness	0.97
$C$	Shaping parameter	55
$G_e$	Autumn density at which $A_{t+1}=A_t$	24

All values are from Matthiopoulos et al. (2003).

## Incorporating predation into models

I incorporated hen harrier predation into both mechanistic models using the MSFR of Asseburg et al. (in review), and set alternative prey abundances to zero to generate a SSFR. Parameter values for the MSFR are given in Table 1 of Chapter 3. The parasite model was modified to include the effects of hen harrier predation by subtracting the FR from the total grouse population. Thus, equation (1) is replaced by:

$$\frac{dN}{dt} = (a - b)N - wN^2 - (\alpha + \delta)T - Hqf_g \quad (6)$$

Where  $H$  is hen harrier density,  $q$  is a scaling constant for the time an individual harrier spends hunting each year and  $f_g$  is the harriers' functional response to the density of grouse chicks.

With the territorial model, simply subtracting the consumption of grouse chicks from the total grouse population would imply that predators only take prey from the recruited population, which is untrue. Instead, I used the FR to update the parameter for breeding success  $d_i$  at different population densities. When hen harriers are present  $d_i$  becomes  $d'$

$$d' = d - \frac{Hqf_g}{G_i} \quad (7)$$

where  $d$  is a constant. To simplify notation, equation (7) can be written as  $d' = d - l$ , where  $l$  represents the total number of chicks taken by harriers from each adult grouse annually. The expression in equation (7) is not guaranteed to be positive. A negative  $d'$  implies that more grouse chicks are consumed than are produced in any given year. I avoided this in the simulations by limiting the minimum value of  $d'$  to zero. However, this restriction was never actually required and therefore did not influence the results.

In both models I used the same AR as had previously been used in the phenomenological model (see Chapter 3)

$$H = 0.00263n_{mp} + 0.00012n_v \quad (8)$$

where  $n_{mp}$  is meadow pipit density and  $n_v$  refers to voles.

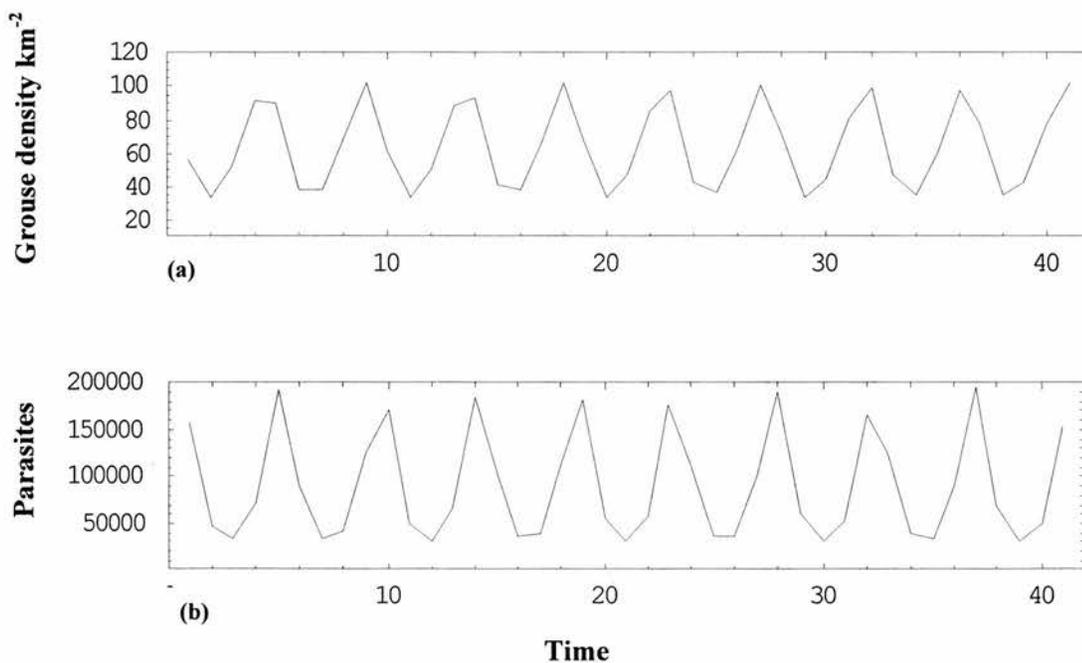
Parameters values for the mechanistic models were set to produce grouse cycles with the same mean and amplitude in the absence of predation, corresponding to the initial conditions set for the phenomenological model (Chapter 3). Simulations were run over 2000 timesteps using the last 40 years to investigate how harrier predation affected grouse population size, cycle amplitude and periodicity, grouse aggressiveness and parasite numbers. Model simulations were carried out using Mathematica 4.1. (See Appendix 4.1 for the ‘host-parasite’ model code and Appendix 4.2 for the ‘aggressive, territorial’ model code).

## Results

### Host-parasite model

#### *No predation*

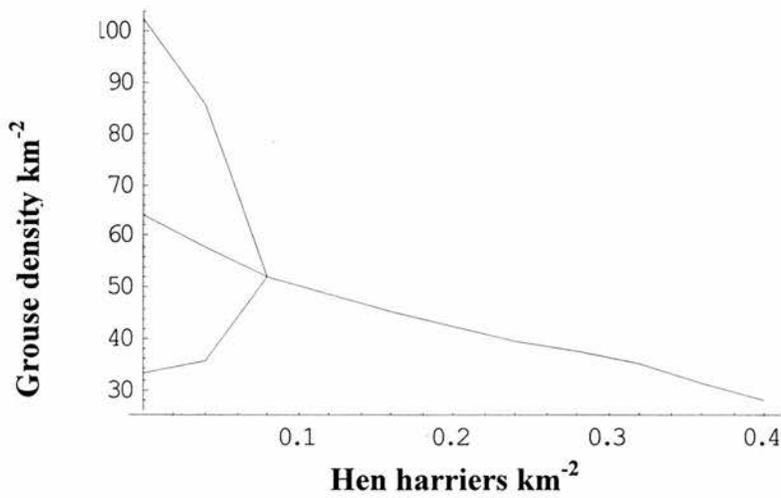
In the absence of predation by hen harriers the host-parasite model predicted the grouse population would cycle with a periodicity of 5 years and amplitude of 3. Population size ranged between 33 and 102 birds  $\text{km}^{-2}$  with a mean of 63 birds  $\text{km}^{-2}$  (Fig. 1a). Parasite burdens increased as the host population neared its peak and declined once the host population crash commenced (Fig.1b).



**Figure 1.** Output from the grouse-parasite model with no hen harriers. The 40-year trajectory shows (a) grouse population density  $\text{km}^{-2}$ , and (b) parasite numbers.

*Predation model using a single-species functional response*

Figure 2 shows the predicted relationship between harrier density and minimum, maximum and mean grouse densities using a SSFR. Mean grouse density and cycle amplitude converged to a stable point equilibrium of 52 grouse  $\text{km}^{-2}$  when there were 0.08 harriers  $\text{km}^{-2}$ , as harrier density increased grouse density gradually declined to 27 birds  $\text{km}^{-2}$  when harriers reached 0.4  $\text{km}^{-2}$ .



**Figure 2.** Variation in minimum, maximum, and mean grouse densities ( $\text{km}^{-2}$ ) with increasing harrier density using a SSFR.

*Predation model using the multi-species functional response and aggregative response for hen harriers*

Table 3 shows how grouse density changed as harrier density increased as a function of meadow pipit and vole numbers. The model predicted that grouse cycles would stabilise at 55 birds  $\text{km}^{-2}$  when there were 0.13 harriers  $\text{km}^{-2}$ . Increasing vole

abundance resulted in a small increase in equilibrium grouse density. However, increasing harrier density had no additional effect on grouse density. Across the range of harrier densities (0-0.4km<sup>-2</sup>), mean grouse density declined by 6.3% when voles were abundant, and 12.3% when voles were absent. Predation had no effect on cycle period.

