EXPLORING THE IMPACT OF COMMON BUZZARD *BUTEO BUTEO* PREDATION ON RED GROUSE *LAGOPUS LAGOPUS SCOTICA*

Richard Michael Francksen

Thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy

School of Biology, Newcastle University

July 2015

Abstract

The relationship between raptors and red grouse *Lagopus Lagopus scotica* is one of the most topical and contentious wildlife management issues in Britain. The common buzzard *Buteo buteo* is a generalist raptor which has increased in population and range in Britain during the last 40 years, which in most areas represents a recovery following historical declines. Increasingly, this has reignited conflict with managers of gamebirds concerned about the impact of buzzard predation. Whilst the impact of buzzards on reared pheasants *Phasianus colchicus* has previously been assessed, the impact of buzzards on red grouse has not been investigated. I aim to address this knowledge gap by providing an insight into the predator-prey relationship between buzzards and red grouse. I have explored the diet, foraging patterns and responses to changing prey abundances of buzzards on a moorland site managed for red grouse in south-west Scotland.

First, I investigated the biases associated with methods of assessing raptor diet. I demonstrated that methodological biases exist and that these can vary over time in relation to natural temporal variations in raptor diet composition. I then investigated functional and numerical responses of buzzards to annual changes in prey abundance. Following declines in vole abundance, buzzards selected a wider range of prey, but consumption of red grouse did not increase, and there was no evidence of a numerical response. Results suggested that buzzard predation of red grouse may be incidental in nature, whereby high vole abundances encouraged buzzards to hunt in red grouse habitats.

Next, I explored buzzard foraging patterns in relation to prey and habitat. Buzzard foraging intensity varied in line with annual variations in vole abundance, and buzzards hunted in areas with more red grouse during the winter. Buzzards avoided heather dominated areas in years when vole abundance was low, but not when vole abundances were high. Results again suggested that incidental buzzard predation of red grouse could increase when vole abundances are high. However, I found no evidence that variations in buzzard foraging intensity influenced grouse mortality indices.

I then described buzzard diet during the winter with the aid of remote tracking methods. Buzzard diet was primarily composed of small mammals, and red grouse were less likely to feature in the diet of buzzards roosting in grassy areas.

Next, I produced estimates of the potential removal of grouse by buzzards using bioenergetics modelling. The results suggested that whilst the removal of grouse by an individual buzzard is likely to be small, the total number of grouse removed could be considerable if buzzard populations are high and predation of grouse is additive to other causes of mortality.

Finally, key results are discussed and placed in a wider context of upland and gamebird management in Britain. Recommendations are made for future study to improve our understanding of these systems, and for testing possible mitigation and management techniques. This study could have wider implications for the management of economically important or threatened species, alongside recovering populations of protected raptors, and may provide a useful framework for studying similar systems elsewhere.

Dedication

This thesis is dedicated to Emma and Owen.

Acknowledgements

First and foremost, I am indebted to my supervisors Dave Baines and Mark Whittingham. Your support, insight and direction have been invaluable in helping me steer through the 'politics' of my project. It has been a pleasure to work with you both.

Throughout my PhD I have had the incredibly fortunate opportunity to discuss my work with some of the most eminent ecologists in my field of research. The Langholm Moor Demonstration Project Scientific and Technical Advisory Group, and Science Contact Group have heard and commented on numerous aspects of my research and I am very grateful to all members. In particular, Robert Kenward, Ian Newton, Steve Redpath, Jeremy Greenwood, Nick Sotherton, Des Thompson, Staffan Roos, Jerry Wilson and Steven Murphy have all personally offered helpful insights and support. Robert Kenward also provided invaluable help in the field during the 2013/14 winter, without which Chapter 5 would not have been possible. Nicholas Aebischer provided valuable statistical advice, particularly on Chapter 2. Thank you all very much.

Langholm Moor itself has been a fantastic place for a budding ecologist to conduct field work, primarily thanks to all the people I was lucky to work with. In particular, Sonja Ludwig and Damian Bubb gave a huge amount of support and help in the field. All of the Langholm Moor gamekeepers offered considerable help, and I am especially grateful to Simon Lester for his support, insight and good humour. All of the RSPB Research Assistants, including Aly McCluskie, Paula Keane, Eimear Rooney, Tommy Pringle, Anna McWilliam and Kirstie Hazelwood helped in numerous aspects during the summer months, and I'm very grateful to all of them. I also had help in the field from a number of MSc and placement students: Zoe Smith, Jon Butler, Ayla Paul, Merlin Becker, Sarah Emerson, Adam Stickler and Emily Trevail, and I'm very grateful for the enthusiasm and help each one of them offered. Many members of the Scottish Raptor Study Group have offered support and valuable insights, in particular Dave and Katie Anderson were generous with their time when teaching me to climb trees and tag buzzards, and Mac Hotson offered endless support and the invaluable use of his 'buzzard eyes' without which many aspects of this study would have been impossible. The Game and Wildlife Conservation Trust hosted me on numerous occasions and their staff offered valuable advice and support on numerous occasions. I am very grateful to the Langholm Moor

Demonstration Project for funding me and giving me this opportunity and to Graeme Dalby, Mark Oddy and Buccleuch Estates for logistical support and access to study sites.

A big thank you to past and present members of Mark's research group who provided support, help and light relief throughout my studies. Thank you to Ailsa, Matt, Caroline, Jon, Mieke, Ibrahim, Nadheer, Kirsty and Rike.

Special thanks to my family, especially Mum and Dad, and Mike, Jane and Hannah for their support and generosity.

Finally, and most importantly, thank you to Emma and (since March 2015) Owen. Your love, support and endless patience throughout this and everything else I do have helped me far more than anything else.

Collaborations

The following people made significant contributions to my thesis: Zoe Smith, Jon Butler, Ayla Paul (MSc Students); Sonja Ludwig and Damian Bubb (Langholm Moor Demonstration Project Lead Scientists), Aly McCluskie and Eimear Rooney (RSPB Research Assistants) all aided in the collection of summer diet data used in Chapters 2 & 3. Data on prey abundances and raptor foraging patterns were collected with the help of Ayla Paul, Sarah Emerson (MSc students), and staff from the Langholm Moor Demonstration Project and Game and Wildlife Conservation Trust. Robert Kenward, Sonja Ludwig and Merlin Becker all offered significant help in the field during the 2013/14 winter for Chapter 5. Data collection for each thesis chapter was coordinated by the author Richard Francksen. Nicholas Aebischer offered statistical advice for Chapter 2. Robert Kenward, Ian Newton and Steve Redpath offered advice on consumption modelling in Chapter 6. Adam Stickler (MSc student) conducted the captive buzzard feeding experiment under supervision from Richard Francksen.

All content was written and analysed by Richard Francksen. Mark Whittingham and David Baines oversaw and directed the research and offered advice and comments on drafts of chapters.

Contents

List of Tables and Figures

Chapter 1: Introduction

Langholm Moor [Photo credit: Making the Most of Moorlands]

“Co-operation requires tolerance, which starts with knowledge”

R. Kenward

(2006)

1.1 Background

Human-wildlife conflict is one of the most challenging and emotive issues in ecology. Conflict can occur when an action by either humans or wildlife has an adverse effect on the other (Conover 2002). Humans may suffer from crop damage, livestock depredation, property damage, loss of income and livelihood, or injury and loss of life. Wildlife may suffer from habitat destruction, detrimental trophic cascades, and ultimately the collapse of populations or reductions in range occupancy (Madden 2004). Contact between humans and wildlife is increasing as human activities expand throughout the world and conservation efforts restore wildlife to some areas of previous occupancy. In many places, this is leading to increased human-wildlife conflict (Woodroffe et al. 2005).

The framing of human-wildlife conflict as situations where wildlife and humans are in direct conflict (Conover 2002) has been criticized as overly simplistic (Madden 2004; Redpath *et al.* 2014) because it ignores the underlying human element and portrays animals as conscious human antagonists (Peterson *et al.* 2010). For example, whilst not conscious antagonists, elephants *Elephus maximus indicus* adversely impacting on the livelihoods of Indian farmers is perhaps an example of a human-wildlife conflict where humans and wild species are in direct conflict (Wilson *et al.* 2015). However, there is also an underlying conflict between interested human groups, in this case elephant conservationists and local farmers. This conflict *between* human interest groups *over* wildlife has been distinguished from 'human-wildife conflict' as a 'human-human conflict' (Madden 2004; Redpath *et al.* 2014). Further examples include the predation of livestock by African lions *Panthera leo,* which leads to conflict between farmers, conservationists and nature tourists (Schuette *et al.* 2013), while the loss of orang-utan *Pongo pygmaeus* habitat for oil palm plantations leads to conflict between developers and conservationists (Swarna Nantha & Tisdell 2009).

The conflict between human interests and predators can often be particularly contentious (Madden 2004; Woodroffe *et al.* 2005). Predators that pose a direct threat to humans or compete for shared resources can produce strong passions among different interest groups. These conflicts can become highly controversial when various human interest groups have different goals, attitudes, or priorities concerning the issue, and if this occurs, a human-human conflict over predators can arise. In some cases, attitudes become entrenched and dialogue between interest groups breaks down (Redpath *et al.* 2013). In order to facilitate communication between interest groups and reach solutions to conflicts, discussions must have access to relevant and current ecological knowledge of the systems in question (Lees *et al.* 2013). Predators and predation issues are some of the most pervasive areas of ecological research, and are increasingly the central theme of studies in the field of Applied Ecology, which is interested in the interface between ecological science and the management of biological resources (Ormerod 2002). The results of these studies can provide useful information to stakeholders engaged in dialogue over conflict (Redpath *et al.* 2010).

1.2 Raptors and gamebirds

Raptors *Falconiformes* are mobile predators that often compete with humans over shared resources (Newton 1979; Woodroffe *et al.* 2005). One such resource is gamebirds *Galliformes*, which are prey for many raptor species (Cotgreave 1995) as well as economically important quarry for humans (Valkama *et al.* 2005; Sotherton *et al.* 2009). Consequently, the relationship between raptors and gamebirds is one of the most topical issues in wildlife management in Britain today (Allen & Feare 2003; Redpath *et al.* 2004; Park *et al.* 2008; Thompson *et al.* 2009; Lees *et al.* 2013). The tenet of this human-wildlife conflict is that raptors reduce the number of gamebirds that would otherwise be available for humans to hunt (Park *et al.* 2008). As a consequence of this impact on gamebirds, perceived or real, raptors are often killed (Redpath *et al.* 2004), which can lead to range reductions or even species extinctions (Woodroffe *et al.* 2005). To explore the roots of the raptor-gamebird conflict, it is first worthwhile exploring the wider context of gamebird hunting and raptors in Britain.

1.2.1 Gamebirds in Britain

The loss, fragmentation and conversion of natural habitats to farmland during the 20th Century is believed to have been the main factor driving declines of many of Britain's wild gamebirds including grey partridge *Perdix perdix*, red grouse *Lagopus lagopus scotica,* and black grouse *Tetrao tetrix* during this period (Hudson & Rands 1988;

Thirgood *et al.* 2000b). Many of Britain's native wild gamebirds continue to decline or remain threatened today, with black grouse, grey partridge and capercaillie *Tetrao urogallus* all on the Red List of UK Birds of Conservation Concern, and red grouse on the Amber List (Eaton *et al.* 2009). Conversely, the number of reared and released non-native gamebirds, principally red-legged partridges *Alectoris rufa* and pheasants *Phasianus colchicus,* has increased throughout the 20th Century (Martin 2011). Today over 35 million pheasants are released each year in Britain (Bicknell *et al.* 2010). The game shooting industry is currently valued at an estimated at £1.6 billion per annum, and brings employment and economic benefits to many rural communities (PACEC 2006).

The context for this study is centred around the management of red grouse on areas of upland heather moorland in Britain.

1.2.2 Red grouse and heather moorland

Figure 1.1: *Red grouse [Photo credit: John Wright]*

Red grouse are a subspecies of willow ptarmigan *Lagopus lagopus* found in upland areas of Britain where heather *Calluna vulgaris* moorland dominates (Snow & Perrins 1998). They predominately feed on the young shoots of heather, but will also eat other plants such as cottongrass *Eriophorum spp.* and bilberry *Vaccinium myrtillus.* Red grouse are monogamous and territorial birds. Hens nest on the ground, generally in mature heather stands with laying beginning in mid/late-April, and family groups are formed until autumn when territories are re-established (Jenkins *et al.* 1963; Hudson 1992).

Red grouse feature in the diet of a number of predators, including foxes *Vulpes vulpes,* corvids *Corvidae spp.* and mustelids *Mustelidae spp.* (Hudson 1992) as well as several raptor species (Park *et al.* 2008). Red grouse also suffer from a number of different parasites, of which the nematode *Trichostrongylus tenuis* is the most significant and causes population cycles when red grouse exist at high densities (Hudson *et al.* 1997).

Long-term declines of red grouse have predominately been associated with loss, fragmentation and degradation of heather-dominated moorland (Thirgood *et al.* 2000b) largely as a consequence of overgrazing and increases in coniferous woodland cover (Thompson *et al.* 1995). Furthermore, declining numbers of gamekeepers, and increasing numbers of many generalist predators including foxes, carrion crows *Corvus corone* and mustelids which are all predators of red grouse and are routinely killed by gamekeepers, have also contributed to red grouse declines (Hudson 1992; Reynolds & Tapper 1996). On short-term and local scales however, when predation from raptors is at high levels, red grouse populations can be limited and population cycles suppressed (Thirgood *et al.* 2000b).

Heather moorland managed principally for the shooting of red grouse is estimated to represent between 5 and 15% of the UK uplands, and between 20 and 40% of all heather-dominated moorland (see Douglas *et al.* 2015 and references therein). Gamekeepers are employed to manage heather moorland to maximise the number of red grouse available for shooting in the autumn. This management involves creating a mosaic of different aged stands of heather to provide food and shelter for grouse, achieved through burning and cutting, and controlling the predators of red grouse (Hudson & Rands 1988). Predators that are legally killed principally include foxes, carrion crows, stoat *Mustela ermine* and weasel *Mustela nivalis*. Birds of prey are killed on some moors despite legal protection (Etheridge *et al.* 1997; Elston *et al.* 2014).

In Europe, extensive heather-dominated landscapes are largely confined to the uplands of the UK and Ireland, where it has considerable economic, conservation, aesthetic and tourism-related value (Thompson *et al.* 1995; Robertson *et al.* 2001). The bird assemblage of Britain's heather moorland contains internationally important populations of breeding and/or foraging species including merlin *Falco columbarius*, golden eagle *Aquila chrysaetos*, peregrine *Falco peregrinus*, hen harrier *Circus cyaneus*, golden plover *Pluvialis apricaria*, curlew *Numenius arquata*, redshank *Tringa tetanus* and ring ouzel *Turdus torquatus* (Thompson *et al.* 1995). Well-managed red grouse moors can help to maintain heather moorland and in doing so help to provide some of these biodiversity benefits (Robertson *et al.* 2001). Red grouse management is also a source of employment and economic benefits to rural communities (McGilvray 1995).

Red grouse shooting in Britain can be divided into two broad types: 'walked-up' and 'driven'. Walked-up shooting involves hunters paying to walk the moorland and shoot grouse as they are encountered. Driven shooting involves a team of employed 'beaters' driving grouse towards a line of paying clients who remain stationary behind 'butts' and shoot the grouse as they fly past or overhead. A key difference between these two models of grouse hunting is the density of grouse and therefore intensity of management required. Driven grouse shooting requires much higher grouse densities than walked-up shooting, and so driven shooting requires a greater intensity of habitat and predator management (Hudson & Newborn 1995). Another key difference is the revenue that each model of hunting generates. The Game & Wildlife Trust's National Gamebird Census (NGC) estimates that driven grouse shooting generates roughly ten times the revenue walked-up shooting does (Sotherton *et al.* 2009). This income reduces the need for landowners to seek alternative sources of income, for example from monoculture forestry or sheep grazing which may have lower conservation benefits than heather moorland (Thompson *et al.* 1995; Robertson *et al.* 2001).

However, there is also concern over the ecological and environmental costs of intensive red grouse management for driven shooting on some moors. In some areas, this management has been linked to damage to blanket bogs, discoloration of drinking water and carbon release associated with intensive heather burning, and with illegal persecution of raptors (Thompson *et al.* 2009). The conflict between red grouse management and hen harriers is well-documented (Redpath & Thirgood 1997, 2009;

Baines & Richardson 2013). Hen harriers have been shown to be capable of limiting the number of red grouse available for shooting (Thirgood *et al.* 2000b), while the distribution of hen harriers is currently limited by their widespread illegal killing on grouse moors (Etheridge *et al.* 1997; Hayhow *et al.* 2013). Solutions to this conflict have been difficult to achieve to-date, but a range of stakeholders have expressed the need to work collectively to find resolutions (Thirgood & Redpath 2008; Sotherton *et al.* 2009; Thompson *et al.* 2009; Elston *et al.* 2014).

In order to inform discussions such as this and those connected to the wider raptor-gamebird conflict, there is a need for robust and current scientific data on the extent of any potential impact of raptor predation on gamebirds, including red grouse (Thirgood & Redpath 2008; Lees *et al.* 2013).

1.2.3 Raptors in Britain

By the late 19th Century, the populations and ranges of most species of diurnal raptor had been greatly reduced, and five out of fifteen breeding species had been eradicated from Britain (marsh harrier *Circus aeruginosus*, goshawk *Accipiter gentilis*, honey buzzard *Pernis apivorus,* white-tailed eagle *Haliaeetus albicilla* and osprey *Pandion haliaetus*). Habitat destruction restricted the range and population sizes of many British raptor species, and their populations were further reduced by persecution from gamekeepers and farmers; accidental poisoning; killing for skins, feathers or eggs, and reductions in prey following agricultural intensification and deforestation (Newton 1979).