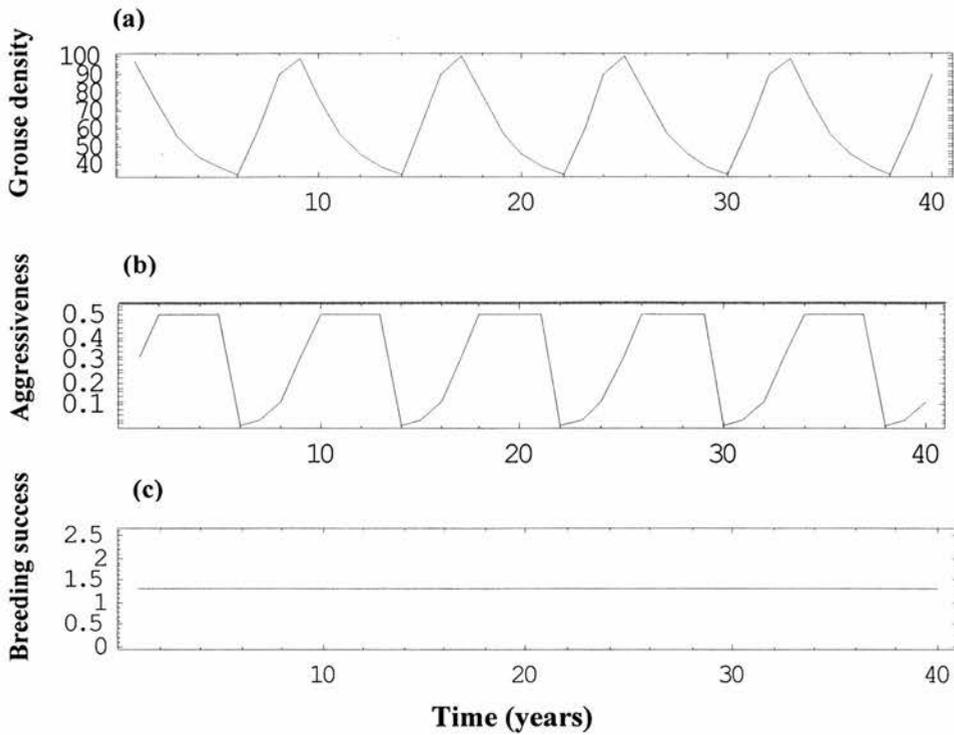
**Table 3.** Mean, minimum and maximum grouse densities for a range of alternative prey and harrier densities.

<b>Meadow pipits km<sup>-2</sup></b>	0			10			50			90			130		
<b>Voles km<sup>-2</sup></b>	0	50	500	0	50	500	0	50	500	0	50	500	0	50	500
<b>Hen harriers km<sup>-2</sup></b>	0	0.006	0.06	0.02	0.03	0.08	0.13	0.14	0.19	0.24	0.25	0.3	0.34	0.35	0.4
<b>Grouse density km<sup>-2</sup></b>															
Mean	63	60	60	62	59	60	55	58	60	55	57	59	55	57	59
Minimum	33	47	49	30	57	55	55	58	60	55	57	59	55	57	59
Maximum	102	76	72	96	62	66	55	58	60	55	57	59	55	57	59

### **Aggressive, territorial model**

#### *No predation*

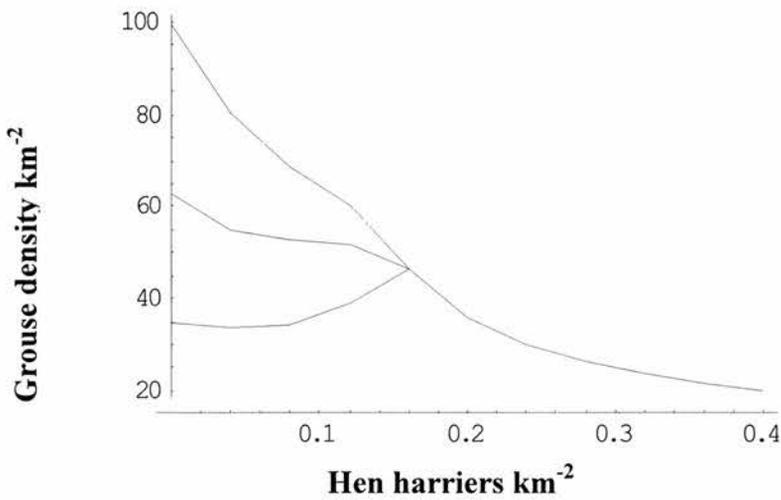
For realistic values of red grouse vital rates ( $s=0.5$  and  $d=1.3$ ) the territorial behaviour model generated a regular cycle period of 8 years with an amplitude of 3 and mean density of 63 grouse km<sup>-2</sup> (Fig. 3a). Aggressiveness was lowest when population size was at a minimum (Fig. 3b). In accordance with the findings of Matthiopoulos et al. (2003), aggressiveness rose when autumn density ( $G_t$ ) exceeded equilibrium density (55 males km<sup>-2</sup> in this case) and fell when autumn density was below the equilibrium level. Breeding success was constant in the absence of harriers (Fig. 3c).



**Figure 3.** Output from the mechanistic grouse model with no hen harriers. The 40-year trajectory shows changes in (a) population density  $\text{km}^{-2}$ , (b) aggressiveness, and (c) breeding success of grouse.

#### *Predation model using a single-species functional response*

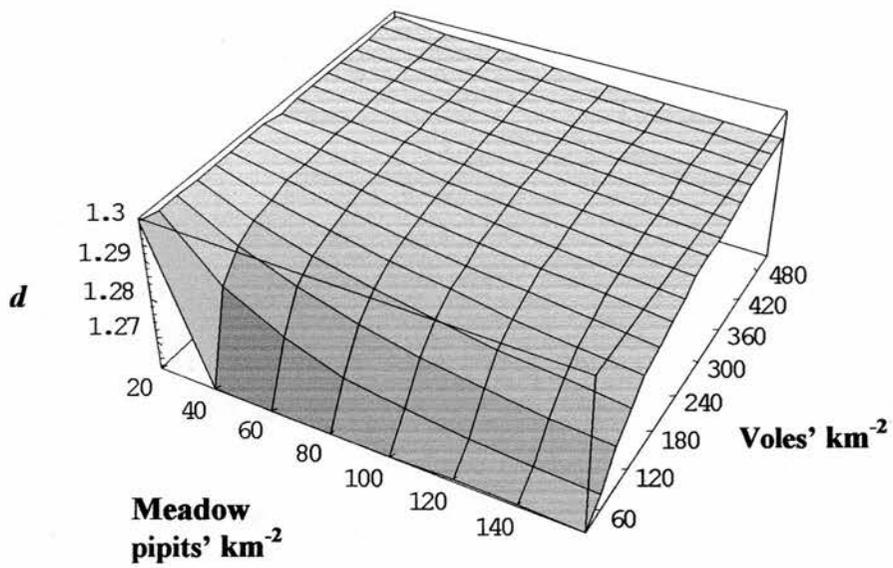
Figure 4 shows predicted mean, minimum and maximum grouse densities using a SSFR. The introduction of low numbers of harriers resulted in a decline in mean grouse density and cycle amplitude, which converged to a stable point equilibrium of  $46 \text{ grouse km}^{-2}$  at  $0.16 \text{ harriers km}^{-2}$ . At maximum harrier density, grouse declined to  $20 \text{ km}^{-2}$ .