Raptors have been legally protected in the UK since 1954 following the introduction of The Protection of Birds Act, although it was not until the introduction of the Wildlife and Countryside Act in 1981 with its greater focus on the killing of birds that many species began to recover. Some species have been aided in their recovery through reintroduction programmes (e.g. red kite *Milvus milvus*, white-tailed eagle and goshawk) (Newton 1979; Carter 2001; Bainbridge *et al.* 2003; Kenward 2006), while the banning of organochlorine pesticides such as DDT has been key in improving the fortunes of others (e.g. peregrine and sparrowhawk) (Newton 1979). The latest Atlas produced by the British Trust for Ornithology (BTO) documents range increases over the last 20 or 40 years for thirteen of Britain's fifteen breeding raptors, with only golden eagle *Aquila chrysaetos* and kestrel *Falco tinnunculus* suffering range contractions over similar periods (Balmer *et al.* 2014). For most of these species, these population and range expansions represent recovery and recolonisation of former range (Newton 1979, 1998).

Nevertheless, some species still have depressed population sizes and restricted ranges in Britain (Baker *et al.* 2006; Balmer *et al.* 2014), while others have undergone more recent declines (Baillie *et al.* 2014). For example, kestrels have declined by 20% in Britain and 65% in Scotland since 1995 (Baillie *et al.* 2014), which is believed to be related to reductions in small mammal availability as a result of agricultural intensification and loss of habitat heterogeneity (Garratt *et al.* 2011). The ranges of common buzzards *Buteo buteo*, hen harrier and golden eagle are all believed to be restricted in part by illegal persecution (Whitfield & Fielding 2004; Gibbons *et al.* 2008; Hayhow *et al.* 2013).

1.3 Impact of raptors on gamebirds

Many raptors are of conservation concern while gamebirds are of economic importance (Newton 1979; McGilvray 1995; Valkama *et al.* 2005; Sotherton *et al.* 2009). Combined with concerns about the impact of raptors on gamebirds, and the illegal persecution of raptors by some gamekeepers, these factors make the raptor-gamebird conflict highly controversial (Redpath & Thirgood 1997; Allen & Feare 2003; Redpath *et al.* 2004; Valkama *et al.* 2005). As a result, a large number of studies have aimed to investigate the impacts of raptor predation on gamebirds (see review in Park *et al.* 2008).

Evidence tends to suggest that losses of reared and released gamebirds to raptors are generally low, but can be substantial on a local scale (Park *et al.* 2008). For example a radio telemetry study of buzzards at pheasant release pens estimated that buzzards accounted for an average of 4% of pheasant mortality, although was as high as 35% at some pens (Kenward *et al.* 2001). Away from release sites, road traffic collisions and predation by foxes tend to be the cause of a greater proportion of total mortality amongst pheasants (Turner & Sage 2003; Lees *et al.* 2013). Turner & Sage (2003) estimated that approximately 0.6% of pheasants killed away from release pens were due to raptor predation whilst 36% were killed or scavenged by foxes.

Wild gamebird species are found in the diet of many British raptors, although it is worth noting that distinguishing between causes of mortality from different raptor species, and between predation and scavenging is a common problem to many studies which look at raptor diet (Park *et al.* 2008). Parish and Sotherton (2007) found that 19% of monitored grey partridges were killed and eaten (herein "predated") by raptors. A study of black grouse in North Wales found that of 33 radio-tracked adults and juveniles, 18 (55%) were predated by raptors (Bowker *et al.* 2007), while in another study 14% of tagged black grouse were predated by peregrines (Warren & Baines 2002). Ptarmigan and capercaillie have been recorded in the diet of golden eagles and buzzards in Scotland (Swann & Etheridge 1995; Watson *et al.* 1998). Whilst few studies have assessed the impact of raptors on these species, one study found that an index of raptor sightings was unrelated to capercaillie productivity in Scottish pine forests (Baines *et al.* 2004).

It is important to note that the occurrence of a gamebird in the diet of a raptor does not equate to there being an overall negative impact of raptor predation at the population level of the gamebird. Nor does a negative correlation between raptor and gamebird abundance provide evidence of causation (Newton 1998). Whilst most of the above studies provide evidence of the occurrence of raptor predation on gamebirds or of correlations between raptors and gamebirds, none of them assess the impact of raptor predation on gamebird breeding densities. However, research on grey partridges on farmland in southern England demonstrated the ability of predators to supress grey partridge breeding density below the level that would occur in the absence of predation (Potts 1986). Models estimated that over-winter raptor predation of grey partridges removed 9.5% of autumn density or 15% of density after shooting, depending on when most raptor predation occurred, which would reduce spring partridge density by 11 – 26% in the absence of shooting (Watson *et al.* 2007).

A wide range of management options aiming to reduce the impact of raptors on prey have been proposed, and many trialled to varying levels of success (FERA 2012). These range from visual or auditory deterrents at the less interventionist end of the scale, to removal of nests, eggs, chicks or adults, either lethally or non-lethally, at the other. The management of systems involving predators and prey that are economically important or of conservation importance requires, at its most fundamental level, current and accurate data of predator-prey dynamics involved (Conover 2002). This is also true of the raptor-gamebird conflict (Thirgood & Redpath 1999; Thompson *et al.* 2009). This research aims to gather such data, and consequently may have value in advocating or discouraging certain management options based on their likely efficacy based on the data. It may also aid in the design of novel methods of limiting losses to buzzards.

1.3.1 The Joint Raptor Study

The Joint Raptor Study (JRS) was conducted between 1992 and 1997 and was based at Langholm Moor in south-west Scotland (Redpath & Thirgood 1997). The study aimed to assess the impact of hen harrier and peregrine falcon on red grouse numbers. Throughout the study, raptors were strictly protected and allowed to breed freely, while control of foxes, carrion crows, stoats and weasels continued. During this time, the number of breeding female hen harriers increased from two in 1992 to twenty in 1997 (Redpath & Thirgood 1999). It was estimated that raptors removed on average 30% of the potential breeding stock of grouse during spring, and hen harriers removed on average 37% of grouse chicks during summer. The study concluded that most of these losses were additive to other causes of mortality, and together they reduced post-breeding grouse populations by 50%, ultimately rendering driven grouse shooting unviable. Subsequently, grouse management was abandoned on Langholm Moor which resulted in an increase in corvid and fox numbers, and breeding hen harrier numbers dropped back to levels observed prior to the JRS (Baines *et al.* 2008). To many, this was a ‘lose-lose’ situation in terms of conservation, economic and cultural activity (Redpath *et al.* 2013).

Whilst the JRS presented arguably the most comprehensive ecological study of the relationship between raptors and their gamebird prey, the debate about the impact of this relationship continues today. Furthermore, since the JRS there have been some notable changes in the raptor community of Britain. Not least of these is the increase in both population and range of the common buzzard (Balmer *et al.* 2014).

1.4 Buzzards

Common buzzard [Photo credit: John Wright]

The common buzzard (herein referred to as 'buzzard') is a medium sized raptor in the family *Accipitridae.* The buzzard is a generalist predator with a wide dietary breadth; selecting prey ranging in size from earthworms and invertebrates to adult pheasants and brown hares *Lepus europaeus.* In Britain, as throughout much of their geographic range, the preferred prey of buzzards are small mammals, especially voles *Microtus* spp. and European rabbits *Oryctolagus cuniculus* (Tubbs 1974; Mañosa & Cordero 1992; Swann & Etheridge 1995; Kenward *et al.* 2001; Selås *et al.* 2007; Rooney & Montgomery 2013). Buzzards nesting on heather moorland in Britain have been shown to predate red grouse alongside their preferred vole and rabbit prey (Graham *et al.* 1995).

In Britain, the buzzard has increased substantially in population and range since the 1970's. The BTO Atlas documents an 81% increase in breeding distribution over the last 40 years, and a 74% increase in winter distribution in the last 30 years, which in most areas represents a recolonisation of previously occupied range (Balmer *et al.* 2014). Reductions in persecution following legal protection, the banning of organochlorine pesticides and the recovery of rabbit populations from myxomatosis have all aided the spread of the buzzard since the 1970's (Parkin & Knox 2010). Recent estimates are that there are now 56 – 77,000 pairs of buzzards in Britain (Musgrove *et al.* 2013), making it the most common diurnal raptor for over a decade (Clements 2002).

This population and range recovery has, in some cases, been coupled with an increase in concern amongst gamekeepers over the impact of buzzards on gamebirds (Parrott 2015). This prompted the UK government to propose, but subsequently withdraw, a study to look at sub-lethal control measures on buzzards to limit the losses of pheasants (Lees *et al.* 2013). There has also been an increase in the number of applications made for licences to reduce the impact of buzzards, deemed to be causing 'serious damage' to gamebirds and livestock (FERA 2012). To date, at least two of these licenses have been issued by Natural England (the UK government department responsible England's natural environment). One was issued authorising the capture and relocation of two buzzards from a free-range poultry farm (Natural England 2013a), and one was issued authorising the removal of four buzzard nests and the eggs contained within (Natural England 2013b).

To date, much of the controversy over buzzards and gamebirds in Britain has centred around their impact, perceived or actual, on reared pheasants (Kenward *et al.* 2001; Lees *et al.* 2013; Parrott 2015). No studies to date have focussed on investigating the potential impact of buzzard predation on red grouse. Considering the importance of red grouse to the management of upland heather moorland (Robertson *et al.* 2001), this presents an important gap in our understanding of the potential impact of recovering buzzard populations on gamebirds and land management in Britain.

1.5 Study site and approach

1.5.1 Langholm Moor

The present study was conducted between 2011 and 2014 on Langholm Moor and its peripheries (55.1 – 55.3°N, 3.0 – 2.8°W) in south-west Scotland. All aspects of the study were conducted within 221 km^2 of the Dumfries and Galloway and Scottish Border regions on land owned by the Buccleuch Estate. This area was chosen to include the 114 km^2 managed under the Langholm Moor Demonstration Project (LMDP) [langholmproject.com] plus a 2 km buffer zone. The buffer zone was chosen in an attempt to incorporate buzzards nesting nearby that may still hunt on the moor from estimates of buzzard home range size at Langholm Moor (Graham *et al.* 1995). The exact area varied slightly between different aspects of the study and this is defined within the text. The site includes 76 km^2 designated as the Langholm – Newcastleton Site of Special Scientific Interest (SSSI) and Special Protection Area (SPA) (Figure 1.1). The SSSI is designated for the site's range of upland habitats and breeding birds, while the SPA is designated for its importance to breeding hen harriers. The habitat within the entire study site consists of rough and acidic grassland (51.0%) and a mosaic of heather and grass moorland (21.6%) with improved grassland (11.1%), commercial coniferous forestry (10.6%) and mixed deciduous woodland (5.1%) occurring on the moor periphery (CEH Land Cover Map 2007; Morton *et al.* 2011).

Historically, Langholm Moor was one of the most productive red grouse moors in Britain. However, since 1948 there were declines in the number of grouse shot, chiefly thought to be due to a 48% reduction in the extent of heather cover on the moor (Thirgood *et al.* 2000b). As outlined above, Langholm Moor was the site of the Joint Raptor Study (JRS) in the 1990's which aimed to measure the scale of raptor predation, chiefly hen harrier and peregrine, on red grouse (Redpath & Thirgood 1997). Langholm Moor is now the site of the Langholm Moor Demonstration Project (LMDP) which aims to "demonstrate an effective means of resolving the raptor-grouse controversy" (Langholm Moor Demonstration Project 2007). To achieve this aim, the LMDP has reinstated grouse moor management alongside strict protection of raptors, thus attempting to achieve the conservation objectives of the SPA/SSSI. Habitat management and control of predators is undertaken by a team of five gamekeepers. The response of the grouse, habitat and raptors is monitored by a team of research scientists. Recognising that there are a range of stakeholders with a shared concern for the future of heather moorland in Britain, the LMDP is a partnership project between Buccleuch Estates, Scottish Natural Heritage, Game and Wildlife Conservation Trust, Royal Society for the Protection of Birds and Natural England.

Prior to the start of the present study and following the reinstatement of moorland management in 2008, red grouse recovery had been slower than expected. Post-breeding grouse density increased during the first years of the project but subsequently levelled off below the predicted level required to shoot 1,000 brace (2,000 birds) currently set as the target (Langholm Moor Demonstration Project 2014). Poor red grouse breeding success, associated with poor chick survival, and high overwinter mortality were identified as key causes for the lack of an expected grouse recovery. Monitoring at Langholm also showed that the majority of recovered grouse carcasses showed signs of raptor predation. Whilst it was not possible to identify which raptors were responsible for this predation, numbers of breeding hen harriers and peregrines were below the levels recorded during much of the JRS (LMDP, unpublished data). The aim of the present study, therefore, was to investigate whether buzzard predation could potentially be impacting on the recovery of red grouse numbers at Langholm Moor following reinstatement of moorland management.

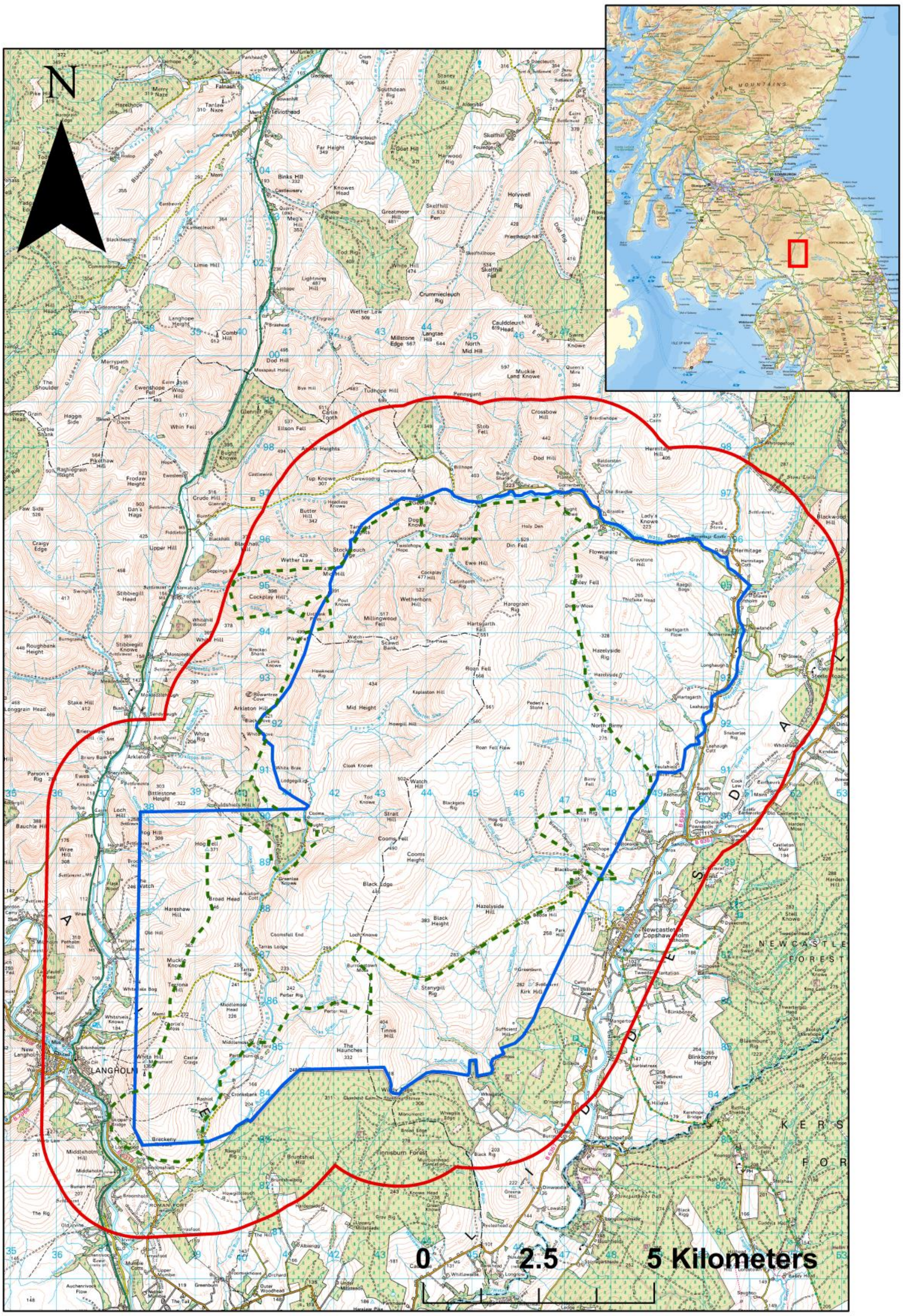

Figure 1.1. The study area (red line) which incorporated the Langholm Moor Demonstration Project (LMDP) area (blue line) and the Langholm-Newcastleton hills SSSI and SPA boundary (green dashed line) in south-west Scotland (inset map). The study area was chosen to include the LMDP area plus a 2 km buffer zone based on home range estimates of buzzard at Langholm Moor (Graham *et al.* 1995).