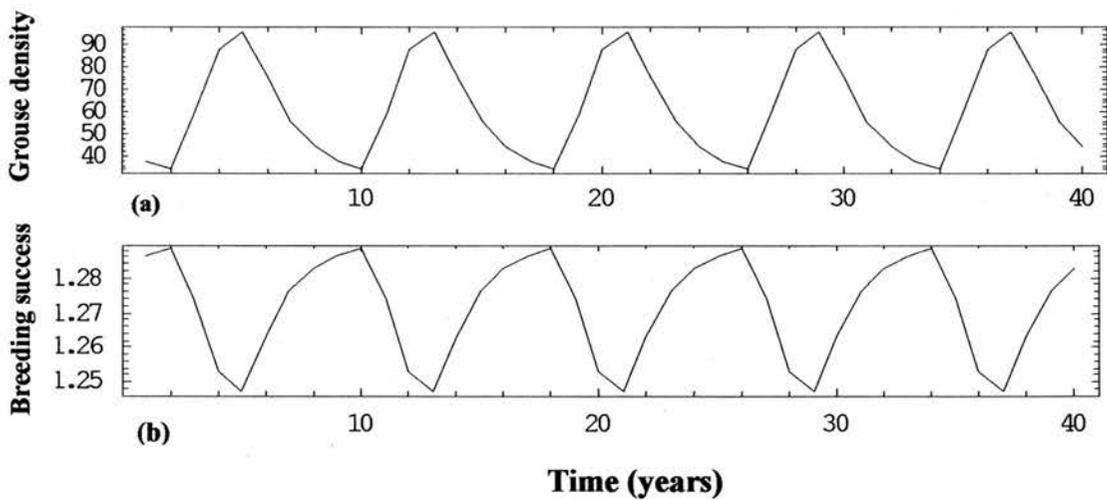
**Figure 4.** Output from the territorial model using a SSFR for harrier consumption of grouse, showing the relationship between harrier density and minimum, maximum, and mean grouse density.

*Predation model using the multi-species functional response and aggregative response for hen harriers*

Under the multi-species model, harrier predation caused fluctuations in grouse breeding success,  $d$ . The density plot in Figure 5 summarises how  $d$  changed as densities of alternative prey varied. Breeding success was at a stable maximum when pipit abundance (and hence harrier abundance) was low, and declined as the number of meadow pipits increased. However, when voles were abundant,  $d$  returned to higher values. Figure 6 shows how the peaks and troughs in breeding success were synchronous with troughs and peaks in population size, suggesting that harrier predation had the greatest impact on breeding success when grouse population density was high.



**Figure 5.** Relationship between grouse breeding success ( $d$ ) and densities of alternative prey, which are positively correlated with harrier density.



**Figure 6.** Grouse breeding success and population density when harrier density is  $0.35 \text{ km}^{-2}$  and vole density is low ( $50 \text{ km}^{-2}$ ).

Across the range of harrier densities, mean grouse density declined by 5% when vole abundance was low (Table 4). However, when vole abundance was high (500 km<sup>-2</sup>) the model suggested that hen harriers had very little effect on the grouse population.

**Table 4.** Mean, minimum and maximum grouse density for a range of alternative prey densities.

<b>Meadow pipits km<sup>-2</sup></b>	0			10			50			90			130		
<b>Voles km<sup>-2</sup></b>	0	50	500	0	50	500	0	50	500	0	50	500	0	50	500
<b>Hen harriers km<sup>-2</sup></b>	0	0.006	0.06	0.02	0.03	0.08	0.13	0.14	0.19	0.24	0.25	0.3	0.34	0.35	0.4
<b>Grouse density km<sup>-2</sup></b>															
Mean	64	61	63	60	62	62	60	61	62	60	61	62	60	61	63
Minimum	33	33	33	27	34	31	33	34	34	31	34	33	33	34	35
Maximum	95	93	95	94	91	94	86	89	91	86	89	93	87	88	90

## Discussion

Mechanisms that drive red grouse cycles have been the subject of intensive study over the last few decades. Two viable hypotheses have emerged: interactions with macroparasites; and intrinsic, behavioural factors. In this paper, I modelled the impact of hen harrier predation on red grouse using models based on both mechanisms, providing a comparison between the intrinsic and extrinsic hypotheses for red grouse cycles. For both models I compared predictions using a SSFR and a MSFR together with the hen harriers' AR. I examined whether model output was sensitive to prey dynamics and compared it with that of a simple phenomenological model for grouse dynamics (Chapter 3).

The host-parasite model assumes that grouse cycles occur when parasites exhibit low degrees of aggregation and parasite-induced reductions in host fecundity are greater than parasite-induced increases in host mortality (Dobson & Hudson 1992). The territorial, aggressive model assumes that population change is due to variations in recruitment of young cocks to the territorial population. Recruitment is inversely related to the interaction between population density and aggressiveness during territorial contests; aggressiveness in one year affects aggressiveness the following year and is influenced by population density (Matthiopoulos et al 2003).

General 'strategic' (May 1974) models, such as the phenomenological model used in Chapter 3, are relatively simple and easy to manipulate, and can be used to form generalizations about ecological systems. However, they do not provide biologically meaningful descriptions of a population and are often considered to be too unrealistic to

be useful for describing specific systems. Mechanistic models on the other hand, lay at what May (1974) calls, the ‘tactical’ end of a spectrum of possible models. Their detail provides some understanding of why phenomena occur and how different variables may interact (Gillman & Hails 1997). Thus, to some extent, they may be considered more ‘realistic’ than phenomenological models. Nevertheless, it is important to note that predictions from the mechanistic models developed here are still generic: they can emerge from any putative mechanism consistent with the assumptions of either Dobson & Hudson (1992), or Matthiopoulos et al. (2003).

Qualitatively, the mechanistic and phenomenological models were in agreement about the effect of hen harrier predation on red grouse dynamics when a SSFR was used. The models predicted that grouse cycles could be stabilised, and that increasing harrier density would result in a decline in equilibrium grouse density to low levels. However, the territorial model required a density of 0.16 harriers  $\text{km}^{-2}$  to stabilise the grouse population while the host-parasite model required only 0.08  $\text{km}^{-2}$  and the phenomenological model 0.06  $\text{km}^{-2}$ .

The impact of predation declined when I modelled the interaction using a MSFR and an AR, indicating that alternative prey have an important influence on this system. The host-parasite model predicted that, at low vole density, grouse cycles would stabilise when harriers reached 0.13  $\text{km}^{-2}$ , and at high vole densities stabilisation would occur when there were 0.19 harriers’  $\text{km}^{-2}$ . Once stabilised, the presence of alternative prey prevented grouse equilibrium density from declining further, even at high harrier densities. The phenomenological model (chapter 3) also predicted that at low vole density grouse dynamics would stabilise at a similar equilibrium density

when there were 0.13 harriers'  $\text{km}^{-2}$ . However, in this model equilibrium grouse density continued to decline as harrier numbers increased, despite the presence of alternative prey. Hence, the two models' predictions about the maximum depression in mean grouse density (i.e. when voles density was low and harrier density high) differed. The host-parasite model predicted that in the worst case scenario, mean grouse density would decline by 12.3%, whereas the phenomenological model predicted a fall of 25%. Output from the territorial model suggested that the availability of very low numbers of alternative prey could prevent harriers from having any impact on grouse dynamics. In the worst case scenario grouse density would decline by 5%.

Whereas results of the mechanistic models showed different trends when using a MSFR and AR, the parasite and phenomenological models concurred that driven grouse shooting was viable up to a maximum of  $\sim 0.2$  harriers  $\text{km}^{-2}$  when voles were abundant and the initial density of grouse in the absence of harriers was  $63 \text{ km}^{-2}$ . Interestingly, Redpath and Thirgood (2003) predicted a similar result (at  $0.3$  harriers  $\text{km}^{-2}$ ) using a simple non-cyclic model for the harrier-grouse interaction.