1.5.2 Study approach

Assessing the impact of predators on their prey is a complex problem which can be addressed in a number of ways (see review in Park *et al.* 2008). The most scientifically rigorous approach to studying predator impact is to experimentally remove the predator from an area and study the response of the prey compared to a similar area, before reversing the treatment (Newton 1998). However, the aim of the LMDP is to demonstrate methods of managing an economically viable grouse moor alongside protection of raptors (Langholm Moor Demonstration Project 2007), and so a removal approach was not appropriate. When predator removal is impractical or inappropriate there are a number of non-experimental approaches that can improve our understanding of the predatory mechanisms involved, and be used to predict impact (Redpath & Thirgood 1997).

Questionnaires given to gamekeepers and land managers can provide information on the number of gamebirds eaten by different predator species (Harradine *et al.* 1997). However, these studies can often be subject to bias, introduced when responses come predominately from those who have been most affected, or by the misidentification of predation versus scavenging events (Park *et al.* 2008). Studies of correlations between predator and prey abundances over multiple areas (Gibbons *et al.* 2008; Amar *et al.* 2010) can provide circumstantial evidence of impact, but cannot derive causal relationships (Park *et al.* 2008). These approaches were also not appropriate for this study focussed on one site at Langholm Moor. Instead, I have focussed on exploring predatory mechanisms and the factors affecting predation rates of red grouse by buzzards.

Optimal Foraging Theory (OFT) can provide invaluable insights and predictions into the manner in which predators hunt for their prey. OFT, originally formulated by MacArthur & Pianka (1966), shows that natural selection has resulted in animals that forage in a manner that maximises their fitness, usually expressed in terms of net energy gain. OFT models predict that animals will selectively choose which food to eat (i.e. optimal diet), and which habitat patches they forage in and for how long (i.e. optimal patch choice) (Pyke *et al.* 1977). In this study, I draw on a number of the fundamental components of

OFT to explore diet and foraging behaviour of buzzards, and obtain initial insights into how these behaviours may affect predation of red grouse.

One of the most commonly used and fundamental methods of exploring a predator-prey relationship is to study the dietary composition of the predator. Dietary composition studies can provide information ranging from a simple assessment of whether a prey occurs in the diet of a raptor, to more detailed assessments of predation rates and timing of predation events (Redpath & Thirgood 1999; Rutz *et al.* 2006; Selås *et al.* 2007; Tornberg & Reif 2007; Park *et al.* 2008). A key part of the present study was to assess the dietary composition of buzzards at Langholm Moor, with particular reference to the occurrence of red grouse in the diet. It was important to investigate dietary composition in winter, as well as summer, owing to the fact that buzzard diet can vary throughout the year (Mañosa & Cordero 1992; Wuczyński 2005).

Vital to any study involving assessment of dietary composition is having an understanding of the inherent biases of the chosen methods. Various methods can either under- or over-estimate the occurrence of particular prey groups based on their persistence, detectability or the manner in which they are handled by the predator (Redpath *et al.* 2001a; Lewis *et al.* 2004). Here I have explored the biases associated with some commonly used techniques in order to better understand how these may have affected my results, as well as the results of similar studies.

There are two central components to any study of the impact of predation on prey: the ‘numerical response’ and the ‘functional response’ (Solomon 1949). The numerical response describes changes in raptor density with variations in prey availability. Raptors, including buzzards, can respond numerically to changes in prey abundances by changing their breeding density or breeding success (Korpimäki & Norrdahl 1991; Redpath & Thirgood 1999; Reif *et al.* 2004), or by spending longer times hunting in a given area, termed the ‘aggregative response’ (Smout *et al.* 2010; Mckinnon *et al.* 2013). Both of these types of numerical response can affect the total impact of raptors on prey. In this study I explore numerical responses of buzzards by investigating how changes in abundances of key buzzard prey groups affect breeding parameters and foraging patterns, and explore how these may influence the impact of buzzards on red grouse.

Dietary assessment also forms the basis of many studies looking at variation in prey choice over time as relative prey availabilities change. This is termed the ‘functional response’, and along with the numerical response, forms the second central component of predation (Solomon 1949; Redpath & Thirgood 1999; Salamolard *et al.* 2000; Reif *et al.* 2004; Park *et al.* 2008; Smout *et al.* 2010). Following on from the predation studies of Holling (1959), three main types of functional response have been classified and defined. Assuming an absence of any numerical response, these three types of functional response can be illustrated by plotting the predation rate of the predator (numbers or proportion of total prey items consumed per unit time) on the y-axis and the density of the prey on the x-axis. These are illustrated in Figure 1.2.

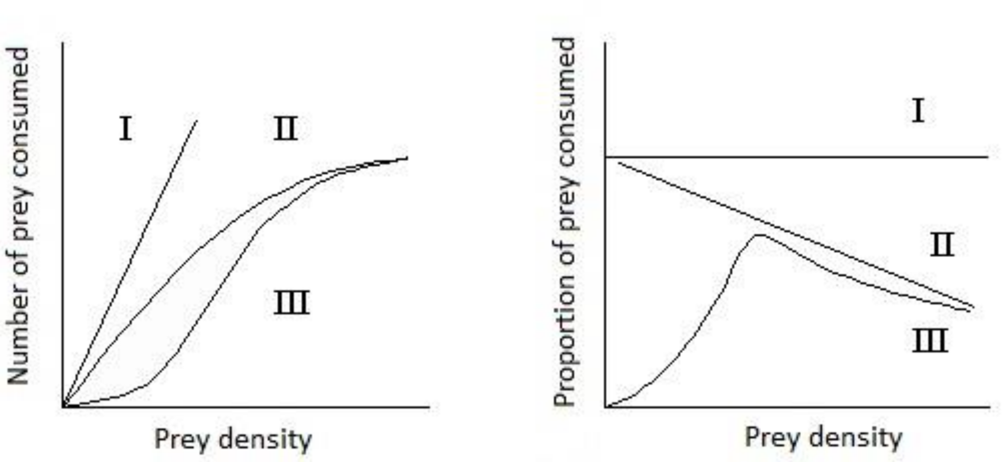

Figure 1.2. Hypothetical relationships between the total number of prey items consumed and prey density (left panel) and the corresponding relationship between the total proportion of prey consumed and prey density (right panel) for three functional responses (types I, II, and III). Adapted from (Crawley 1992).

A type I functional response describes a linear relationship between the number of prey items consumed and prey density. This equates to a constant relationship between the proportion of total prey killed and prey density, termed ‘density independence’. Type I functional responses have been documented for raptors specialising in small mammal predation (Korpimäki & Norrdahl 1991), and suggest that the proportion of prey killed by predators is unaffected by prey density. Type II functional responses show a convex or hyperbolic relationship between numbers of prey consumed and prey density, whereby there is a steep rise in the number of prey consumed with increasing (low) densities, after which the numbers killed reaches an asymptote. This equates to a decelerating predation rate, also termed 'inverse density dependence', and suggests that the impact of predation is greatest at low prey densities. These type II responses are more commonly found for generalist predators (Dale *et al.* 1994; Redpath & Thirgood 1999; Smout *et al.* 2010). Type III functional responses describe a concave or sigmoidal relationship between numbers of prey killed and prey density. Like type II responses, this means that the number of prey killed reaches a plateau at high prey densities (or decelerating predation rate), although unlike type II relationships predation rate accelerates at low prey densities. This means that predation is density dependent at low prey densities, but inverse density dependent at high prey densities. This situation results in an increasing impact of predation as prey density increases *to a point,* after which the proportion of prey killed begins to decline, and has been suggested for goshawk predation on grouse species (Linden & Wikman 1983). Clearly, knowledge of the shape of the functional response of predators is key in determining the impact of predation on prey (Redpath & Thirgood 1999; Valkama *et al.* 2005; Park *et al.* 2008).

Optimal Foraging Theory shows that the foraging distribution of any animal will be non-random in a patchy environment (MacArthur & Pianka 1966). Understanding the factors that determine the foraging patterns of raptors can provide useful information on how they may impact on prey and how any negative impacts could be mitigated (Thirgood *et al.* 2003). The relative attractiveness of an area to foraging raptors will determine the number of raptors and duration that they hunt the area (aggregative response) (Smout *et al.* 2010; Mckinnon *et al.* 2013). In this study I have investigated buzzard foraging patterns and the aggregative response of buzzards by exploring the key factors influencing buzzard foraging distributions.

The energetic requirements of an organism can be estimated using bioenergetic calculations. These account for the age, size, demographics and behaviour of an animal in order to estimate the energy and food required to sustain it while behaving normally in its natural environment (Masman *et al.* 1988; Warkentin & West 1990; Nagy *et al.*

1999). When combined with information on dietary composition and population size, bioenergetic calculations can be used to estimate the total number of prey items taken by a predator population. These models can be valuable in estimating the total possible impact of predation (Phillips *et al.* 1999; Roby & Lyons 2003). In this study I use bioenergetics calculations, with data on buzzard diet and population, to estimate the maximum number of red grouse that buzzards could be removing from Langholm Moor.

1.6 Thesis aims

The overall aim of this thesis is to improve our understanding of the mechanisms influencing the predator-prey relationship between a raptor with an expanding range and recovering population, the common buzzard, and red grouse on an area of upland heather moorland in south-west Scotland. For the reasons outlined above, an experimental approach was not possible, yet alternative approaches were available which will help to explore buzzard impact on red grouse. Specifically, the aims of my thesis are to:

1. evaluate the biases associated with some common methods of assessing the dietary composition of raptors;
2. investigate the numerical and functional responses of buzzards to variations in prey abundance during the breeding season;
3. determine what explains the foraging distribution of buzzards, and whether variations in foraging patterns correlate with patterns of red grouse mortality;
4. assess the home ranges and dietary composition of buzzards during the winter, and ask what factors determine whether a buzzard eats red grouse;
5. estimate the number of red grouse removed by buzzards from Langholm Moor.

Finally, I will discuss the main findings of the thesis and their relevance to the wider study system, and recommend future research directions.

1.7 Thesis outline

Following this general introduction, the thesis is arranged into five chapters, each one attempting to address each of the five aims above. A general discussion concludes the study. Firstly, I investigate the biases associated with some commonly used methods of assessing raptor diet. I compare buzzard diet composition between three methods and discuss how differences may affect the conclusions of impact studies such as this one (Chapter 2). I then investigate numerical and functional responses of buzzards during the breeding season. I assess yearly variation in buzzard breeding density, breeding success, and dietary composition with special focus on the occurrence of red grouse, in relation to yearly fluctuations in prey abundance (Chapter 3). Next, I explore buzzard foraging patterns during both summer and winter in relation to variations in prey and habitat. I also use a correlative approach to examine relationships between buzzard foraging patterns and indices of red grouse mortality (Chapter 4). I return to describing buzzard diet composition, but this time during winter which to date has received much less consideration than the breeding season from raptor diet studies. I also investigate the factors leading to the presence of red grouse in buzzard diet during the winter (Chapter 5). I then bring many of these results together by combining dietary composition and population estimates with calculations of bioenergetics requirements, in order to produce the first estimates of the total number of red grouse that buzzards could remove from Langholm Moor (Chapter 6). Finally, I discuss key results and place them in the context of both Langholm Moor and gamebird management in Britain (Chapter 7).

The key aim of my thesis is to improve our understanding of the predator-prey dynamics of buzzards and red grouse at Langholm Moor. These results may have wider implications for the management of economically important or threatened species, alongside increasing populations of protected raptors. While solutions that are acceptable to all stakeholders in the raptor-grouse conflict have been both few and challenging to achieve (Redpath *et al.* 2010), there is on-going dialogue between interested parties, as exemplified by the Langholm Moor Demonstration Project. Key to this dialogue is having an understanding of the ecological dynamics behind the system in question (Lees *et al.* 2013). Therefore, I hope that this study can contribute to discussions aimed at resolving the raptor-grouse conflict.

Chapter 2. Prey delivered to common buzzard nests: comparing methods for assessing diet composition during the breeding season

Note: An edited version of this chapter is published as: **R. M. Francksen, M. J. Whittingham & D. Baines.** (2016) Assessing prey provisioned to common buzzard *Buteo buteo* chicks: a comparison of methods. *Bird Study*. Available at: http://dx.doi.org/10.1080/00063657.2016.1183111.

2.1 Abstract

Accurate and unbiased estimates of diet are important for many aspects of raptor ecology. Recent increases in the population and range of common buzzards *Buteo buteo* have generated interest regarding their potential impact on gamebirds. Understanding biases associated with chosen methods of dietary assessment is crucial for investigating the impact of predation. Data on diet composition were collected from 32 buzzard nests on and around an area of upland heather moorland managed for red grouse *Lagopus lagopus scotica* between 2011 and 2013. Data obtained from direct observations using motion-triggered nest cameras were compared with two commonly used indirect methods of assessing diet: collection of prey remains and analysis of regurgitated pellets. Dietary composition differed between methods in all three study years, and these methodological differences varied between years, most likely in relation to changes in prey abundance. Small mammals were underestimated by prey remains in all years, while reptiles and amphibians were underestimated by prey remains and pellets in two of the three study years. Large birds, including gamebirds, tended to be overestimated by prey remains, significantly so in one year. Pellets overestimated the frequency of invertebrates in all study years. Future studies should consider not only how chosen methods may affect results, but also how effects can differ between years.

2.2 Introduction

Evaluating the diet of raptors has formed an important component of many studies, including those concerned with reproduction, energetics, dietary overlap and the impact of predation (Newton 1979; Warkentin & West 1990; Redpath & Thirgood 1999; Park *et al.* 2008; Rooney & Montgomery 2013). A range of techniques are available for assessing raptor diet which can be broadly separated into 'direct' and 'indirect' methods. Direct methods involve the observing of individuals during foraging or feeding of their young. Examples of the use of direct methods include the studies of Redpath & Thirgood (1999) who conducted observations of hen harriers *Circus cyaneus* from hides to obtain data on the composition of prey delivered to chicks in the nest; Kenward *et al.* (1981a) who tracked goshawks *Accipiter gentilis* using radio telemetry methods and obtained direct observations of individuals at the remains of their prey; while Lewis *et al.* (2004), Reif & Tornberg (2006) and Selås *et al.* (2007) all deployed cameras in the nests of buzzards and goshawks to observe prey delivered to chicks in the nest. Indirect methods involve the collection of evidence from past predation events to infer the composition of diet. Examples of the use of indirect methods include Swann & Etheridge (1995), Graham *et al.* (1995) and Rooney & Montgomery (2013) who all collected prey remains and regurgitated pellets from buzzard nest sites; Pietersen & Symes (2010) who analysed the stomach contents of dead Amur falcons Falco amurensis and lesser kestrels Falco naumanni; and Resano-Mayor *et al.* (2014) who compared data from regurgitated pellets with stable isotope analysis of feathers collected from nestling Bonelli's eagles *Aquila fasciata*.

It is generally assumed that raptor diet is most accurately estimated through direct methods (Redpath *et al.* 2001a; Rutz 2003; Lewis *et al.* 2004; Tornberg & Reif 2007), yet due to the greater time and cost implications associated with the use of direct methods, most raptor diet studies have employed indirect methods (Tornberg & Reif 2007). Recently however, the development and reduction in cost of video camera technology mean that this method is now a viable option for more researchers interested in raptor diet (Reif & Tornberg 2006; Steen 2009) and nest monitoring (Bolton *et al.* 2007). Due to the wide range of techniques available, it is important to understand the inherent biases of chosen methods.

The impact of raptors on gamebirds is a contentious and topical issue (Thirgood *et al.* 2000a). Consequently, a great number of published studies have sought to assess impacts on UK gamebird populations, both introduced and native, arising from raptor predation (see review in Park *et al.* 2008). Assessment of raptor diet is an important component of many of these studies, however Park *et al.* (2008) highlight that inherent biases in methods is a recurring limitation. Improving the accuracy of future studies therefore depends on having informed knowledge of the most appropriate methods.

Recently, the impact of common buzzards *Buteo buteo* (herein 'buzzard') on gamebirds has been the subject of intense debate (Lees *et al.* 2013). During the past 40 years, buzzards have expanded their range by an estimated 81% in Britain (Balmer *et al.* 2014), and have been the most abundant diurnal raptor in Britain for over a decade (Clements 2002) with an estimated population of 56-77,000 breeding pairs (Musgrove *et al.* 2013). This expansion has been accompanied by an increase in applications for control licenses (FERA 2012), which in part has led to calls for increased rigour when assessing the impact of buzzards on gamebirds (Lees *et al.* 2013). Despite this, methodological biases have not been assessed for buzzard diet studies in the UK before, which is pertinent considering the increased interest in this species.

The aim of this study is to explore whether assessment of buzzard diet varies between direct and two commonly used indirect methods. I then identify key areas where biases occur, and investigate whether these differences are consistent between years.

2.3 Methods

2.3.1 Study site

The study was carried out at Langholm Moor (55.1 – 55.3°N, 3.0 – 2.8°W) in south-west Scotland. The study site is owned by Buccleuch Estates and encompasses 221 km^2, which included 114 km^2 covered by the Langholm Moor Demonstration Project (LMDP), as well as 76 km^2 designated as the Langholm – Newcastleton SSSI and SPA. Within the LMDP area, moorland management to benefit red grouse is undertaken by a team of five gamekeepers which includes rotational burning and cutting of heather, and control of corvids, foxes and mustelids. For more study site details see Chapter 1, Section 1.5.1.

2.3.2 Buzzard nests

Forestry, wooded gullies and isolated trees and crags were systematically searched for the presence of active buzzard nests, particularly within known territories. Nest searches began in February or March each year. Nests were considered active if they were either freshly lined, had fresh prey remains and/or pellets nearby, or if territorial adults were heard calling (Tubbs 1974; Hardey *et al.* 2009). Between 2011 and 2013, 58 active buzzard nests were recorded within the study site. Prey remains and pellets were collected from 46 of these nests once failed attempts and discoveries after chicks had fledged were excluded. Of these 46 nests, camera footage was also collected from the 32 nests located on or closest to the LMDP site, as these were of most interest for assessment of impact on red grouse for a concurrent study (Chapter 3). For the purposes of this study, comparisons between direct and indirect methods were conducted with data from these 32 nests. All nests fell into either the LMDP project area or within 1 km from the project boundary (see Figure 1.1 in Chapter 1). All diet data were collected between April and August in each year. Any nests discovered after chicks had hatched were not included in this study to reduce bias associated with nest discovery date.

2.3.3 Measuring diet – Camera images

Images from high-resolution waterproof cameras formed the direct method of diet estimation at 32 buzzard nests (2011 = 11, 2012 = 10, 2013 = 11). Cameras were attached with a bracket to a branch within 1 – 2 meters of the nest to allow the entire nest platform to be observed (Reif & Tornberg 2006). Motion in the nest triggered cameras to record colour video clips of 1-5 minutes in duration, recorded on a high-definition video recording unit at the base of the nest tree. Six recording units (model: Mini HDVR LS-H720) were rotated systematically between nests. Recording units were deployed at each nest for a minimum of three days during the following periods: during the first week post-hatching; between one and four weeks post-hatching; and from four weeks post-hatching until young had fledged and ceased to be fed at the nest (mean nestling period of 32 nests = 50 days, *s.e.* = 0.74). Equipment was powered by a 12v car battery and footage was stored on a 32 gigabyte mini-SD card before being downloaded and analysed. Prey were recorded as 'unknown' if obscured by a chick, adult or branch and couldn't be identified.

2.3.4 Measuring diet – Prey remains and pellets

Prey remains and pellets formed the indirect methods of diet estimation. Concurrent to cameras recording prey deliveries, searches for prey remains and regurgitated pellets were conducted at the same 32 nests. Searches were conducted within a 50 m radius of the nest five times during the nestling period: when hatching was confirmed, during each of the three recording unit rotation periods, and during the first week post-fledging. Searches within the nest itself were conducted three times: during camera installation; when chicks were ringed; and again during the first week post-fledging when cameras were removed. Prey remains were recorded and removed from the search area to prevent double counting. Pellets were frozen and dried prior to dissection and analysis.

Mammal hairs and bones found in pellets and feathers in pellets and prey remains were identified following Teerink (2004) and Brown *et al.* (2003) respectively. Prey were identified to the lowest possible taxonomic level. Prey identified in remains and pellets were assumed to represent one individual prey item unless it was obvious that more than one individual was present. In some cases, especially with larger prey items, it may be that this approach overestimated the number of individual prey items if one item constituted numerous meals and was therefore represented in successive pellets (Rooney & Montgomery 2013). However, in order to retain consistency between prey items and with other studies, each prey item in pellets was assumed to represent one individual unless otherwise obvious.

Since pellets usually contained more than one prey item (2.2 ± 0.1 items), it was possible to derive two measures of prey frequency data from pellet analysis: the percentage of pellets containing a given prey type (pellet frequency); and the number of occurrences of a particular prey type as a percentage of all identified items (pellet relative frequency) (Redpath *et al.* 2001a). To retain comparability with the other two methods used in this study as well as those in other studies, pellet relative frequency is used here.

2.3.5 Data analysis

Prey were assigned to one of seven groups (average weights of birds used for classification were taken from Snow & Perrins (1998) and Robinson (2005)):

- Small mammals (field vole *Microtus agrestis;* bank vole *Myodes glareolus;* wood mouse *Apodemus sylvaticus*; common mole *Talpa europaea;* common shrew *Sorex araneus;* unidentified small mammals).
- Large mammals (*Lagomorph spp.; Mustela spp.;* brown rat *Rattus norvegicus;* grey squirrel *Sciurus carolinensis*).
- Small bird (*Passeriformes* and other small birds of $\leq$ 100g average adult weight).
- Large bird (*Galliformes spp.; Corvidae spp.; Charadriformes spp.; Columbidae spp.;* other large birds of >100g average adult weight).
- Herpetofauna (common frog *Rana temporaria;* common toad *Bufo bufo;* common lizard *Zootoca vivipara;* adder *Vipera berus;* slow worm *Anguis fragilis*).
- Invertebrates (beetles *Coleoptera spp.* (largely *Carabidae spp.* and *Scarabidae spp.*)*;* earthworms *Megadrilacea spp.*).
- Unknown prey. Items which could not be identified to at least Order level.

Gamebirds (*Galliformes spp.*: red grouse and pheasants) were not separated from other large birds in analysis due to their similar size, and therefore presumably similar manner in which they are handled by buzzards at the nest, and in order to maintain larger group sample size in analysis.

In recognition that prey proportions are a composition of groups totalling 100%, compositional analysis was used (Aebischer *et al.* 1993b). Prey proportions from each assessment method were expressed as the percentage of total prey at each nest (N = 32).

The data were proportions of six prey groups (small mammals, large mammals, small birds, large birds, herpetofauna and invertebrates). Unidentified prey in camera images (N = 136) were removed prior to analysis.

Each six-part composition of prey identified at each nest was transformed into five log-ratios with the sixth prey group used as the denominator in the transformation. The analysis does not depend on which group is used as the denominator group (Aebischer *et al.* 1993b), and small mammals were used as the denominator group here because this group contained the fewest non-zero values. Any zeros in the dataset were replaced with 0.1 to allow calculation of log-ratios.

To assess whether assessment method affected the composition of buzzard diet, multivariate analysis of variance (MANOVA) was used, specifying 'nest' as a blocking factor, and year and method as predictors of differences in prey composition. An interaction term 'year × method' was also fitted to assess whether differences between methods varied between years. Since MANOVA does not support multi-stratum analysis of variance, it is not valid to test 'year' as a fixed effect across the whole data set (Crawley 2007). However, since I was not interested in the effect of 'year' other than through its interaction on 'method', this was not a problem for the analysis. Significance values of model terms were assessed using a Pillai-Bartlett statistic (Λ) (Crawley 2007) and accepted as significant at $p < 0.05$. Main effects were tested with interaction effects removed from the model. Mardia's tests revealed that there was no significant kurtosis ($p = 0.90$) or skewness ($p = 0.18$) indicating multivariate normality of the data.

To identify which prey groups caused any differences between assessment methods, ranking matrices were constructed by comparing the pairwise differences between log-ratios, following the approach of Aebischer *et al.* (1993a). To achieve this, all 30 possible log-ratios were calculated using each of the six prey groups as a denominator to the other five numerator groups. Prey groups were then compared using contrast analysis to identify differences between camera images and each of the indirect assessment methods in turn. All analyses were conducted using 'R' statistical software 3.1.2.

2.4 Results

A total of 2,320 hours of footage were collected from the 32 nest cameras deployed over the three years (mean per nest per year 79.5 ± 15.1 hours) yielding 1,005 prey deliveries (mean deliveries per nest 31.4 ± 2.6). Of these deliveries, 136 (13.5%) could not be identified, and were invariably smaller items which were blocked from view by the chicks, adults or foliage and consumed quickly. Small mammals were the most frequent prey item recorded on camera images (51.3%). A total of 486 prey remains were recovered from inside and around the 32 nests (mean items per nest = 15.2 ± 1.0). In prey remains, large birds were the most numerously found prey group (40.7%). A total of 217 pellets were collected from the same 32 nests (mean pellets per nest 6.8 ± 0.5), yielding 476 prey items. Pellet analysis revealed small mammals to be the most frequently occurring prey (44.7%) In all methods used, gamebirds formed the greatest proportion of the 'large birds' category (cameras: 46.5%; prey remains: 53.0%; pellets: 71.9% of all 'large birds' recorded) (Table 2.1, Figure 2.1).

As an average of identified prey items by nest (N = 32), small mammals constituted the largest average percentage on camera images (60.2% ± 2.9 SE) and in pellets (49.2% ± 2.7 SE), yet only constituted an average of 13.1% (± 2.2 SE) of prey remains across all nests. Large birds formed the largest average percentage of prey remains across all nests (39.5% ± 3.5 SE), but averaged only 4.6% (± 0.9 SE) of camera images and 7.0% (± 1.3 SE) of prey identified from pellets across all nests. Large mammals were more likely to be found in prey remains at nests (21.7% ± 2.9 SE) than in camera images (9.5% ± 1.5 SE) or pellets (13.2% ± 1.8 SE) from the same nests, whilst invertebrates were much more likely to be identified from pellets (22.5% ± 1.6 SE), than from prey remains (2.4% ± 0.8 SE) and were very rarely identified from camera images (0.5% ± 0.2 SE).

There was a significant interaction between assessment method and year on buzzard diet composition at the 32 nests ($\Lambda = 0.372$, $p = 0.026$). Therefore, the effect of method was assessed in each year separately. In all three years, method had a significant effect on diet composition (2011: $\Lambda = 1.439$, $p < 0.001$; 2012: $\Lambda = 1.327$, $p < 0.001$; 2013: $\Lambda = 1.403$, $p < 0.001$). Ranking matrices were constructed for comparisons between camera images and each indirect method in turn, using data from each of the three years. The resulting six matrices were used to rank prey groups and identify which groups differed between methods (Tables 2.A1 & 2.A2 in Chapter Appendix, summarised in Table 2.2).

Matrices revealed that compared to camera images, prey remains significantly underestimated the frequency of small mammals and herpetofauna relative to all other prey groups in two out of three years (2011 & 2013), and significantly underestimated small mammals alone in one year (2012). Prey remains overestimated the frequency of large birds relative to all other prey groups in all years, significantly so in 2011. (See Table 2.A1 a – c in Chapter Appendix for ranking matrices. Results from ranking matrices are summarised in Table 2.2).

Matrices revealed that compared to camera images, pellet analysis significantly underestimated herpetofauna relative to all other prey groups in 2011 & 2012, and they were also the most underestimated group in 2013 though not significantly. Pellet analysis significantly overestimated invertebrates relative to all other prey groups in all years. (See Tables 2.A2 a – c in Chapter Appendix for ranking matrices. Results from ranking matrices are summarised in Table 2.2).

The analysis was repeated using 0.01 and then 1 as the replacement for zero values in the dataset. In both cases this did not alter any significance values of the MANOVAs. Alternative non-zero values also didn’t affect significance values in matrix rankings, although in three cases the order of matrix rankings was affected. However, since none of the prey groups differed significantly beforehand, the effect was purely cosmetic and would not alter the conclusions of the study.

Table 2.1. Prey identified at 32 buzzard nests during the breeding season at Langholm Moor between 2011 and 2013. Data are pooled within methods and presented as frequency (N) and % of total frequency (%).

	Camera images		Prey remains		Prey items in pellets	
Prey item	**N**	**%**	**N**	**%**	**N**	**%**
Small mammals						
Field vole	308	30.6	28	5.8	142	29.8
Common mole	91	9.1	20	4.1	33	6.9
Other small mammals	117	11.6	9	1.9	38	8.0
Subtotal	**516**	**51.3**	**57**	**11.8**	**213**	**44.7**
Large mammals						
Lagomorph spp.	45	4.5	105	21.6	76	16.0
Mustela spp.	15	1.5	1	0.2	0	0
Brown rat	16	1.6	0	0	0	0
Grey squirrel	0	0	2	0.4	0	0
Subtotal	**76**	**7.6**	**108**	**22.2**	**76**	**16.0**
Small birds	**88**	**8.8**	**84**	**17.3**	**37**	**7.8**
Large birds						
Pheasant	10	1.0	77	15.8	6	1.3
Red grouse	10	1.0	28	5.8	17	3.6
Corvidae spp.	12	1.2	52	10.7	2	0.4
Charadriformes spp.	7	0.7	8	1.6	2	0.4
Columbidae spp.	4	0.4	25	5.1	1	0.2
Other large birds	0	0	8	1.6	3	0.6
Subtotal	**43**	**4.3**	**198**	**40.7**	**32**	**6.7**
Herpetofauna						
Amphibian spp.	114	11.3	25	5.1	5	1.1
Reptile spp.	27	2.7	1	0.2	0	0
Subtotal	**141**	**14.0**	**26**	**5.3**	**5**	**1.1**
Invertebrates						
Coleoptera spp.	3	0.3	12	2.5	113	23.7
Megadrilacea spp.	2	0.2	1	0.2	0	0
Subtotal	**5**	**0.5**	**13**	**2.7**	**113**	**23.7**
Unidentified	**136**	**13.5**	**0**	**0**	**0**	**0**
Total	**1005**		**486**		**476**	

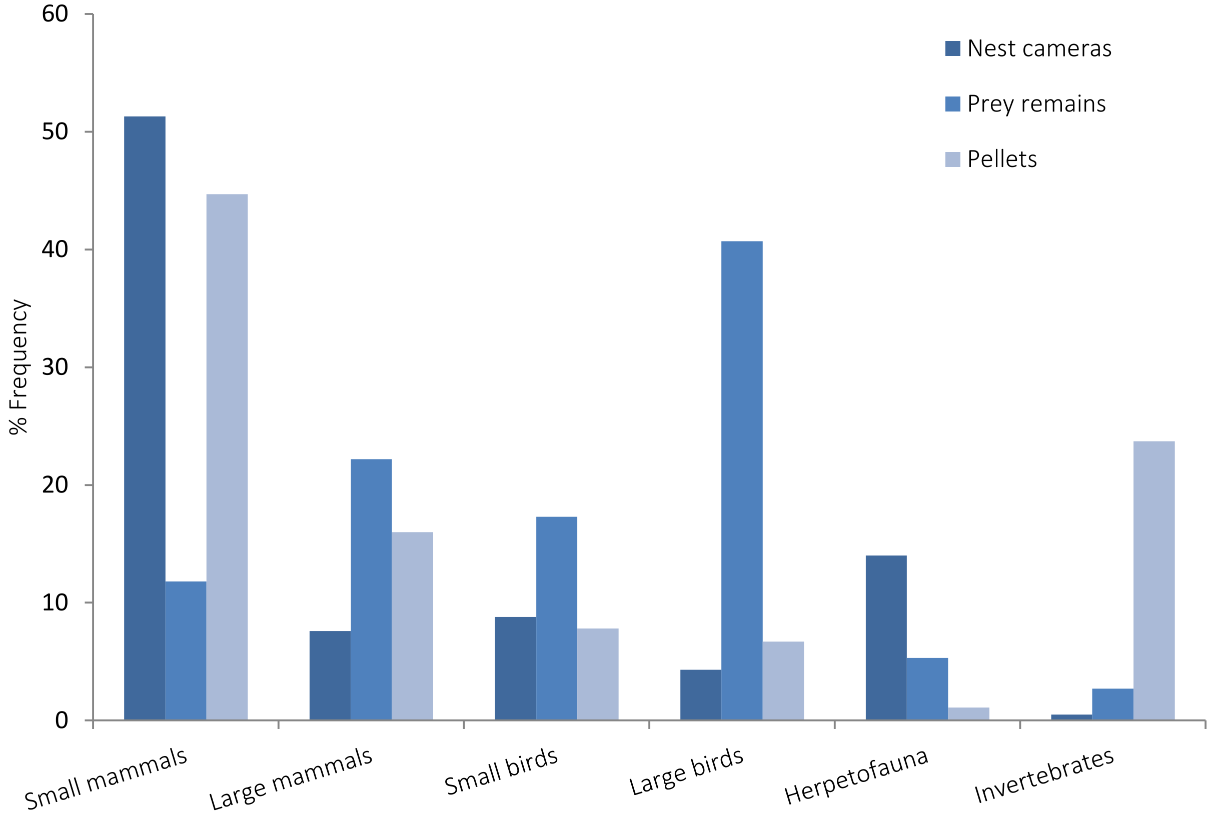

Figure 2.1. Percentages of six prey groups identified at 32 buzzard nests at Langholm Moor between 2011 and 2013 (data pooled across all nests in all years). Bars show percentages by frequency from three prey assessment methods. Unidentified prey were excluded.

Table 2.2. Rankings of apparent importance of six prey groups derived from pairwise comparisons of biases associated with prey remains and pellets compared to camera images in 2011 – 2013. Rankings were calculated from ranking matrices (Tables 2.A1 & 2.A2 in Chapter Appendix) where <<< denotes a significant difference ($p < 0.05$) between adjacent ranks.

	Prey group estimation ranking
a) Prey remains	
2011	Small mammals < Herpetofauna <<< Invertebrates < Large mammals < Small birds <<< Large birds
2012	Small mammals <<< Herpetofauna < Invertebrates < Small birds < Large mammals < Large birds
2013	Small mammals < Herpetofauna <<< Small bird < Large mammals < Invertebrates < Large birds
b) Pellets	
2011	Herpetofauna <<< Small mammals < Small birds < Large birds < Large mammals <<< Invertebrates
2012	Herpetofauna <<< Small birds < Small mammals < Large birds < Large mammals <<< Invertebrates
2013	Herpetofauna < Large mammals < Small birds < Small mammals < Large birds <<< Invertebrates

2.5 Discussion

Collecting accurate information on dietary composition is a prevalent challenge in field ecology (Redpath *et al.* 2001a). There are a range of techniques for assessing the dietary composition of raptors, and deciding which is used will depend on the aims of the study, as well as considerations of time and cost. Direct methods of diet assessment are considered to present the most accurate description of the diet of raptors, but are relatively time consuming and expensive (Redpath *et al.* 2001a; Reif & Tornberg 2006) and so the inferences from indirect methods are commonly used (e.g. Swann & Etheridge 1995; Graham *et al.* 1995; Pietersen & Symes 2010; Rooney & Montgomery 2013; Resano-Mayor *et al.* 2014). Understanding how indirect methods differ from direct methods, and how these differences may affect conclusions, is important for all researchers interested in raptor diet. This is especially pertinent at a time of increasing interest in the effects of predation on economically important gamebirds by recovering populations of raptors.