The results from the phenomenological and host-parasite models support the hypothesis that generalist predators can stabilize cyclical prey populations (Hanski et al. 1991; Redpath & Thirgood 1999). All three models demonstrated that single-species and multi-species functional responses generate different predictions about the effect of a predator on its prey, and support the conclusions of Asseburg et al. (in review ) that using a SSFR to model the behaviour of a generalist predator can result in a

misleading impression of the predator's effect on its prey. Interestingly all three models predicted a different outcome in a worst case scenario.

Structural variations between models prevented me from setting exactly the same cycle period for each model. However, this constraint did not affect the results because predation had no impact on periodicity. Results of the territorial model differed from the parasite and phenomenological models when a MSFR and AR were used because of the way recruitment, and hence predation, were modeled. In the parasite and phenomenological models predation affected total chick numbers. However, in the territorial model, the FR influenced the parameter for breeding success,  $d$ . The territorial model is recognized as being inherently sensitive to small changes in parameter values (Matthiopoulos et al. 2003). Introducing even small numbers of alternative prey into the MSFR, resulted in a switching of predation away from grouse, effectively nullifying the impact of predation on  $d$ . Work is currently underway to refine the sensitivity of this model (Matthiopoulos pers.comm.).

In developing the mechanistic models, I was interested in the way in which predation might affect parasite levels or aggressiveness in red grouse. The results suggested that the interaction was indirect in both models, with predation influencing parasite numbers and aggressiveness via its affect on grouse density. Hudson et al. (1992) developed a model in which the susceptibility of grouse to predation increased with intensity of their parasite burden. However, susceptibility was related to increased scent emission in heavily infected birds and therefore only affected predation by mammalian predators that hunt by scent.

I have investigated the impact of harrier predation on red grouse dynamics using simple and complex models, different hypotheses for cycles, different sets of parameter values modeled in discrete and continuous time, and single and multi-species functional responses. Predictions of the phenomenological and parasite models were qualitatively and, to some extent, quantitatively similar, suggesting that simple and complex models of red grouse dynamics may respond to predation by harriers in similar ways. The results from the territorial model suggest that, in its current form, it may underestimate the effect of predation. From a management viewpoint, we should be cautious about the accuracy and realism of any of the models, largely because of parameter uncertainty associated with the FR and AR, and also because the models are yet to be validated with observed grouse data.

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## Appendix 4.1. Mathematica code for the host-parasite model

```
fMeanPop[rmp_, nv_] :=
Module[{k = 900, h = rmp*0.00263 + nv*0.0001241,
  ag = 0.0007025, amp = 1.82139, av = 3.7569, tg = 2.6944,
  tmp = 1.6995, tv = 2.24958, mg = 2.505, mmp = 1.19986,
  mv = 1.134, bg, bmp, bv, a = 2.24, b = 1.055,  $\alpha = 2.27 * 10^{-4}$ ,
   $\delta = 5.031 * 10^{-4}$ ,  $\lambda = 8.5$ ,  $\gamma = 9$ ,  $\beta = 0.1$ ,  $\sigma = 0.2$ ,  $\mu a = 0.6$ ,
   $\theta = 50$ ,  $\mu p = 1.24$ ,  $w = 0.0023$ ,  $\kappa = 0.5$ ,  $H_0 = \gamma / \beta$ ,
  inithosts = 40, (*initfree=0*) initpara = 100,
  initarrested = 10, grouse, parasites},
  bmp = amp * tmp;
  bv = av * tv;
  bg = ag * tg;
  tmin = 860;
  tmax = 900;

  sol =
  NDSolve[
    {H'[t] == (a - b - w * H[t]) H[t] - ( $\alpha + \delta$ ) P[t] -
      (h * k
        (ag * (a * H[t] ^ mg) /
          (1 + bg * (a * H[t] ^ mg) + bmp * rmp ^ mmp +
            bv * nv ^ mv))),
      A'[t] ==  $\frac{\lambda P[t] H[t]}{(H[t] + H_0)}$  - ( $\mu a + b + \theta$ ) A[t] -
       $\alpha (P[t] A[t]) / H[t]$ ,
      P'[t] ==  $\theta A[t] - (\mu p + b + \alpha) P[t] -$ 
       $\alpha (P[t]^2 / H[t]) (\kappa + 1) / \kappa$ ,
      H[0] == inithosts, P[0] == initpara,
      A[0] == initarrested}, {H, A, P}, {t, 0, tmax},
    MaxSteps -> 100000, AccuracyGoal -> 35, PrecisionGoal -> 6];
```

```

grouse = Table[Evaluate[{H[t]} /. sol][[1, 1]],
  {t, tmin, tmax}];
parasites = Table[Evaluate[{P[t]} /. sol][[1, 1]],
  {t, tmin, tmax}];

Return[{grouse, parasites}];

(*Return[Mean[grouse]]*)
(*Return[Max[grouse]/Min[grouse]]*)
(*sp=Abs[Fourier[grouse]];
sp[[1]]=0;
per=N[(tmax-tmin)/Position[sp,Max[sp]][[1,1]]];
Return[per];*)

];

```

## Appendix 4.2. Mathematica code for the aggressive-territorial model

```
fMeanPop[nmp_, nv_] :=
Module[{s = 0.495,
  cH = 1.73,
  cL = 0.97,
  c = 55,
  pm = 24,
  k = 900, h = nmp*0.00263 + nv*0.0001241, ag = 0.0007025,
  amp = 1.82139, av = 3.7569, tg = 2.6944, tmp = 1.6995,
  tv = 2.24958, mg = 2.505, mmp = 1.19986, mv = 1.134,
  bg, bmp, bv, bi, p, a, ps},
  bmp = amp*tmp;
  bv = av*tv;
  bg = ag*tg;
  pert = 10;

  tmin = 860;
  tmax = 900;
  ki = .1;
  p = Table[.1, {i, 1, tmax}];
  a = Table[1, {i, 1, tmax}];
  prod = 1.3;

  bi = Table[0, {i, 1, tmax}];

  ps = {};
  For[t = 5, t <= tmax - 1, t++,
    If[
      prod <=
        (h*k
          (ag*(prod*p[[t]]^mg) /
            (1 + bg*(prod*p[[t]]^mg) + bmp*nmp^mmp +
              bv*nv^mv)) / p[[t]], Print["Negative"]];
```

```

b =
  Max[0,
    prod -
      (h * k
        (ag * (prod * p[[t]] ^ mg) /
          (1 + bg * (prod * p[[t]] ^ mg) + bmp * nmp ^ nmp +
            bv * nv ^ mv)) / p[[t]])];

bi[[t]] = b;

mH = 0.5 + Random[Real, {-10^-pert, 10^-pert}];
mL = .005 + Random[Real, {-10^-pert, 10^-pert}];
If[mH < a[[t]] (1 + cH), fH = mH - a[[t]], fH = cH a[[t]];
If[mL > a[[t]] (1 - cL), fL = a[[t]] - mL, fL = cL a[[t]];

p[[t+1]] =
  p[[t]] (s + b / (1 + ki a[[t]] * p[[t]] (1 + b)));

a[[t+1]] = a[[t]] - fL +
  (fH + fL) fL p[[t+1]] ^ c / (pm ^ c fH + fL p[[t+1]] ^ c);
If[a[[t+1]] <= 0, a[[t+1]] = 0.005];

];

ps = Table[{a[[t]], p[[t]]}, {t, tmin, tmax - 1};
a = Table[a[[t]], {t, tmin, tmax - 1};
p = Table[p[[t]], {t, tmin, tmax - 1};
bi = Table[bi[[t]], {t, tmin, tmax - 1};

Return[{p, a, bi}];

(*Return[Mean[p]]*)
(*Return[Max[p]/Min[p]]*)
(*sp=Abs[Fourier[p]]);
sp[[1]]=0;
per=N[(tmax-tmin)/Position[sp,Max[sp]][[1,1]]];
Return[per];*)

];