This study highlighted the wide dietary breadth of buzzards, previously established elsewhere (Mañosa & Cordero 1992; Graham *et al.* 1995; Reif *et al.* 2004; Rooney *et al.* 2014). In this study buzzards ate prey ranging in size from ground beetles *Coleoptera* spp. and earthworms *Megadrilacea* spp. to adult pheasants *Phasianus colchicus* and brown hares *Lepus europaeus*, with the largest prey item discovered being an adult lesser black-backed gull *Larus fuscus.* Small mammals, especially field voles, were the dominant prey type in camera image and pellet data, whilst large birds and large mammals were most important numerically in prey remains. To a lesser extent, Herpetofauna (in camera data) and invertebrates (in pellet data) were also important buzzard dietary components, again confirming a number of earlier studies (Mañosa & Cordero 1992; Swann & Etheridge 1995; Selås 2001).

Between method differences in diet assessment can be caused by a number of factors, which can be both methodological and ecological. Methodological differences arise due to inherent differences in the ability of one method to record a given prey type relative to other prey types when compared to another method. For example, longer persistence periods and greater conspicuousness of remains of large prey are both likely to result in their overestimation in prey remains compared to a direct observation method (Lewis *et al.* 2004; Tornberg & Reif 2007). Between method differences can also arise due to ecological effects, which may vary between species, geographic area and over time. For example, differences in digestibility between prey groups and in digestive efficiency between predators can both lead to between method differences. Buzzards have a high digestive efficiency (Barton & Houston 1993), and the near complete digestion of soft-bodied herpetofauna is likely to render these prey largely unidentifiable in pellet analysis. Equally, indigestible and conspicuous invertebrate wing cases and exoskeletons could lead to an overestimation of invertebrates in pellet analysis, compared to direct observations in which they may be hidden or too small to identify. Ecological effects leading to potential between method differences may also arise if certain prey items are eaten by predators at the capture site rather than being brought back to a nest, which can lead to biases if methods are focussed purely on the nest site rather than on the individual predator (Simmons *et al.* 1991). Similarly, since diet composition may naturally vary between breeders and non-breeders (Rutz *et al.* 2006; Penteriani *et al.* 2013), bias may be introduced by using methods that only collect data from breeding individuals, such as surveys at nests, compared to methods that collect data irrespective of breeding status, such as collection of pellets from winter roosts (Marquiss & Booth 1986, Chapter 5) or remote telemetry tracking (Kenward *et al.* 1981b; Rutz *et al.* 2006). Many of these factors are likely to have been at least partly responsible for the between method differences observed in this study. The large bird category in this study was largely composed of gamebirds in all three methods employed, and their relative overestimation in prey remains documented here will be an important consideration in future studies investigating the potential impact of raptor predation on gamebirds.

The diet of generalist raptors such as buzzards is known to vary between years in relation to natural fluctuations of preferred and alternative prey, termed the ‘functional response’ (Korpimäki & Norrdahl 1991; Redpath & Thirgood 1999; Salamolard *et al.* 2000; Reif *et al.* 2004). Accurate assessments of functional responses in raptors are important for a number of areas of ecological research, including the study of potential impact of raptor predation on gamebirds (Redpath & Thirgood 1999; Valkama *et al.* 2005; Park *et al.* 2008). This study highlighted that the same few prey groups were consistently over- or under-estimated in the extreme when compared to direct observations. Nonetheless, the results also showed that more subtle methodological biases can differ between years which could affect the accuracy of assessments of functional responses in raptors. The results of this study showed that large birds were significantly overestimated in prey remains relative to all other prey in the first year (2011), but not in either subsequent year when compared to camera images. It may be notable that 2011 was a peak vole abundance year in the three – four year vole cycle at Langholm (Redpath & Thirgood 1999; Chapter 3). It is possible that as buzzards responded functionally to higher vole abundance, a considerable number of the voles delivered to buzzard nests in 2011 were missed during prey remain searches whilst the large birds remained conspicuous for reasons outlined above. This may have led to the overestimation of large birds in prey remains during 2011 compared to nest cameras, the latter of which are more likely to record vole deliveries. Simmons, Avery & Avery (1991) propose 'correction factors' for obtaining a more accurate estimate of 'true' diet when direct methods are not used. Similarly, Lewis *et al.* (2004) propose collecting data from a sub-sample of nests using direct observations and then using these data to 'calibrate' data from a larger sample using indirect methods. Provided this is conducted within years, this may be a sensible way of improving data accuracy while reducing costs. However, the results of the present study suggest that the effects of calibration could differ between years leading to inaccurate estimations if applied across years. Researchers should consider not only how their chosen methods may introduce bias into their findings, but also how these biases may differ in relation to the duration of study.

The results of this study may not hold for other raptors, nor for buzzard populations elsewhere. Buzzards are generalist and opportunistic in their feeding habits (Tubbs 1974), so results may differ for other populations with alternative habitats and prey resources. Furthermore, 14% of prey deliveries captured on camera images were not identified, showing that any method of diet analysis, including direct assessment methods that are assumed to provide the most accurate assessment, involve inherent bias. The results of this study would benefit from being tested with buzzard populations elsewhere, and with other diet assessment methods, both direct and indirect, before conclusions are extrapolated.

In conclusion results confirm the findings of numerous studies showing that method choice can affect assessment of raptor diet composition. Importantly, whilst indirect methods consistently biased the same prey groups at the extreme ends of the bias rankings, significant methodological differences varied over time in relation to other less drastically biased prey groups. This was most likely caused by changes in relative abundance of prey resources in the environment. Future studies should consider methodological biases and how these might vary over time when attempting to draw conclusions about the potential impact of raptor predation on gamebirds.

2.6 Appendix

Tables 2.A1 a-c. Matrices of t-values from contrast analysis between **camera images** and **prey remains** in 2011 (a); 2012 (b) and 2013 (c) for six prey groups. Reading across rows, positive t-values imply overestimation and negative values imply underestimation in prey remains compared to camera images for that prey group relative to other groups (significant at $p < 0.05$ in bold). Rankings are calculated by the total number of positive values in each row, e.g. large birds rank five implying that they are overestimated in prey remains relative to the five other groups compared to camera images. (“S.”= small; “L.” = large, see text for definitions).

(a) 2011

	Denominator						
Numerator	S. mammal	L. mammal	S. bird	L. bird	Herpetofauna	Invertebrate	**Rank**
S. mammal		**-2.277**	**-3.02**	**-6.077**	-0.049	**-3.112**	0
L. mammal	**2.277**		-0.634	**-3.3**	**2.278**	0.182	3
S. bird	**3.02**	0.634		**-2.513**	**2.485**	0.921	4
L. bird	**6.077**	**3.3**	**2.513**		**5.843**	**3.842**	5
Herpetofauna	0.049	**-2.278**	**-2.485**	**-5.843**		**-2.842**	1
Invertebrate	**3.112**	-0.182	-0.921	**-3.842**	**2.842**		2

(b) 2012

	Denominator						
Numerator	S. mammal	L. mammal	S. bird	L. bird	Herpetofauna	Invertebrate	**Rank**
S. mammal		**-3.595**	**-3.172**	**-5.119**	**-2.089**	**-3.25**	0
L. mammal	**3.595**		1.088	-1.125	1.668	1.432	4
S. bird	**3.172**	-1.088		**-2.341**	0.673	0.044	3
L. bird	**5.119**	1.125	**2.341**		**3.143**	**2.511**	5
Herpetofauna	**2.089**	-1.668	-0.673	**-3.143**		-0.748	1
Invertebrate	**3.25**	-1.432	-0.044	**-2.511**	0.748		2

(c) 2013

	Denominator						
Numerator	S. mammal	L. mammal	S. bird	L. bird	Herpetofauna	Invertebrate	**Rank**
S. mammal		**-4.206**	**-4.468**	**-5.729**	-0.211	**-5.897**	0
L. mammal	**4.206**		0.789	-1.382	**4.313**	-0.554	3
S. bird	**4.468**	-0.789		**-2.444**	**3.382**	-1.355	2
L. bird	**5.729**	1.382	**2.444**		**6.08**	0.955	5
Herpetofauna	0.211	**-4.313**	**-3.382**	**-6.08**		**-4.423**	1
Invertebrate	**5.897**	0.554	1.355	-0.955	**4.423**		4

Tables 2.A2 a-c. Matrices of t-values from contrast analysis between **camera images** and **pellet analysis** in 2011 (a); 2012 (b) and 2013 (c) for six prey groups. Reading across rows, positive t-values imply overestimation and negative values imply underestimation in pellet analysis compared to camera images for that prey group relative to other groups (significant at $p < 0.05$ in bold). Rankings are calculated by the total number of positive values in each row. ("S."= small; "L." = large, see text for definitions).

(a) 2011

	Denominator						
Numerator	S. mammal	L. mammal	S. bird	L. bird	Herpetofauna	Invertebrate	**Rank**
S. mammal		1.775	1.607	-0.708	**3.151**	**-5.737**	3
L. mammal	-1.775		-0.16	**-2.26**	0.863	**-6.2**	1
S. bird	-1.607	0.16		-1.993	0.865	**-5.704**	2
L. bird	0.708	**2.26**	1.993		**3.315**	**-3.28**	4
Herpetofauna	**-3.151**	-0.863	-0.865	**-3.315**		**-8.945**	0
Invertebrate	**5.737**	**6.2**	**5.704**	**3.28**	**8.945**		5

(b) 2012

	Denominator						
Numerator	S. mammal	L. mammal	S. bird	L. bird	Herpetofauna	Invertebrate	**Rank**
S. mammal		-1.175	0.296	-0.129	**2.634**	**-4.558**	2
L. mammal	1.175		1.521	1.076	**3.746**	**-3.28**	4
S. bird	-0.296	-1.521		-0.397	**2.452**	**-4.887**	1
L. bird	0.129	-1.076	0.397		**2.99**	**-4.03**	3
Herpetofauna	**-2.634**	**-3.746**	**-2.452**	**-2.99**		**-7.805**	0
Invertebrate	**4.558**	**3.28**	**4.887**	**4.03**	**7.805**		5

(c) 2013

	Denominator						
Numerator	S. mammal	L. mammal	S. bird	L. bird	Herpetofauna	Invertebrate	**Rank**
S. mammal		**-2.043**	-0.715	-0.537	**4.599**	**-7.098**	1
L. mammal	**2.043**		1.411	1.333	**6.618**	**-3.59**	4
S. bird	0.715	-1.411		-0.002	**4.963**	**-4.994**	2
L. bird	0.537	-1.333	0.002		**5.083**	**-5.051**	3
Herpetofauna	**-4.599**	**-6.618**	**-4.963**	**-5.083**		**-9.513**	0
Invertebrate	**7.098**	**3.59**	**4.994**	**5.051**	**9.513**		5

Chapter 3. Numerical and functional responses of breeding common buzzards on Langholm Moor

3.1 Abstract

Generalist predators are often assumed to increase their predation of alternative prey when abundances of their preferred prey are low. However, this assumption may not apply to all alternative prey groups in patchy landscapes. The manner in which generalist predators respond to changing prey abundances influences the impact of their predation on prey. I studied the numerical and functional responses of common buzzards *Buteo buteo*, a generalist raptor with an expanding British range, in relation to changes in prey abundance over three years on an area of upland moorland managed for red grouse *Lagopus lagopus scotica.* In Britain, field voles *Microtus agrestis* form a principal component of the diet of buzzards. I was particularly interested in how fluctuating vole abundance affected buzzard predation on red grouse. Breeding parameters and diet composition were monitored at 13 – 16 buzzard nests each year using motion triggered cameras and collection of prey remains and regurgitated pellets. During the study, field vole abundance declined significantly indicating a decline phase in the vole cycle. Results suggested that buzzards did not respond numerically, in terms of breeding density or breeding success, to declining vole abundance. However, the proportion of voles in buzzard diet decreased in line with vole indices. Rather than predation on red grouse increasing when vole abundance declined, grouse remains became less frequent in buzzard prey remains and pellets, and showed no trend in camera images. Instead, buzzards switched to eating more lagomorphs, moles, shrews and corvids: prey groups typically associated with moorland fringe and farmland habitats. This may suggest that when provisioning their chicks, buzzards take red grouse only incidentally while hunting for voles within moorland habitats. These results demonstrate the functional response of an opportunistic predator whereby natural declines in their preferred vole prey led to reductions in incidental predation of red grouse as a wider range of alternative prey were selected. I suggest that when investigating predator diet and impacts on prey, knowledge of all resources and habitats that are available to predators is important.

3.2 Introduction

Predators may respond to fluctuations in prey abundance either numerically or functionally (Solomon 1949). Numerical responses involve a change in predator density, which can occur either through changes in nesting density and breeding success (Redpath & Thirgood 1999; Reif *et al.* 2004) or through changes in the intensity at which predators forage in a given area (the 'aggregative response') (Kenward *et al.* 1981b). Functional responses involve a change in individual predation rates, and hence dietary composition (Solomon 1949; Andersson & Erlinge 1977). As such, numerical responses are influenced by the mobility, reproductive potential and generation time of the predator, while functional responses are influenced by the ability of the predator to shift to alternative prey and interspecific competition for prey (Andersson & Erlinge 1977; Korpimäki & Norrdahl 1991; Redpath & Thirgood 1999). Knowledge of the functional and numerical responses of predators can provide a useful conceptual framework for exploring predator-prey systems (Redpath & Thirgood 1999; Tornberg *et al.* 2012).

Predicting how predator responses may impact on prey populations is a well-studied subject in Applied Ecology (Ormerod 2002), for which a number of theoretical hypotheses have been developed. The Main Prey Hypothesis (MPH) predicts that specialist predators, through a delayed numerical response, can cause inverse density-dependent declines in their main prey (Tornberg *et al.* 2012). The Alternative Prey Hypothesis (APH) predicts that generalist predators will switch to alternative prey when their main prey resource declines (Angelstam *et al.* 1984), and has been used to explain apparent switches to alternative prey as main prey densities diminish (Reif *et al.* 2001; Votier *et al.* 2004b; Tornberg *et al.* 2012). This may result in either increased predation on a single alternative prey resource, or an increased diet breadth as a range of alternative prey are selected (Schoener 1971; Pyke *et al.* 1977; Salamolard *et al.* 2000). Furthermore, predation of alternative prey may also increase during phases of high main prey abundance, as densities of non-selective (generalist) predators increase due to their numerical response, termed the Shared Predation Hypothesis (SPH) (Norrdahl & Korpimäki 2000; Reif *et al.* 2004).

Optimal Diet Theory predicts that generalist predators rank prey in terms of profitability (Pyke *et al.* 1977), and so ‘preferred prey’ are those for which energy gain per unit handling time is greatest. Accordingly, the selection of less profitable (alternative) prey depends on the abundance of preferred prey (Krebs & Davies 1993). Therefore, theoretical models predict that predation of alternative prey is relaxed during years of high preferred prey abundance. However, even in relatively simple ecosystems, the availability of numerous alternative prey resources can lead to complex interactions between predators and prey. The nature of any response will depend on the range of habitats and prey available to generalist predators, as well as their relative profitability as prey resources to the predator in question (Smout *et al.* 2010).

In systems involving mobile generalist predators, heterogeneous habitats and numerous available prey resources, predator response can also affect the predation rate of incidental prey (defined by Cornell (1976) as less profitable alternative prey which are not the focus of a directed search by the predator). This is termed the Incidental Prey Hypothesis (IPH). If incidental prey have similar habitat requirements to the main prey, predation may increase on these incidental prey groups when densities of the main prey group are high (Selås 2001). Conversely, if incidental prey coexist in space with important alternative prey groups, incidental predation may be higher when main prey density is low (Mckinnon *et al.* 2013).

The shape of the functional response curve describes how predation rates vary with prey density (Crawley 1992) and knowledge of this is critical in assessing the impact of predation on prey (Redpath & Thirgood 1999). Type I functional responses (linear relationships) have been recorded in vole specialist raptors (Korpimäki & Norrdahl 1991) although type II responses (asymptotic or convex relationship) are more common in generalist predators (Redpath & Thirgood 1999; Salamolard *et al.* 2000). Type III responses (sigmoidal or concave relationship) have been found for predators of grouse including goshawks (Linden & Wikman 1983) and hen harriers (Redpath & Thirgood 1999). Knowledge of predator responses, both numerical and functional, and how these change with varying prey densities, can provide valuable information about the potential impact of predators on prey (Redpath & Thirgood 1997).

The common buzzard *Buteo buteo* (herein ‘buzzard’) is a mobile, generalist predator whose preferred prey are small mammals, especially voles *Microtus* spp., and where available in large numbers, European rabbits *Oryctolagus cuniculus* (Tubbs 1974; Swann & Etheridge 1995; Graham *et al.* 1995; Reif *et al.* 2001, 2004; Rooney & Montgomery 2013). Buzzards nesting on heather moorland in Britain have been shown to predate red grouse *Lagopus lagopus scotica* alongside their preferred vole and rabbit prey (Graham *et al.* 1995). The population increase and recolonisation of previous range by buzzards in Britain (Musgrove *et al.* 2013; Balmer *et al.* 2014) has, in some cases, created concern amongst game managers about the impact of predation by buzzards on gamebirds (Lees *et al.* 2013; Parrott 2015). Red grouse are an economically important gamebird in parts of upland Britain (Hudson 1992), and understanding predatory mechanisms is an important aspect of reaching conservation and economic objectives (Kenward 1999).

Buzzard predation of grouse species *Tetraoninae* has previously been described with the APH, whereby predation on grouse increased during the low phase of the vole cycle (Reif *et al.* 2001; Valkama *et al.* 2005; Tornberg *et al.* 2012). However these studies, like the majority of studies of predator-rodent mediated food web interactions to date, were conducted in boreal ecosystems (Zárybnická *et al.* 2015). Highly modified and patchy landscapes, such as those found in upland areas of Britain (Thompson *et al.* 1995), and their associated patchy prey resources (Thirgood *et al.* 2003; Wheeler 2008), may elucidate different and complex predator responses. Considering this, the interest in the raptor-red grouse system (Thirgood *et al.* 2000a; Elston *et al.* 2014) and the increasing concern over the impact of buzzard predation on gamebirds (Lees *et al.* 2013; Parrott 2015), it is pertinent to explore how any response of buzzards to naturally fluctuating vole abundance may influence predation rates on red grouse.

In this study I investigate the numerical and functional responses of buzzards on an area of heather moorland managed for red grouse and the farmland and forest peripheries. I aim to explore how any observed response could influence predation of red grouse by buzzards, accounting for annual and spatial variation in grouse density.

3.3 Methods

3.3.1 Study area

This study was conducted at Langholm Moor in south-west Scotland during three summers (2011 – 2013). The 221 km^2 site includes the Langholm Moor Demonstration Project (LMDP), and the Langholm – Newcastleton SSSI and SPA. Within the LMDP area, moorland management including heather habitat management and predator control of corvids, foxes and mustelids is undertaken by a team of gamekeepers to benefit red grouse. The study site included the LMDP area plus a 2 km buffer zone, which is the maximum distance buzzards are considered to hunt from their nests from nearest neighbour distances at Langholm (Graham *et al.* 1995). Langholm Moor consists of rough and acidic grassland (51.0%) and a mosaic of heather *Calluna vulgaris* and grass moorland (21.6%) with improved grassland (11.1%), commercial coniferous forestry (10.6%) and mixed deciduous woodland (5.1%) occurring on the moor periphery (CEH Land Cover Map 2007; Morton *et al.* 2011; see Chapter 1 Section 1.5.1 for more details of the site).

3.3.2 Prey abundances

I was interested in the variation in prey abundances between years as a context for assessing buzzard numerical and functional responses. Published literature on buzzard diet throughout the British Isles suggests that small mammals, especially voles (*Microtus* spp.) and lagomorphs are important components of buzzard diet, with passerines and larger birds such as red grouse featuring where they are available as alternative prey (Swann & Etheridge 1995; Graham *et al.* 1995; Rooney & Montgomery 2013). Therefore, I focussed on abundances of voles, lagomorphs, passerines and red grouse.

Red grouse were counted twice each year within ten 0.5 km^2 blocks using pointer dogs, first in spring to assess pre-breeding densities and again in July to assess post-breeding densities. Transects 1 km long and spaced 150 metres apart were walked through each block with a pointer dog quartering 100 metres either side of the transect. All grouse flushed by the dog were counted and recorded to calculate densities in each block (Thirgood *et al.* 2000c).

Vole abundance was assessed using snap trapping on ten lines of 50 unbaited traps set over two nights in March of each year between 2011 and 2013, which previous work has shown to provide an accurate index of small mammal abundance (Redpath *et al.* 1995). Field vole *Microtus agrestis* abundance at Langholm is known to cycle over a three to four year period (Redpath & Thirgood 1999), and over all trap lines field voles comprised 83% of all small mammals trapped. Therefore, the mean number of field voles caught per 100 trap nights from the ten sites was used as an index of vole abundance in each year. All ten small mammal trap lines were within 500 metres of the ten grouse count areas.

Passerines were counted in sixteen 1 km^2 National Grid squares using a modified breeding bird survey method (modified from Thirgood *et al.* 1995b). Two parallel 1 km transects were walked once in April/May and again in May/June and the number of passerines detected were recorded. Meadow pipits *Anthus pratensis* dominated numerically and comprised 63% of the total number of passerines detected on surveys. An index of meadow pipit abundance was therefore derived by taking a mean of the total number of meadow pipits counted in the two surveys in each year (Baines *et al.* 2008). Ten of the passerine survey squares included the ten grouse count areas, the other six were distributed across Langholm Moor within the LMDP area.

Lagomorphs, which on Langholm Moor include rabbit *Oryctolagus cuniculus* and brown hare *Lepus europaeus,* were also recorded during passerine surveys. These revealed that lagomorph abundance on the moor was low in all three years (<0.1 individuals / km). Therefore, I conducted lagomorph surveys using a modified methodology described in Graham, Redpath & Thirgood (1995). Pilot counts and data collected during grouse and passerine surveys suggested that lagomorphs were largely confined to the improved grassland plots on the moorland periphery. Twelve 1 km transects placed in these grassland plots were walked in June between 05:00 and 09:00, excluding any days of strong wind or rain. Combined numbers of rabbit and brown hare seen per transect were used as a measure of relative abundance to compare between years. Over all surveys, rabbits comprised 94% of the total number of lagomorphs seen. Lagomorph surveys were instigated in 2012.

I tested for variation in abundances of all prey between years using one-way ANOVA (t-tests for lagomorph data). I arcsine transformed the small mammal data to achieve normality before analysis.

3.3.3 Numerical response

I was interested in the numerical response of buzzards in relation to yearly variations in prey abundance. If a numerical response to high vole abundance occurred, buzzards would be expected to nest at a higher density, and/or raise more chicks to fledging (Redpath & Thirgood 1999; Reif *et al.* 2004). Raptors can also respond numerically by spending more time hunting in areas of high prey profitability, the so called ‘aggregative response’ (Kenward *et al.* 1981a), however this type of response is not investigated here, and instead is the subject of Chapter 4.

Active buzzard nests were located by systematically searching forestry, wooded gullies and isolated trees and crags, particularly within known territories and where displaying buzzards were seen. Buzzard breeding density was expressed as the mean nearest-neighbour distance (NND) within year, based on distances between active nests measured by inputting nest locations into ArcGIS version 10.3. NND was assessed using active buzzard nests located in early spring over the three years, where we were certain that all neighbouring nests had been located. Two measures of breeding success were calculated: ‘chicks fledged per successful nest’ (nests at which at least one chick fledged), and ‘chicks fledged per breeding attempt’ (all nesting attempts including those that fledged no chicks). ‘Chicks fledged per breeding attempt’ was the same as chicks per pair because no pairs were observed to lay repeat clutches if their first attempt failed (pers. obs.). Chicks were considered to have fledged if seen outside of the nest at $\geq$ 4 weeks old (Hardey *et al.* 2009). Breeding density was compared between years with one-way ANOVA. Breeding success data could not be normalised with standard procedures so were analysed for differences between years using non-parametric tests.

3.3.4 Functional response

I was interested in assessing the functional response of buzzards to yearly variation in prey abundances. The existence of a functional response would involve changes in diet composition of buzzards as relative prey abundances changed. Of particular interest was how the proportion of prey deliveries consisting of red grouse varied between years as prey densities changed, accounting for variation in grouse density.

All methods of assessing raptor diet carry inherent bias (Simmons, Avery & Avery 1991; Redpath *et al.* 2001; Rutz 2003; Lewis, Fuller & Titus 2004; Tornberg & Reif 2007), which may also affect the reliability of comparisons between years (Chapter 2). In order to reduce the bias of using just one method, data were obtained from three sources: motion-triggered nest cameras, prey remains, and analysis of regurgitated pellets found at nests. Between 2011 and 2013, 58 active buzzard nests were recorded within the study site. Prey remains and regurgitated pellets were collected from 46 of these nests, excluding failed attempts and discoveries late in the nestling period that yielded few remains (Figure 3.1). Camera footage was collected from the 32 nests discovered before hatching that were closest to the LMDP area.

High-resolution waterproof cameras were fitted to oversee buzzard nests within the study site (number of nests with cameras: 2011 = 11, 2012 = 10, 2013 = 11). Cameras were attached with a bracket to a suitable branch above the nest to allow the entire nest platform to be captured in the image. Cameras recorded colour video clips of 1-5 minutes in length when motion was detected in the nest. Footage was recorded on high-definition video recording units connected at the base of the nest tree before being downloaded for analysis. Six high-definition video recording units (model: Mini HDVR LS-H720) were rotated systematically between nests. Recording units were deployed at each nest for a minimum of three days during the following periods: during the first week post-hatching, between one and four weeks post-hatching and from four weeks post-hatching until young had fledged and ceased to be fed at the nest (mean nestling period of 32 nests = 50 days ± 0.74). Equipment was powered by a 12v car battery and footage was stored on a 32gb mini-SD card before being downloaded and analysed. A total of 2,320 hours of footage were collected from 32 nest cameras (mean per nest 79.5

± 15.1 hours) yielding 1,005 prey deliveries (mean deliveries per nest 31.4 ± 2.6). Of these prey deliveries, 136 (13.5%) could not be identified, and were invariably smaller items which were blocked from view and consumed quickly. The proportion of unidentified deliveries declined between years (2011 = 29%; 2012 = 15%; 2013 = 6%) as camera placement and image quality were improved.

Concurrent to cameras recording prey deliveries, searches for prey remains and regurgitated pellets were conducted at the same 32 nests where cameras were deployed, plus the additional 14 nests to increase sample sizes of prey remains and pellets (number of nests searched: 2011 = 15, 2012 = 13, 2013 = 18). Searches within a 50 metre radius of the nest were conducted once when hatching was confirmed, once during each of the three periods of recording unit rotation, and once during the first week post-fledging. Searches within the nest were conducted when hatching was confirmed and again during the first week post-fledging.

Prey remains were recorded and removed from the search area to prevent double counting. Pellets were frozen and dried prior to dissection and analysis. Mammal hairs and bones found in pellets were identified using methods described in Teerink (2004). Feathers in pellets and prey remains were identified using Brown *et al.* (2003). Prey were identified to the lowest possible taxonomic level. Prey identified in remains and pellets were assumed to represent one individual prey item unless it was obvious that more than one individual was present.

Disturbance was minimised by ensuring all visits to nests lasted less than one hour and were only conducted in calm, mild weather to reduce the risk of exposure to chicks (Hardey *et al.* 2009), and cameras were installed after hatching was completed to reduce the chance of nest abandonment (Reif & Tornberg 2006). During this study, only one observed nest was abandoned, and in this case cameras recorded adults returning to the nest numerous times before abandonment occurred. Methods therefore did not appear to affect the natural behaviour of buzzards.

Predator diet was expressed both as the proportion of items in a given prey group (frequency) and as a proportion of the total prey weight of a given prey group (biomass).

Both measures are important when assessing predator diet; frequency measures can reveal the extent to which prey are selected (Redpath & Thirgood 1999; Thirgood *et al.* 2000c; Amar *et al.* 2008) while biomass measures can reveal the importance of different prey groups to the predator (Newton 1979; Cumberland *et al.* 2001; Rooney & Montgomery 2013). When calculating proportions of diet by biomass, weights of mammals were derived from values for adult individuals in Aulagnier *et al.* (2009) and Salamolard *et al.* (2000), unless it was obvious that the prey item was a young individual, in which case these were halved (Rooney & Montgomery 2013). Bird weights were taken from Snow & Perrins (1998) and Robinson (2005). Averages of sexes were used for prey items where the sex could not be reliably determined. The weight of a field vole was used for small mammals unidentified to species level, European rabbit was used for *Lagomorph spp.* unidentified to species, and meadow pipit was used for passerines unidentified to species because these were all the most common species on surveys for these groups (this study). Weights of invertebrates, amphibians and reptiles were taken from Salamolard *et al.* (2000), Rooney & Montgomery (2013) and ARKive [www.arkive.org]. Percentages of prey deliveries were calculated for each year with each method, in terms of frequency and biomass.

Pellet analysis is known to carry inherent bias in the estimation of diet composition (Simmons, Avery & Avery 1991; Redpath *et al.* 2001; Lewis, Fuller & Titus 2004, Chapter 2). To reduce the bias that pellet analysis had on results, correction factors were applied to the results. Correction factors were derived from a controlled feeding trial involving captive buzzards conducted in 2014. This experiment found that red grouse were detectable in 51.8% of buzzard pellets produced following a grouse meal, when analysed with conventional analysis techniques described in Yalden & Morris (2009). The trial also found that small mammals were detectable in 99% of pellets produced following a small mammal meal although the number of small mammal individuals detected was 53% of the number eaten by the buzzard prior to pellet production (Stickler *et al.* unpublished data - see Thesis Appendix, section A1 for further details). Using these detectability values, I corrected numbers and presence of prey identified in pellets prior to analysis. All birds identified to species were assumed to have the same detectability rates in pellets as grouse, whereas bird remains that were unidentifiable to species were assumed to have detectability rates of 94% as per values from the experiment. Detectability rates of lagomorphs and invertebrates were unknown and were unchanged.

Dietary breadth of generalist predators can change with variations in relative prey abundance (Salamolard *et al.* 2000). Therefore I also explored yearly variation in mean diet breadth using each assessment method. Diet breadth was assessed using a Levins' index (Levins 1968) calculated as:

$$Diet\ breadth = \frac{1}{\sum {p_j}^2}$$

where p_j is the proportion of total frequency of prey group *j*.

The index is a scale from 1 – n with n available prey groups, where a breadth of 1 would occur when just 1 prey group was found in the diet (i.e. a specialist), whereas a breadth of *n* represents all available groups contributing equally to the diet (i.e. a generalist). Diet breadth was calculated for each nest using each of the three assessment methods and compared between years using data from each method separately.

To explore buzzard predation rates on red grouse I considered yearly variation in presence of red grouse in buzzard diet accounting for variation in grouse density. To avoid multiple testing, and because records of red grouse in camera images and pellets were too few for models to be reliable, I only considered variation in the presence of red grouse in prey remains data. Prey remains can over-estimate large birds relative to other prey groups when compared to other methods (Redpath *et al.* 2001a; Lewis *et al.* 2004; Chapter 2). However, since the aim here was to explore temporal changes in the occurrence of red grouse in buzzard diet, this was not deemed to be a problem. A General Linear Mixed Model (GLMM) was constructed with binomial errors and a logit-link function using the proportion of prey records consisting of red grouse as response variable. The sample size (n) was the number of successful buzzard nests at which prey remains were collected (46). 'Territory' was included as a random effect to account for sampling nests within the same territory in successive years. Predictor variables were year and grouse density in a 1 km radius of each buzzard nest, which represents an average territory size of buzzard pairs at Langholm (Graham *et al.* 1995). Grouse density around each buzzard nest was estimated using a modified approach of that taken by Redpath & Thirgood (1999), whereby the mean July grouse density (grouse / km^2) for each year, estimated from counts in the ten blocks, was multiplied by the proportion of heather dominated vegetation within a 1 km radius of each buzzard nest using data from the Landcover Map (2007) (Morton *et al.* 2011). I included interaction terms between year and grouse density to explore whether the relationship between grouse density and the presence of grouse in buzzard diet varied between years. Prior to model construction I checked that variation in sample size did not affect the results. Significance of interaction terms was assessed by deletion and model comparison using log-likelihood tests and Chi^2 statistics (Whittingham *et al.* 2006).

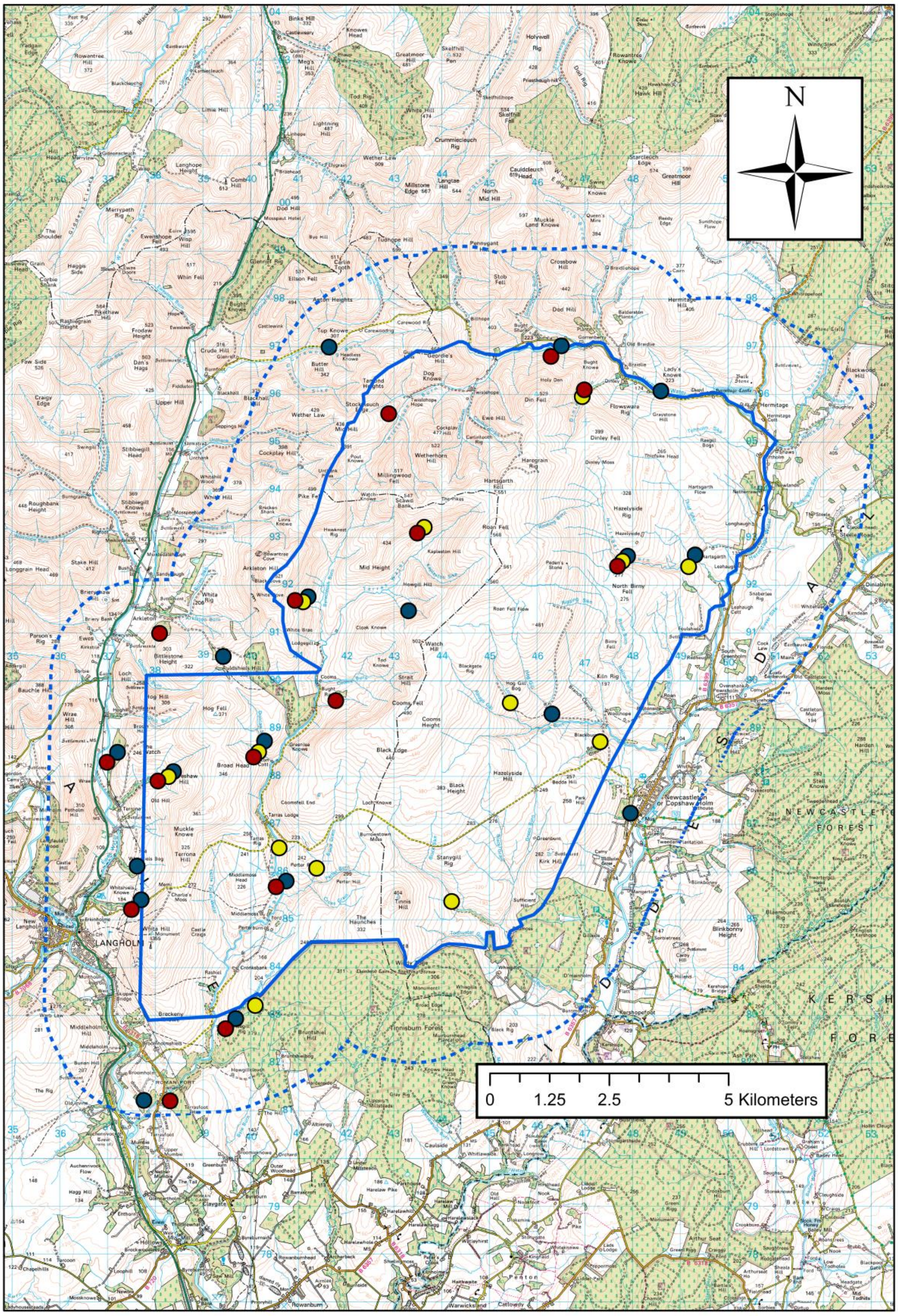

Figure 3.1. Locations of 46 buzzard nests at Langholm Moor (2011 – 2013) used for diet analysis. Diet data were collected from 15 nests in 2011 (red dots); 13 nests in 2012 (yellow dots) and 18 nests in 2013 (blue dots) (see text for details of methods used). All nests were within the LMDP area (solid blue line) or within a 2 km buffer zone (dashed blue line).