```

## **CHAPTER 5**

---

### **Incorporating parameter uncertainty in predation functions, into models of the hen harrier-red grouse system**

---

#### **Abstract**

*In this chapter I tested the robustness of predictions from three deterministic models by comparing them with the results of stochastic models for the harrier-grouse system. The results of the deterministic models were quantitatively robust. All three models predicted very different depressions in red grouse density under a worst case scenario. They also recorded different degrees of uncertainty in this metric, however this was reduced when biological mechanisms were incorporated into the models. Future work to validate the results requires fitting models to observed data for grouse populations, with and without hen harriers.*

## Introduction

Uncertainty is ubiquitous in natural systems. In the last decade ecologists have become increasingly preoccupied with understanding and dealing with sources of uncertainty, not least because the relatively 'young' discipline of ecology is constantly unearthing complexity. But, this preoccupation is also a result of the fact that uncertainty erodes our ability to make predictions about the future, and hence, inform decision-makers and influence policy (Dovers & Norton 1996; Haines 1998; Harwood & Stokes 2003). Nowhere is this truer than in the case of global climate change. The presence of uncertainty associated with this science has been interpreted as an undermining of scientific authority and as a hindrance to policy (Shackley & Wynne 1996). Akçakaya et al. (2000) suggested that uncertain data has led to inconsistent IUCN classifications about the conservation status and management of species. Kokko et al. (1997) noted that failure to deal with uncertainty can lead to misleading or false conclusions. They evaluated harvesting strategies for seal populations in the Baltic and showed that deterministic models could give a false impression of safety, while the same strategies were judged to be risky when a more realistic, stochastic model was used.

Mathematical models have long been used to aid understanding of ecological processes and systems. However, they have been mostly deterministic, relying on point estimates and means to make predictions, while ignoring basic variability in biological processes, or at least assuming it to be negligible (Chesson 1978; Regan 2004). Deterministic models have their place in ecology, however, when an adequate degree of realism is required, for instance, to facilitate management decisions,

uncertainty must be considered. Akçakaya et al. (1997) suggest that mathematical models for populations require explicit treatment of both the deterministic and stochastic mechanisms that effect them.

To include aspects of stochasticity in a model, it is necessary to first construct a deterministic model to characterise the processes important for the dynamics of a population (Burgman et al. 1993), and then to identify the principal sources of stochasticity. Stochasticity can then be incorporated into mathematical population models by replacing deterministic parameters, such as means, with random variables selected from predetermined probability distributions (Regan 2004).

Uncertainty has many different sources but may be classified into two main categories: epistemic and linguistic. The first is uncertainty in things that can be measured including, parameter uncertainty, systematic error, natural variation and model uncertainty. Linguistic uncertainty arises because of ambiguities or vagueness in language used to describe or classify desired states (Harwood & Stokes 2003). It is rarely possible to treat both epistemic and linguistic uncertainty simultaneously (Regan et al. 2002). As a result, the latter is often ignored and only epistemic uncertainty is considered (Chesson 1978; Shaffer 1987; Burgman et al. 1993; Regan et al. 2002).

In this chapter I investigate the effect of one source of epistemic uncertainty on predictions about the impact of hen harrier predation on red grouse dynamics. Using the three deterministic models from Chapters 3 and 4, I incorporate parameter uncertainty into the hen harrier's MSFR and AR, and look at the robustness of the

deterministic models' predictions about the maximum depression in mean grouse density, when hen harriers are abundant but alternative prey (field voles) are low. This metric, otherwise considered a 'worst case scenario', is of particular interest to managers of the harrier-grouse system. A robust estimate of maximum grouse depression may provide a useful starting point for management planning. Examining uncertainty in the two predation functions is an obvious place to begin, firstly because predation is the main theme of this thesis, secondly, we have good information about the variation in the parameters for the MSFR and AR, and finally, because the uncertainty associated with these functions covers individual variation in predation and measurement error.

## Methods

### Incorporating parameter uncertainty

To fit an MSFR to the hen harrier consumption data and to assess uncertainty in the resulting parameter estimates, Asseburg et al. (in review) employed computer-intensive methods. A by-product of this approach was a large sample of sets of parameters for the MSFR. Each such set, fully parameterised the MSFR and its occurrence in the sample reflected that set's likelihood under the data. In this chapter, I obtained a measure of the uncertainty in the MSFR, by using the entire sample of sets of parameters. It is important to note that the likelihood of a set of parameters is not affected independently by changes in each parameter and therefore treating each set as an entity maintains the connectivity between values and provides a more faithful representation of likelihood under the data than random sampling from the individual parameter distributions.

To obtain a corresponding sample of sets of parameters for the AR (which regulates the number of predators), I used the variance-covariance matrix estimated from a linear regression fitted to abundance data for meadow pipits, field voles and hen harriers. Given the mean and variance, I then randomly generated 200 pairs of numbers from a multi-normal distribution to create a new data set of coefficients to measure the relationship between hen harrier and alternative prey abundance. A multi-normal distribution was used because we are dealing with two types of alternative prey.

For each of the harrier-grouse models (phenomenological, territorial, host-parasite) parameters values were set to give an initial mean grouse density of  $63 \text{ birds km}^{-2}$  in

the absence of predation (parameter values are given in Chapters 3 & 4) Combinations of sets of parameter values for the predation functions (i.e. the MSFR & AR) were then sampled independently, with the implicit assumption is that there is no relationship between the parameters of the MSFR and AR: the two functions were fitted independently from two data studies, with no information about possible links between them. However, the parameters within each of the two functions were not selected independently. For each combination of values, the models looked at an extensive range of values of alternative prey densities (0-130 meadow pipits km<sup>-2</sup> and 0-500 field vole km<sup>-2</sup>) and recorded the lowest predicted mean grouse density. Equation (1) was used to measure the maximum depression in grouse density

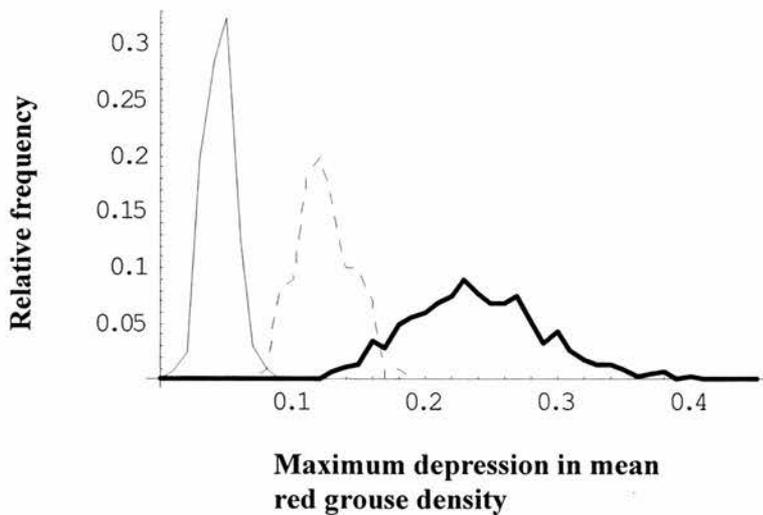
$$1/(M(M - Min(data))) \tag{1}$$

where M is mean grouse density km<sup>-2</sup> in the absence of predation, and *Min(data)* is the minimum density of grouse recorded for each set of combinations of values for the MSFR and AR.