3.4 Results

3.4.1 Prey abundances

Field voles varied in density between years ($F_{2,27} = 7.09$, $p = 0.003$). Vole abundance peaked in 2011 and crashed in 2013, demonstrating a decline period in the vole cycle at Langholm Moor during this study. There were no variations between years in the densities of red grouse in spring ($F_{2,27} = 0.10$, $p = 0.915$), red grouse in July ($F_{2,27} = 2.54$, $p = 0.097$), meadow pipits ($F_{2,45} = 0.72$, $p = 0.492$) or lagomorphs (T = -0.29, N = 12, $p = 0.779$) (Table 3.1).

Table 3.1. Mean ± *s.e.* abundances of key buzzard prey groups at Langholm Moor between 2011 - 2013. Note that prey densities are presented in different units.

	Voles / 100 trap nights* (N = 10)	Spring grouse / 0.5km^2 (N = 10)	July grouse / 0.5km^2 (N = 10)	Meadow pipits / km^2 (N = 16)	Lagomorphs / km (N = 12)
2011	**7.0 ± 1.9**	16.7 ± 1.6	25.4 ± 4.9	24.6 ± 1.8	N/A
2012	**4.0 ± 1.0**	15.4 ± 3.0	26.6 ± 3.5	21.5 ± 2.0	8.0 ± 1.2
2013	**0.6 ± 0.3**	15.8 ± 1.8	38.0 ± 4.6	23.8 ± 1.9	8.3 ± 1.9

* significant variation between years ($p < 0.05$) highlighted in bold (see text)

3.4.2 Buzzard numerical response

Mean nearest neighbour distance (NND) was assessed using 48 of the total 58 active nests at which the nearest neighbouring nests was confidently discovered based on intensive searches. Mean NND across all years was 1.72 km (± 0.12 *s.e.*), and did not vary between years ($F_{2,45} = 1.53$, $p = 0.227$) (Table 3.A1 – Chapter Appendix). During the same period, the mean number of chicks fledged from all breeding attempts (N = 58) was 1.52 ± 0.11 (range 0 – 3), and the mean number of chicks fledged from all successful nests (N = 50) was 1.76 ± 0.09 (range 1 – 3) (Table 3.A2 – Chapter Appendix). There was no variation between years in chicks per breeding attempt (Kruskal-Wallis ANOVA: H = 1.12, d.f. = 2, $p = 0.570$), or chicks per successful nest (H = 0.16, d.f. = 2, $p = 0.923$). Thus there was no evidence of a numerical response by buzzards to changing vole abundances, both in terms of nesting density and number of chicks fledged.

3.4.3 Buzzard functional response

A total of 2,320 hours of footage were collected from the 32 nest cameras deployed over the three years (mean per nest per year 79.5 ± 15.1 hours) yielding 1,005 prey deliveries (mean deliveries per nest 31.4 ± 2.6). Of these deliveries, 136 (13.5%) could not be identified, and are excluded here. Field voles were the most frequently recorded prey item on camera images in all years. There was a downward trend in the number of voles delivered to buzzard nests from 52% of total identified prey deliveries in 2011 to 20% in 2013, which declined in line with vole abundance. There were corresponding increases in the frequency of other small mammals (moles, shrews and mice) from 14% of prey in 2011 to 34% in 2013, and other large birds (corvids, waders and pigeons) from 0% in 2011 to 5% in 2013. There was no trend in the frequency of red grouse delivered to buzzard nests, which varied between 0% in 2011 (no records) and 2.6% in 2012. In terms of biomass, lagomorphs were the dominant prey group in all years. Voles declined from 14% of total prey biomass in 2011 and 15% in 2012 to just 4% in 2013, which corresponded with the crash in vole abundance during this study. Biomass of ‘other large birds’ increased in proportion of prey by biomass from 0% in 2011 to 14% in 2013. Again there appeared to be no trend in red grouse biomass in buzzard diet assessed using camera images (Table 3.A3, Chapter Appendix).

Searches inside and around 46 successful buzzard nests yielded 664 prey remains (mean items per nest = 14.4 ± 0.8). Lagomorphs were the dominant prey in each of the three years both in terms of frequency and biomass. This contrasts to the previous result (Chapter 2) and is probably explained by a combination of the larger sample of nests used in the current study that were in the moorland periphery which contains higher densities of lagomorphs (this study; Graham *et al.* 1995), as well as the separation of red grouse from other large birds. Voles declined from 16% of all prey remains in 2011 to 1% in 2013, which was in line with declines in vole abundance. There were corresponding increases in proportions of lagomorphs from 21% in 2011 to 28% in 2013, other large birds from 9% in 2011 to 22% in 2013 and moles from 2% in 2011 to 5% in 2013. However, red grouse declined in proportion of prey remains from 12% in 2011 to 2% in 2013, which was the equivalent of a decline in total biomass from 13% to 2% (Table 3.A4, Chapter Appendix).

Analysis of 295 pellets collected from the same 46 successful buzzard nests (mean ± *s.e.* pellets per nest 6.4 ± 0.6) yielded 655 prey items (mean ± *s.e.* prey items per pellet = 2.3 ± 0.1). Data from initial pellet analysis are given in Table 3.A5, and data following the application of correction factors are given in Table 3.A6 (Chapter Appendix). After correction factors were applied to initial pellet analysis data, voles were numerically the dominant prey type in pellets in each year. Voles decreased in proportion of total estimated prey items from 58% in 2011 to 38% in 2013, which was equivalent of a decline in total biomass from 19% to 6%, in line with declines in vole abundance. There were concurrent increases in lagomorphs from 2% of items in 2011 to 12% in 2013, equivalent of an increase in total biomass from 20% to 62%, as well as increases in other small mammals from 8% of items in 2011 to 18% in 2013. As with prey remains, there were declines in the proportion of red grouse remains found in pellets from 6% in 2011 to 3% in 2013, which was equivalent to a decline in total biomass from 21% to 5%.

Diet breadth assessed using camera images differed significantly between years ($F_{2,29}$ = 6.64, $p = 0.004$). Post hoc comparisons indicated a significant increase in diet breadth in 2013 (mean = 4.72, *s.d.* = 1.03) compared to both 2011 (mean = 3.24, *s.d.* = 0.61; p = 0.004) and 2012 (mean = 3.64, *s.d.* = 1.22; $p = 0.046$). Diet breadth also differed significantly between years when assessed with pellet analysis ($F_{2,43}$ = 5.02, $p = 0.011$). Post hoc comparisons indicated a significant increase in diet breadth in 2013 (mean = 2.61, *s.d.* = 0.82) compared to 2011 (mean = 1.79, *s.d.* = 0.57; $p = 0.008$), but diet breadth in 2012 was not significantly different to either other year ($p > 0.17$). Diet breadth did not vary between years using prey remains data ($F_{2, 43}$ = 1.18, $p = 0.316$).

Thus, there was evidence of a functional response by buzzards to declining vole abundance in which buzzards ate a wider variety of prey including more other small mammals, lagomorphs (assessed by prey remains and pellets) and large birds (cameras and prey remains), but buzzard consumption of red grouse either declined (prey remains and pellets) or showed no obvious trend (camera images).

3.4.4 Red grouse in buzzard diet

The proportion of grouse in prey remains was not related to the number of prey items found at each nest ($F_{1,43} = 2.17$, $p = 0.148$), confirming that the number of prey items collected from each nest did not significantly affect the results. There was a significant interaction between grouse density and year (GLMM $\chi^2_1 = 10.55$, $p = 0.005$, ΔAIC = 6.56), indicating that the relationship between the proportion of red grouse in buzzard diet and grouse density around each buzzard nest differed between years. Inspection revealed that grouse density around each buzzard nest had a significant positive effect on the proportion of grouse in buzzard diet during the peak vole year (2011) ($F_{1,13} = 24.67$, $p = <0.001$), but no effect during either other year (2012: $F_{1,11} = 0.39$, $p = 0.544$; 2013: $F_{1,16} = 1.26$, $p = 0.279$) (Figure 3.2). Although not analysed for statistical significance to avoid multiple testing and due to low sample sizes, relationships for pellet and camera data are shown in the chapter appendix (Figures 3.A1 & 3.A2).

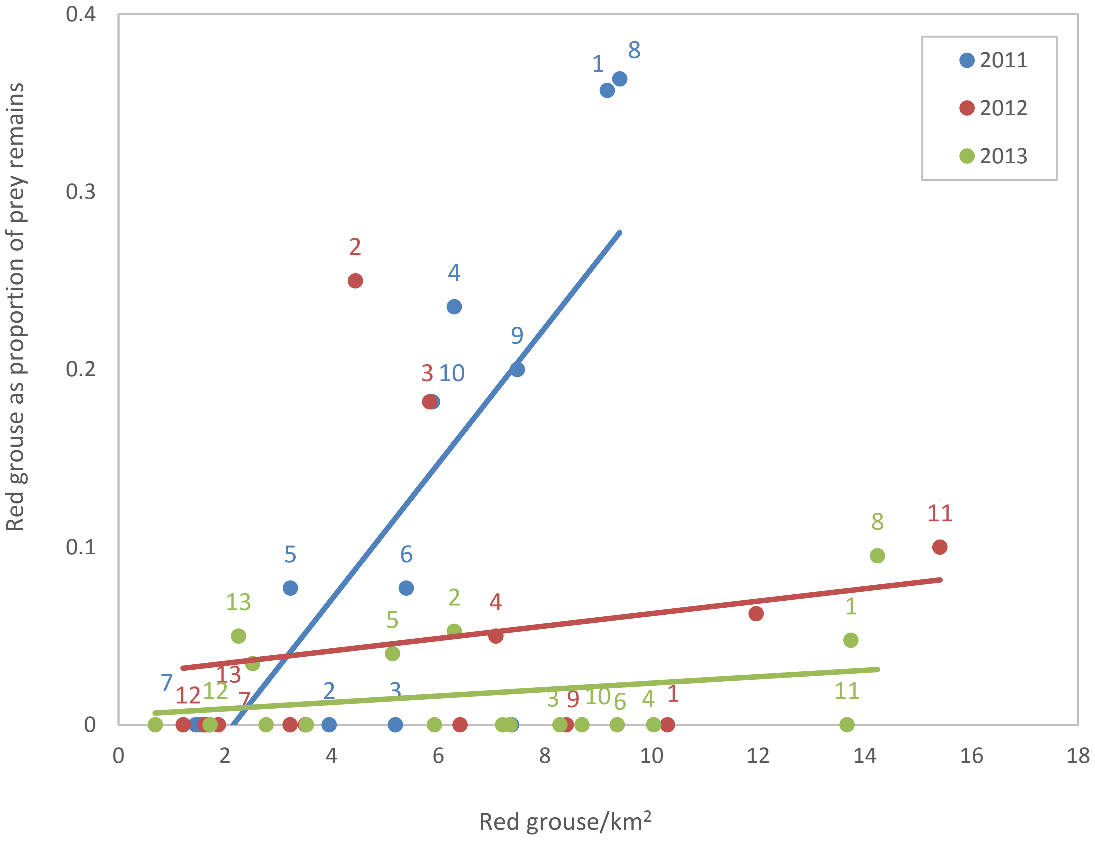

Figure 3.2. Relationship between the proportion of prey remains consisting of red grouse and estimated grouse abundance within a 1 km radius of each nest during a peak vole year (2011: n = 15), an intermediate vole abundance year (2012: n = 13) and a vole crash year (2013: n = 18). Grouse density had a significant positive effect on the proportion of grouse in prey remains at buzzard nests in 2011 (the peak vole year), but not in either other year (see text). Numbers above data points refer to territories where nests were surveyed in multiple years.

3.5 Discussion

The impact of predation on prey populations depends largely on the numerical and functional responses of predators (Solomon 1949). Documenting the responses of raptors to variations in prey density has been highlighted as a key area of research required to increase understanding of raptor impacts on gamebirds (Park *et al.* 2008). In this study I demonstrated evidence of a functional response of breeding buzzards to significant temporal variation in the abundance of their main vole prey. When vole abundance diminished, buzzards appeared to increase their predation on a wider range of alternative prey groups such as lagomorphs, corvids, columbids, shrews and moles. Conversely, predation on red grouse appeared to either decrease or not change in response to vole decline, depending on the dietary assessment method used. Results therefore support the predictions of the Alternative Prey Hypothesis (APH) by showing an apparent switch in dietary choice when vole abundance declined. Equally, my results supported the predictions of the Incidental Prey Hypothesis (IPH), whereby buzzards incidentally predated more grouse when vole abundance was high on the moor. I have demonstrated evidence that a spatial coexistence of voles and red grouse on the heather-grass mosaic at Langholm moor (Redpath & Thirgood 1997) is likely to promote incidental predation of red grouse by buzzards when vole indices are high.

Previous studies have demonstrated increased predation of grouse species *Tetraonidae* by buzzards when vole *Microtus spp.* abundance declined (Reif *et al.* 2001; Tornberg *et al.* 2012). However, like many APH studies, these were conducted in relatively homogenous landscapes with lower alternative prey resource diversity (Zárybnická *et al.* 2015). The present study was conducted in a heterogeneous landscape comprising upland heather moorland with a mosaic of ericaceous vegetation and acid grassland surrounded by farmland, improved grassland and woodland (Redpath & Thirgood 1997). In this mixed landscape, prey resources will be patchy in their distribution, which can affect predation on incidental prey when predators are able to switch their dietary choice (Selås 2001; Mckinnon *et al.* 2013). It is notable that many of the prey groups that increased in buzzard diet as vole abundance declined are typically associated with farmland and improved grassland habitats rather than moorland (Glue 1967; Swann & Etheridge 1995; Rooney & Montgomery 2013). This suggests that during periods of low vole availability, buzzards switched to hunting alternative prey in habitats away from the moorland, thus reducing incidental predation on red grouse associated with moorland habitats. Similarly, during years of intermediate and low vole abundance, the presence of grouse in buzzard diet was not related to the density of grouse in the vicinity of the buzzard nest, presumably as buzzards switched to increased predation of alternative prey occurring outside of grouse habitats. My results suggest that systems involving heterogeneous landscapes with mobile predators may produce more complex interactions than are predicted in more homogenous landscapes.

I found no evidence of a numerical response to temporal variation in vole abundance in breeding buzzards. Neither breeding density nor breeding success varied between years as vole abundance declined. This may suggest that buzzards are sufficiently generalist in their feeding habits to be able to switch to alternative prey in order to offset declines in their preferred prey, so that breeding performance is not affected (Reif *et al.* 2004). Although heather moorland generally contains a relative paucity of suitable buzzard nesting sites (Hardey *et al.* 2009), it is unlikely that this had a major effect on results here because Langholm Moor is surrounded by woodland and intersected with numerous wooded gullies (Redpath & Thirgood 1997), many of which were vacant despite their apparent suitability to nesting buzzards (pers. obs.). Disentangling these effects on buzzard breeding performance, as well as other influences such as weather conditions will require more data over several years and prey abundance cycles.