Using Mathematica 4.2, 2000 iterations were run and the minima were used to plot a frequency histogram of worst case scenarios: in other words, a distribution of the maximum depression in mean grouse density. From the previous deterministic models, the worst case scenario is likely to involve a high density of meadow pipits (e.g. 130 km<sup>-2</sup>) and hence hen harriers (e.g. 0.34 km<sup>-2</sup>), and an absence of voles. Confidence intervals were obtained using the 95<sup>th</sup> percentile. The results were compared with the worst case scenarios predicted by the deterministic models.

## Results

Figure 1 shows the distributions of maximum depression in mean red grouse density for three stochastic models. The maximum depression was 0.049 with confidence interval (0.029, 0.072) under the territorial model; 0.129 with a confidence interval (0.093, 0.169) under the host-parasite model; and, 0.244 with a confidence interval (0.155, 0.350) under the phenomenological model. The confidence limits are widest for the phenomenological model and narrowest for the territorial model, suggesting that we can be more confident we are close to the true value in the latter model. Uncertainty is mapped differently for each of the three models, there is very little overlap in the distributions. All three distributions are symmetric.



**Figure 1.** Comparative plot showing the distribution of the maximum depression in mean red grouse density for three stochastic models: (-----) Territorial model; (.....) Host-parasite model; (——) Phenomenological model.

## Discussion

In this chapter I tested the robustness of predictions from three deterministic models by comparing them with the results of stochastic models for the same predator-prey system. The metric I chose to use was a worst case scenario: the maximum depression in mean red grouse density when hen harriers are very abundant and alternative prey low. Table 1 compares the results of the deterministic and stochastic models.

**Table 1.** Predicted maximum depression in mean red grouse density

Type of model	Territorial	Host-parasite	Phenomenological
Deterministic	0.047	0.123	0.253
Stochastic	0.049	0.129	0.244

The results of the stochastic models were quantitatively similar to those of the deterministic models, suggesting that the predictions of the latter were robust, regardless of uncertainty in the parameters of the predation functions. The predictions of the three models were significantly different from each other: the territorial model predicted that in the worst case, hen harriers could cause a 5% depression in grouse density, the host-parasite model predicted a 13% depression, and the phenomenological model, a 25% depression. A surprising feature is that, despite all three models starting with the same mean density of red grouse, using the same functions for predation and accounting for the same amount of uncertainty, they all ended up with a different degree of uncertainty. This is likely to be a consequence of the way in which predation was incorporated into the models, as discussed in chapters 3 and 4.

Figure 1 suggests that when biological complexities, in this case, mechanisms of cyclicity, are introduced into the model, the quantitative impact on the red grouse population is reduced, as is the uncertainty about its effects. The confidence intervals for the two mechanistic models were much smaller than those for the phenomenological model. On this basis, we might have expected the uncertainty in the predictions of the phenomenological model to encompass that of the other models. In fact there was no overlap, and this may be an indication that the phenomenological model is not biologically reasonable.

If depressions in grouse density greater than 0.07 and 0.17 are observed in real systems, this may be an indication that the territorial and host-parasite hypotheses, respectively, are insufficient to explain grouse dynamics. However, the converse is not true: because Figure 1 is a plot of maximum depression in grouse density, a depression of less than 0.10 does not mean that the host-parasite hypothesis is invalid. We might also infer from these results that, if red grouse dynamics are determined primarily by social factors (i.e. the territorial hypothesis), then the population will be fairly robust to predation by hen harriers.

From this work, it is not possible to conclude which of the mechanistic models is most 'realistic'. Validating the results would involve fitting models to empirical data for populations of red grouse, both with and without predation by hen harriers. Presently, there are no data of this kind available. Future work might look at how strongly the results here depend upon the specific parameters used for grouse in the models. For instance, would predictions change significantly if the initial density of red grouse were changed? To my knowledge, the density used here is feasible for a grouse moor,

although actual observed levels can range widely. I would expect any changes in initial density to have a proportional effect on the results. Current discourse suggests that both territorial and host-parasite mechanisms may both play a role in grouse dynamics. Recent work by Mougeot et al. (in press) showed that the two processes suspected to cause the unstable population dynamics of red grouse interact and could both influence autumn recruitment, which regulates subsequent breeding density. Hence, it may be worth investigating whether the impact of predation might also lie between the predictions of these models. As yet, more complicated population models for grouse, such as a multifactor hypothesis for dynamics, do not exist. Other models could investigate the frequency with which the maximum depression in red grouse density ends up being below the threshold required for shooting. However, because the system changes when there is hunting, the model would need to incorporate information about how grouse density is depleted through this activity.

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## Appendix 5.1. Mathematica code for stochastic models

```
(*Generic model*)
fMeanPop1[nmp_, nv_, tmax_, i_, j_] :=
Module[{a = 0.0191, b = 1.9, c = 3.3
, k = 900, h = nmp*nr[[j, 2]] + nv*nr[[j, 1]], th = 5.1,
ag = fr[[i, 7]], amp = fr[[i, 9]], av = fr[[i, 8]],
tg = fr[[i, 4]], tmp = fr[[i, 6]], tv = fr[[i, 5]],
mg = fr[[i, 1]], nmp = fr[[i, 3]], mv = fr[[i, 2]], bg, bmp, bv, pdel, pt},
bmp = amp*tmp;
bv = av*tv;
bg = ag*tg;

pdel = NestList[#[[2]], (#[[2]] + c*#[[2]] - h*k*
(ag*(c*#[[2]])^mg)/(1+bg*(c*#[[2]])^mg
+ bmp*nmp^nmp + bv*nv^mv) *
(1+a*#[[1]])^(-b)) &, {40, 30}, tmax];
pt = Transpose[pdel][[1]];

pt = Table[pt[[ii]], {ii, tmax-100, tmax}];

Return[pt]
];
```

(\*Behavioural model\*)

fMeanPop2[nmp\_, nv\_, tmax\_, i\_, j\_] :=

Module[{s = 0.495,

cH = 1.73,

cL = 0.97,

c = 55,

pm = 24, ii,

k = 900, h = nmp\*nr[[j, 2]] + nv\*nr[[j, 1]], ag = fr[[i, 7]],

amp = fr[[i, 9]], av = fr[[i, 8]], tg = fr[[i, 4]],

tmp = fr[[i, 6]], tv = fr[[i, 5]], mg = fr[[i, 1]],

nmp = fr[[i, 3]], mv = fr[[i, 2]], bg, bmp, bv, bi, p, a, ps},

bmp = amp\*tmp;

bv = av\*tv;

bg = ag\*tg;

pert = 10;

tmin = tmax - 100;

ki = .1;

p = Table[.1, {ii, 1, tmax}];

a = Table[1, {ii, 1, tmax}];

prod = 1.3;

bi = Table[0, {ii, 1, tmax}];

ps = {};

For[t = 5, t ≤ tmax - 1, t++,

If[prod ≤ (h\*k (ag\* (prod\*p[[t]] ^ mg) / (1 + bg\* (prod\*p[[t]] ^ mg)  
+ bmp\*nmp ^ nmp + bv\*nv ^ mv)) / p[[t]], Print["Negative"]];

b = Max[0, prod - (h\*k (ag\* (prod\*p[[t]] ^ mg) /  
(1 + bg\* (prod\*p[[t]] ^ mg)  
+ bmp\*nmp ^ nmp + bv\*nv ^ mv)) / p[[t]]];

bi[[t]] = b;

```

mH = 0.5 + Random[Real, {-10^-pert, 10^-pert}];
mL = .005 + Random[Real, {-10^-pert, 10^-pert}];
If[mH < a[[t]] (1 + cH), fH = mH - a[[t]], fH = cH a[[t]];
If[mL > a[[t]] (1 - cL), fL = a[[t]] - mL, fL = cL a[[t]];

p[[t + 1]] = p[[t]] (s + b / (1 + ki a[[t]] * p[[t]] (1 + b)));

a[[t + 1]] = a[[t]] - fL + (fH + fL) fL p[[t + 1]]^c /
  (pm^c fH + fL p[[t + 1]]^c);
If[a[[t + 1]] <= 0, a[[t + 1]] = 0.005];

];
p = Table[p[[t]], {t, tmin, tmax - 1}];
Return[p];

];

```

(\*Parasite model\*)

```

fMeanPop3[nmp_, nv_, tmax_, i_, j_] :=
Module[{k = 900, h = nmp * nr[[j, 2]] + nv * nr[[j, 1]],
  ag = fr[[i, 7]], amp = fr[[i, 9]], av = fr[[i, 8]],
  tg = fr[[i, 4]], tmp = fr[[i, 6]], tv = fr[[i, 5]],
  mg = fr[[i, 1]], mmp = fr[[i, 3]], mv = fr[[i, 2]],
  bg, bmp, bv, a = 2.24, b = 1.055,  $\alpha = 2.27 * 10^{-4}$ ,
   $\delta = 5.031 * 10^{-4}$ ,  $\lambda = 8.5$ ,  $\gamma = 9$ ,  $\beta = 0.1$ ,  $\sigma = 0.2$ ,
   $\mu a = 0.6$ ,  $\theta = 50$ ,  $\mu p = 1.25$ ,  $w = 0.0025$ ,  $\kappa = 0.5$ ,
  Ho, inithosts = 40, (*initfree=0*) initpara = 100,
  initarrested = 10, grouse, parasites, sol, t, H, A, P, tmin},
  bmp = amp * tmp;
  bv = av * tv;
  bg = ag * tg;
  tmin = tmax - 100;
  Ho =  $\gamma / \beta$ ;

```

```

sol = NDSolve[{H'[t] == (a - b - w * H[t]) H[t] - (alpha + delta) P[t] -
  (h * k (ag * (a * H[t] ^ mg) / (1 + bg * (a * H[t] ^ mg) + bmp *
    rmp ^ rmp + bv * nv ^ nv))),
  A'[t] == (lambda * P[t] H[t]) / (H[t] + Ho) - (mu a + b + theta) A[t] - alpha (P[t] A[t]) / H[t],
  P'[t] == theta A[t] - (mu p + b + alpha) P[t] - alpha (P[t]^2 / H[t])
  (kappa + 1) / kappa,
  H[0] == inithosts, P[0] == initpara, A[0] == initarrested}
, {H, A, P}, {t, 0, tmax}, MaxSteps -> 100000, AccuracyGoal -> 30,
PrecisionGoal -> 6];

```

```

grouse = Table[Evaluate[{H[t]} /. sol][[1, 1]], {t, tmin, tmax}];
parasites = Table[Evaluate[{P[t]} /. sol][[1, 1]], {t, tmin, tmax}];

```

```

Return[grouse];
];

```

```

<< Graphics`Legend`
<< Graphics`Graphics`
<< Statistics`DescriptiveStatistics`

```

## Uncertainty

```
hist = {};  
For[k = 1, k ≤ 10, k++,  
  i = Random[Integer, {1, Length[fr]}];  
  j = Random[Integer, {1, Length[nr]}];  
  data = {};  
  For[voles = 0, voles ≤ 500, voles += 100,  
    For[pipits = 0, pipits ≤ 130, pipits += 20,  
      rg = fMeanPop3[pipits, voles, 150, i, j];  
      data = Append[data, Mean[rg]];  
    ];  
  ];  
  hist = Append[hist, 1/63 * (63 - Min[data])];  
  If[k/10 == Round[k/10], Histogram[hist]];  
];
```

```
hist >> "H:\Parasites.ma";
```

## Comparative plots

```
hist1 = << "H:\Generic.ma";  
hist2 = << "H:\Social.ma";  
hist3 = << "H:\Parasites.ma";
```

```

bins1 = Table[{i, 0}, {i, 0, 0.45, 0.01}];
bins2 = bins3 = bins1;
bins = bins1;
hist = hist1;
For[i = 1, i ≤ Length[hist], i++,
  For[j = 2, j ≤ Length[bins], j++,
    If[hist[[i]] ≥ bins[[j - 1, 1]] &&
      hist[[i]] < bins[[j, 1]],
      bins[[j - 1, 2]] += 1 / Length[hist]; Break[]];
  ];
g1 = ListPlot[bins, PlotJoined → True,
  PlotStyle → {Thickness[0.01]};

bins = bins2;
hist = hist2;
For[i = 1, i ≤ Length[hist], i++,
  For[j = 2, j ≤ Length[bins], j++,
    If[hist[[i]] ≥ bins[[j - 1, 1]] &&
      hist[[i]] < bins[[j, 1]],
      bins[[j - 1, 2]] += 1 / Length[hist]; Break[]];
  ];
g2 = ListPlot[bins, PlotJoined → True];

bins = bins3;
hist = hist3;
For[i = 1, i ≤ Length[hist], i++,
  For[j = 2, j ≤ Length[bins], j++,
    If[hist[[i]] ≥ bins[[j - 1, 1]] &&
      hist[[i]] < bins[[j, 1]], bins[[j - 1, 2]] += 1 / Length[hist]; Break[]];
  ];
g3 = ListPlot[bins, PlotJoined → True,
  PlotStyle → {Dashing[{0.02, 0.02}]}];
Show[g1, g2, g3, PlotRange → All];

```

## Confidence Intervals

```
mg = Mean[hist1];
ug = Sort[hist1][[Round[Length[hist1] * 0.975]]];
lg = Sort[hist1][[Round[Length[hist1] * 0.025]]];
Print["Expected maximum depression under generic model
is ", mg, " with C.I. (", lg, ",", ug, ")."];
ms = Mean[hist2];
us = Sort[hist2][[Round[Length[hist2] * 0.975]]];
ls = Sort[hist2][[Round[Length[hist2] * 0.025]]];
Print["Expected maximum depression under social model is
", ms, " with C.I. (", ls, ",", us, ")."];
mp = Mean[hist3];
up = Sort[hist3][[Round[Length[hist3] * 0.975]]];
lp = Sort[hist3][[Round[Length[hist3] * 0.025]]];
Print["Expected maximum depression under parasite model is
", mp, " with C.I. (", lp, ",", up, ")."];
```

## General Discussion

---

Applied issues with predators offer some of the largest current challenges to basic ecology (see Introduction) (Ormerod 2002). Issues involving predators of conservation concern that impact upon economically valuable resources, such as game and livestock, pose an urgent challenge worldwide. Not only do they pit human communities that wish to reduce predator levels against those who seek to preserve or restore wildlife populations, but also because the frequency and economic costs of such conflicts appears to be on the increase in many areas (Mech 1998; Karanth 2002; Treves et al. 2002). As a result, many species now face accelerated extinction risks (Weber & Rabinowitz 1996).

In recent decades, the world's attention has been drawn to the need to maintain biological diversity, and there has been a profound shift in attitudes and indeed approaches to managing human-predator-prey conflicts (Weber & Rabinowitz 1996; Linnell et al. 1999; Treves & Karanth 2003). Aesthetic and conservation arguments against lethal control of predators have encouraged the development of non-lethal approaches to the management of predator-related problems. Further, it is no longer acceptable to base management strategies simply on economic interests or fear, as has often been the case in the past. The development of effective solutions for human-predator-prey conflicts requires a clear understanding of predators-prey interactions, the factors that influence them, and measures of both the ecological and economic impacts of predation (Treves & Karanth 2003; Ormerod 2002).

In this thesis, I examined current understanding of human-predator-prey conflicts, specifically those involving economically valuable prey species, and looked at whether advances in our understanding of population dynamics and behavioural ecology have been incorporated into this emerging field of conflict management. I reviewed a wide range of case studies, looked at the type of data that has been collected, examined the evidence of ecological and economic impacts of predators on prey species, and identified gaps in our knowledge. Using data from a particularly well studied predator-prey system I also developed a series of models to investigate the impact of predation and the possible implications for management. This thesis highlights the type of information that may be useful to scientists and managers and how this information can be incorporated into models to quantify the impact of predation and inform current debates surrounding human-predator-prey conflicts.

In Chapter 1, I surveyed the literature on human-predator-prey conflicts involving livestock and game species, since these are among the most common predator control problems worldwide. Where possible, I collected data on ecological and social factors, such as, predator abundance, prey abundance, methods of husbandry and human population density, and examined statistically whether prey losses to predators and patterns of resource management could be linked to these factors. Surprisingly few studies actually reported numerical data on losses to predators. However, from the case studies that did report this, I found that livestock and game losses to predators were generally low and were negatively associated with net primary productivity and predator home range size. I also found that variations in husbandry were associated with prey losses and predator density, although husbandry had no effect on the level of prey losses. Inconsistent and sparse data across the range of case studies limited the

ability to identify other important factors or patterns and lead to the conclusion that there is presently no reliable framework for identifying the type of data that should be collected for assessing human-predator-prey conflicts. Overall, there were very few attempts to quantify the impact of predation, and thus it was not possible to draw any firm conclusions about whether or not predators are a problem. Furthermore, it appears that the baseline data required to do this, such as predator and prey densities and predator consumption rates, were unavailable in most cases.

Calls for ecosystem-based approaches to management have emerged over the last decade, following a growing realisation that traditional species-level approaches are inadequate for conserving biodiversity (Christensen et al. 1996; Estes 1996; Yodzis 2000). Yodzis (1994) suggested that modelling interactions between species may make managed systems more predictable. However, the type of data required to do this can be difficult to collect as well as costly in terms of time and money. Few of the case studies I reviewed described the multi-species communities in which conflicts occurred, most described direct effects arising from simple 1-predator 1-prey interactions. Hence, little is known about how alternative prey and multiple predators influence these systems.

In Britain, one of the most controversial human-wildlife issues involves raptor predation on economically valuable gamebirds. There is widespread debate and concern regarding the impact and management of raptors. The perception that they can limit or reduce gamebird numbers and affect shooting activities has resulted in widespread, illegal persecution of many raptor species. Whilst a number of studies have addressed raptor-gamebird issues in Britain, none have specifically addressed

these issues for Scotland. In Chapter 2 I undertook research, commissioned by Scotland's Moorland Forum, to review evidence for impacts of raptors on gamebird numbers and productivity, and the economic implications and relative impacts of other factors on these interests in Scotland.

Although there is a wealth of strongly held opinion surrounding various raptor-gamebird systems, I found that very few quantitative studies have been conducted into the impact of raptors on gamebird populations both in the UK and elsewhere. There is some evidence that hen harriers and peregrines have impacts on red grouse breeding and post breeding densities, and that sparrowhawks can affect grey partridge, when population densities of these gamebird species are low. However, there is little evidence of any kind for any significant ecological impact of raptors on red-legged partridge, pheasant, capercaillie or black grouse. Excepting pheasant, no attempts have been made to directly link ecological impacts to economic effects for any gamebird population.

Much of the research that has been conducted on gamebird and raptor species over the last few decades has investigated the basic ecology and population dynamics of species. There is also a wealth of information on causes of mortality other than predation by raptors, including disease, habitat loss and other predators (e.g. foxes, mustelids). Studies that have attempted to document impacts of raptors include questionnaire surveys to gamekeepers, and correlations between time series of predator and prey numbers. A number of studies have assessed the proportion of gamebird deaths attributable to raptors. However, these studies have not shown a link to subsequent reductions in breeding density and were commonly conducted in areas

where the true impact of raptors is likely to have been reduced through illegal killing of raptors. Much of the literature reports on the diet of raptors, but is often impossible to identify the importance of individual gamebird species. Furthermore, the usefulness of many dietary studies in assessing impacts is constrained by the absence of data on predator and prey abundances. Predator removal experiments have not been conducted for raptors, due to their protected status, and simple predator-prey models have only been developed for two systems: hen harriers and red grouse; and sparrowhawk and grey partridge.

Chapters 1 and 2 clearly highlight that our understanding of human-predator-prey conflicts is still in its infancy. The fact that the impact of predators on different prey species has not been assessed in many cases, suggests that few systems are sufficiently understood and that many conflicts are based on a presumption that predators must have a negative impact on prey stocks and thus pose a threat to people's livelihoods. An absence of data suggests that ecologists have not had sufficient resources to undertake this research.

In cases where predators of concern are legally protected, it may not be possible to experimentally manipulate numbers in order to test hypotheses of predation limitation. A valid alternative is to model predator-prey interactions. Key components of these models are the functional and numerical responses of predators. Because many predators (all in the case studies we reviewed) are generalists, it is important to describe their responses to changes in the abundance of both the primary prey and alternative prey species (Yodzis 1998). Asseburg et al. (in review) suggested that ignoring the effects of alternative prey could give a misleading impression of the

predator's effect on its prey. Very few studies have collected long-term data on these metrics. One of the few systems for which some of this data is available is the hen harrier-red grouse system. In Chapters 3 and 4, I developed three models to quantify the impact of hen harrier predation on red grouse. These are the first models to investigate predation on a cyclic grouse population, and to incorporate information about the hen harriers functional and aggregative response to alternative prey. The mechanistic models presented in Chapter 4 also provided the first comparison between the intrinsic and extrinsic hypotheses for red grouse cycles.

When I incorporated a single-species functional response of hen harriers to grouse into the models, all three models predicted that grouse cycles would stabilise and equilibrium density would decline as harrier density increased. The results of the phenomenological (Chapter 3) and host-parasite (Chapter 4) models were quantitatively similar, suggesting that stabilisation could occur at low harrier densities, whilst the territorial model (Chapter 4) required higher densities of harriers to suppress cycles.

To improve the realism of the models I incorporated the harrier multi-species functional response and aggregative response to alternative prey. This time the models predicted that high densities of alternative prey could substantially reduce the impact of predation, and stabilisation of grouse cycles would occur only at very high harrier densities. Hence, in contrast with the simple, single-species models, the multi-species models suggested that driven grouse shooting would still be viable at high harrier densities, presenting a win-win outcome for both hunting stakeholders and conservationists. This work highlighted the importance of alternative prey in the

harrier-grouse system, and showed that ignoring multi-species interactions can lead to very different predictions about the impact of predation.

Finally, I used the deterministic models to predict the maximum depression in grouse numbers in a worst case scenario, that is, when harrier density was high and voles were absent. The outcome was very different under all three models, with the phenomenological model predicting the largest depression and the territorial model the least. The impact of predation was reduced when mechanisms for grouse cycles were incorporated into the models. In Chapter 5, I incorporated parameter uncertainty in the predation functions into the models and showed that the predictions of the deterministic models were robust, although the degree of uncertainty surrounding the predictions was different in each case. From the results of the multi-species models, we might conservatively recommend that managers focus their efforts on maintaining high densities of alternative prey by manipulating or maintaining grassland habitat, in order to reduce the impact of hen harriers on red grouse populations.

The models developed here are the first dynamical models of the harrier-grouse interaction and have provided a very useful step in understanding the system, as well as illustrating the importance of a multi-species approach. It is hoped that this approach to modelling predator-prey interactions will be applicable to other systems. Future work should focus on validating the results with observational data. This will provide managers with a more secure understanding of the likely outcomes of a range of management strategies, and may also provide a reliable basis for estimating the true economic costs of harrier predation on red grouse.

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