There are a few reasons to treat the results here with caution. Firstly, as with many studies involving investigations of raptor diet, distinguishing between predation and scavenging is a limitation of the methods used here (Park *et al.* 2008). Buzzards are known to kill and scavenge prey (Tubbs 1974), and distinguishing between the two may require other methods such as focussed and intensive following of buzzards to record kill rates (Kenward *et al.* 1981a, 2001; Rutz 2003). Secondly, the effect of microhabitat variables on the vulnerability of grouse to buzzard predation was not considered here. Insufficient cover from predators or habitat fragmentation can increase grouse vulnerability to predation from raptors (Thirgood *et al.* 2002; Whittingham & Evans 2004; Arroyo *et al.* 2009). The functional response documented here should also be confirmed by studying buzzard response over a greater range of grouse densities, in order to confirm whether the observed responses occur at higher grouse density. This will be important for assessing the functional response curve shape, for which my data are too restricted to make reliable conclusions about (Redpath & Thirgood 1999). This could be achieved by collecting data over a longer time period as grouse densities at Langholm vary over time, or by collecting data from other grouse moors with different grouse densities than Langholm (Redpath & Thirgood 1999). Studying the responses of buzzards over multiple vole and grouse cycles would improve the accuracy of my results. It is also important to note that the functional response documented here came from observations of breeding birds only, and there are no data on changes in the dietary composition of non-breeding buzzards. This factor, as well as other sources of bias inherent in the methods here, such as an inability to quantify prey eaten away from the nest (Redpath & Thirgood 1999; Chapter 2), mean that my results should only be considered in the context of the changes in the composition of prey brought to nests. However, a concurrent study of foraging habits found evidence that buzzards, which included both breeding and non-breeding individuals, hunted at higher intensities on the heather moor when vole indices were high (Chapter 4). This gives further evidence that higher vole density may lead to increased incidental predation of red grouse by buzzards. Finally, and importantly, it is unknown whether these observations would differ elsewhere. It is probable that the heather-grass mosaic at Langholm Moor promotes high vole densities (Wheeler 2008) which may in turn promote incidental predation of grouse as buzzards hunt for voles. Studying the response of buzzards on other grouse moors with different habitat and prey resource compositions could improve our understanding of the IPH in these systems.

The observation that incidental predation of red grouse by buzzards may be linked to elevated vole abundance has potential implications for those interested in mitigating grouse losses to raptors. For example, it may be possible to deter buzzards from hunting in grouse habitats by exploiting the natural flexibility of buzzard foraging behaviour. This could be achieved by making grouse habitats less attractive to forage in, by increasing heather cover and therefore reducing their value as vole rich habitats (Wheeler 2008). Conversely, the relative attractiveness of habitats that are spatially separated from grouse habitats could be increased by maintaining vole rich habitats on the moorland periphery. Similarly, buzzards could be attracted away from grouse habitats by artificially providing supplementary food away from the moorland, which may also reduce the need to hunt natural prey (Redpath *et al.* 2001b; Rooney *et al.* 2014). Further research is needed to test the efficacy of some of these proposed management solutions aimed at mitigating raptor impacts on red grouse (Thirgood & Redpath 2008). My results suggest that studies investigating predator-prey dynamics and their management should consider all resources and habitats available to predators.

3.6 Appendix

Table 3.A1. Mean nearest neighbour distances of buzzard nests at Langholm Moor between 2011 – 2013. NND was similar between years (see text).

	N	Mean NND ± *s.e.* (km)	Min. NND (km)	Max. NND (km)
2011	15	1.61 ± 0.21	0.55	3.80
2012	12	2.06 ± 0.23	0.90	3.55
2013	21	1.62 ± 0.20	0.21	4.12

Table 3.A2. Measures of buzzard breeding success at 58 breeding attempts and at 50 successful nests at Langholm Moor between 2011 and 2013. Successful nests are nests where at least one chick was fledged.

	Chicks per breeding attempt		Chicks per successful nest	
	N	Mean ± s.e. (range)	N	Mean ± s.e. (range)
2011	16	1.56 ± 0.22 (0-3)	14	1.79 ± 0.19 (1-3)
2012	16	1.69 ± 0.20 (0-3)	15	1.80 ± 0.18 (1-3)
2013	26	1.39 ± 0.18 (0-3)	21	1.71 ± 0.14 (1-3)

Table 3.A3. Percentages of prey recorded with **camera images** delivered to 32 buzzard nests in three years (2011 = 11; 2012 = 10; 2013 = 11). Data are presented as percentages by frequency and percentages of total biomass. Data are pooled across nests within year. Unidentified prey (N = 136) were removed prior to calculating percentages.

	Frequency			Biomass		
	2011	2012	2013	2011	2012	2013
N (Identified prey items)	249	266	354			
Small mammals						
Field vole	52.2	40.2	20.1	13.6	14.8	3.9
Mole	9.2	10.5	11.3	8.0	13.0	7.3
Other small mammals	5.2	9.4	22.3	0.4	1.1	1.4
Large mammals						
Lagomorph spp.	4.8	1.5	8.2	41.9	18.5	52.7
Other large mammals	4.4	4.9	2.0	9.3	13.2	4.8
Small passerines	10.8	7.5	11.6	1.8	1.7	1.4
Large birds						
Red grouse	0.0	2.6	0.8	0.0	4.9	2.4
Pheasant	2.0	0.8	0.8	20.8	11.0	6.5
Other large birds	0.0	1.9	5.1	0.0	10.9	14.4
Other prey						
Invertebrates	0.8	0.8	0.3	0.0	0.0	0.0
Herpetofauna	10.4	19.9	17.5	4.1	10.9	5.3

Table 3.A4. Percentages of **prey remains** collected at 46 buzzard nests in three years (2011 = 15; 2012 = 13; 2013 = 18). Data are presented as percentages by frequency and percentages of total biomass. Data are pooled across nests within year.

	Frequency			Biomass		
	2011	2012	2013	2011	2012	2013
N (Identified prey items)	160	169	335			
Small mammals						
Field vole	15.6	5.9	0.9	0.9	0.3	0.0
Mole	1.9	3.0	5.4	0.4	0.5	0.9
Other small mammals	1.3	3.6	0.9	0.0	0.1	0.0
Large mammals						
Lagomorph spp.	20.6	21.9	28.4	39.6	40.7	45.1
Other large mammals	1.9	0.0	0.6	1.5	0.0	0.1
Small passerines	15.6	17.8	14.0	0.6	0.6	0.4
Large birds						
Red grouse	11.9	5.3	2.1	13.2	5.6	1.6
Pheasant	15.0	17.2	17.9	35.4	37.3	34.0
Other large birds	9.4	15.4	21.8	8.3	14.2	17.5
Other prey						
Invertebrates	5.6	1.8	3.6	0.0	0.0	0.0
Herpetofauna	1.3	8.3	4.5	0.1	0.6	0.3

Table 3.A5. Percentages of prey identified from analysis of **pellets** collected at 46 buzzard nests in three years (2011 = 15; 2012 = 13; 2013 = 18). Data are presented as percentages by frequency and percentages of total biomass. Data are pooled across nests within year. Data are from initial pellet analysis, without correction factors. Data post-application factors are shown in Table 3.A6.

	Frequency			Biomass		
	2011	2012	2013	2011	2012	2013
N (identified prey items)	128	141	386			
Small mammals						
Field vole	50.8	38.3	30.6	15.9	7.5	3.8
Other small mammals	7.0	12.8	14.5	0.7	0.8	0.9
Large mammals						
Lagomorph spp.	3.1	10.6	17.9	32.6	69.1	73.6
Small passerines	6.3	9.2	9.6	1.2	1.1	0.7
Large birds						
Red grouse	4.7	2.8	2.3	17.0	6.4	3.0
Pheasant	1.6	0.7	2.3	19.4	5.5	11.4
Other large birds	2.3	2.8	3.1	12.5	9.4	6.5
Other prey						
Invertebrates	22.7	22.0	19.2	0.0	0.0	0.0
Herpetofauna	1.6	0.7	0.5	0.7	0.2	0.1

Table 3.A6. Pellet analysis data from Table 3.A5 with correction factors applied using results from a buzzard feeding experiment (Stickler *et al.* unpublished data - see Thesis Appendix, section A1). Data were corrected assuming detectability rates of 53% for small mammals and 52% for identified birds (94% for unidentified birds). Values for lagomorphs and invertebrates were unchanged. Data are presented as percentages by frequency of the total number of prey items estimated post-application of correction factors, and percentages of total biomass. Data are pooled across nests within year (2011 = 15; 2012 = 13; 2013 = 18).

	Frequency			Biomass		
	2011	2012	2013	2011	2012	2013
N (estimated prey items after correction factors)	202	223	588			
Small mammals						
Field vole	58.3	45.6	37.8	18.5	11.0	6.0
Other small mammals	8.1	15.2	18.0	0.8	1.2	1.4
Large mammals						
Lagomorph spp.	1.9	6.7	11.7	20.1	53.9	61.5
Small passerines	6.9	10.4	11.2	1.4	1.6	1.1
Large birds						
Red grouse	5.5	3.4	2.9	21.0	10.0	5.0
Pheasant	1.8	0.9	2.9	23.0	8.2	18.3
Other large birds	2.7	3.4	2.5	14.8	14.1	6.6
Other prey						
Invertebrates	13.8	13.9	12.6	0.0	0.0	0.0
Herpetofauna	1.0	0.4	0.3	0.4	0.2	0.1

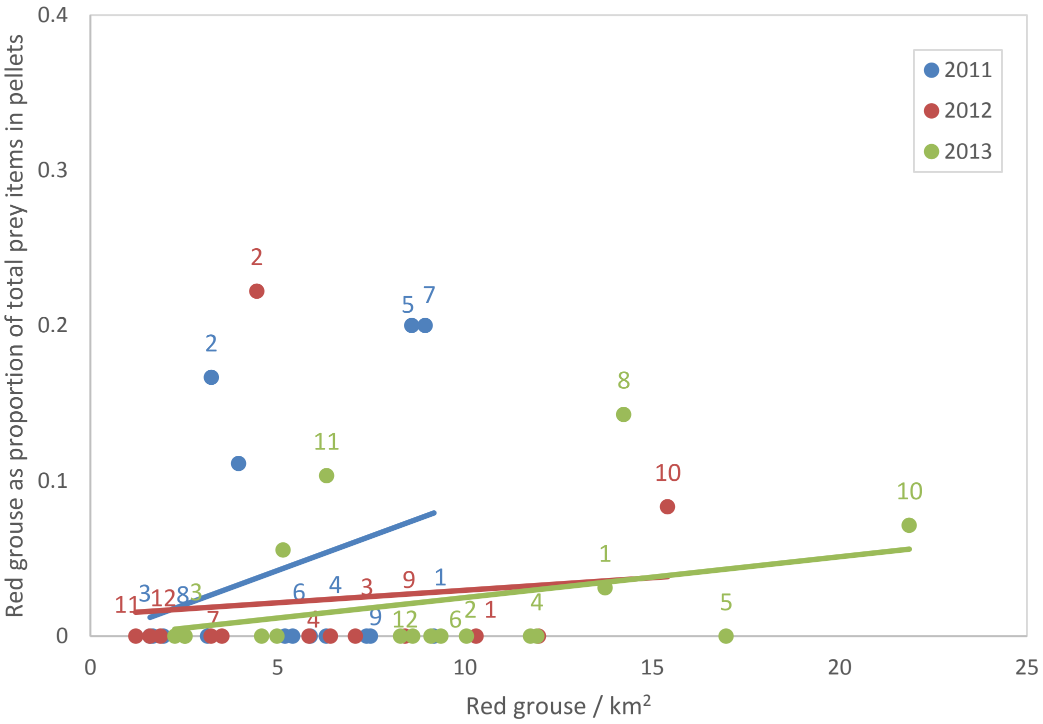

Figure 3.A1. Relationship between the proportion of prey items in pellets consisting of red grouse and estimated grouse abundance in a 1 km radius of each nest in three years (2011: n = 15, 2012: n = 13, 2013: n = 18). Relationships were not tested for significance (see text). Numbers above data points refer to territories where nests were surveyed in multiple years.

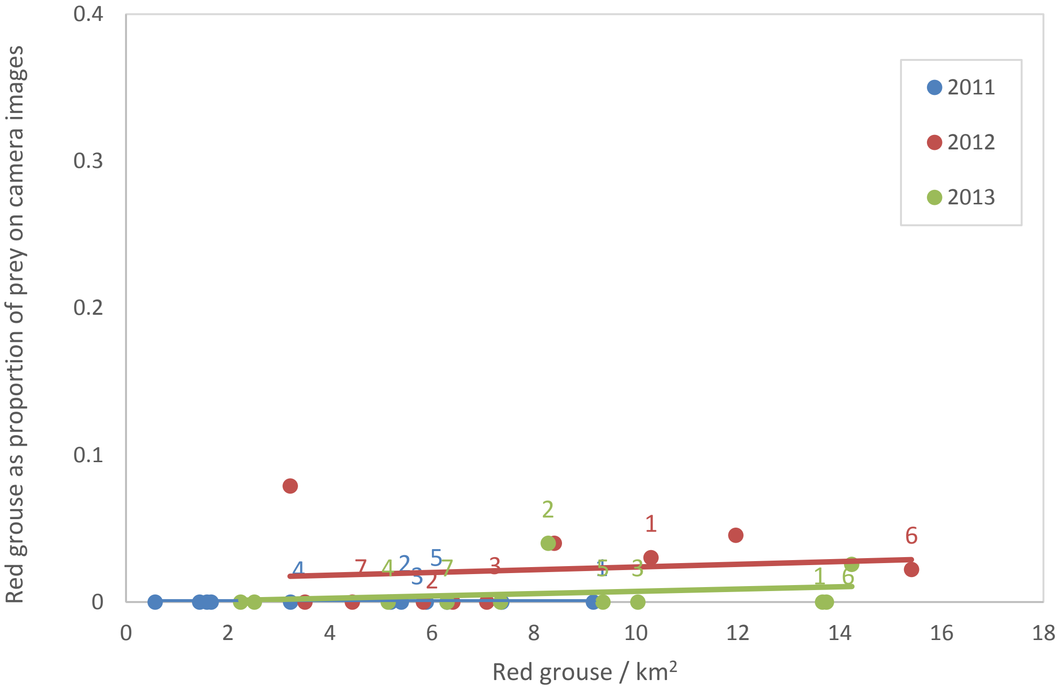

Figure 3.A2. Relationship between the proportion of prey items on camera images consisting of red grouse and estimated grouse abundance in a 1 km radius of each nest in three years (2011: n = 11, 2012: n = 10, 2013: n = 11). Relationships were not tested for significance (see text). Numbers above data points refer to territories where nests were surveyed in multiple years.

Chapter 4. Correlates of common buzzard foraging patterns and relationships with mortality indices of red grouse

4.1 Abstract

Optimal Foraging Theory predicts that mobile predators inhabiting heterogeneous landscapes will hunt in habitats yielding the greatest net energy gains. However, the relative importance of habitats may vary over time as prey abundances change. Here I test these hypotheses on an area of upland heather moorland managed for red grouse in south-west Scotland. I explore the key factors influencing the foraging distribution of common buzzards in summer and winter, and how these vary between years as prey abundances change. I also use a correlative approach to explore relationships between foraging patterns of buzzards and indices of grouse mortality. Buzzards showed significant yearly variation in foraging density in line with fluctuating vole abundance. I found no significant influence on buzzard foraging patterns of the spatial variation in voles or meadow pipits, but buzzards hunted in areas with more red grouse during winter. Buzzards hunted in areas with less heather when vole abundance was reduced, but during a peak vole abundance year no effect of habitat composition on buzzard foraging patterns was detected. I found no evidence of any relationship between grouse mortality indices and the foraging distributions of buzzards or all large bird-eating raptors, although it was not possible to distinguish between mortality and emigration in the grouse mortality index. Results suggest that predation of red grouse by buzzards may increase when vole abundances are high by promoting buzzard foraging in red grouse habitats. These results could provide a useful framework for further study of buzzard impact on economically important or threatened prey.

4.2 Introduction

Optimal Foraging Theory predicts that animals will preferentially forage in areas with maximum net energy gains (Stephens & Krebs 1986). Raptors are mobile predators that often inhabit heterogeneous landscapes with unevenly distributed prey (Newton 1979). As such they are predicted to forage in a non-random pattern, concentrating foraging effort in areas delivering the greatest net energy gain (Pyke *et al.* 1977). The tendency for a raptor to forage in a given area will be influenced by a range of factors, of which the abundance and availability of prey are key (Baker & Brooks 1981; Preston 1990).

Raptors will often respond numerically to relative changes in densities of their prey. Numerical responses can occur through changes in breeding density or success, or by individuals preferentially hunting in areas of maximum net energy gains (Solomon 1949; Stephens & Krebs 1986; Korpimäki & Norrdahl 1991; Redpath & Thirgood 1999; Salamolard *et al.* 2000; Reif *et al.* 2004). This latter response is termed the 'aggregative response', and the degree to which this occurs can influence predation rates on main, alternative and incidental prey (Mckinnon *et al.* 2013).

An understanding of the relative attractiveness of habitats to predators is essential for effective management of populations of both predators and their prey (Morrison *et al.* 2012). However, as the aggregative response shows, the relative attractiveness of habitats can vary over time as prey density and availability changes. Lõhmus (2003) calls this the "year-effect of habitat relationships", and found that year × habitat interactions were analysed in only 5% of raptor and owl habitat preference studies. Estimating the impact of raptors on prey resources requires an understanding of the factors affecting the foraging patterns of raptors (Thirgood *et al.* 2003) as well as the degree to which these factors change over time in response to annual variations in prey abundances (Lõhmus 2003).

Common buzzards *Buteo buteo* (herein 'buzzard') have expanded in range by an estimated 81% in range since the 1970s (Balmer *et al.* 2014) and are the most common diurnal raptor in Britain (Musgrove *et al.* 2013). Increasingly, this has brought them into conflict with game managers concerned about impact on gamebirds (Harradine *et al.*

1997; FERA 2012). Buzzards are generalist raptors whose preferred prey are voles *Microtus* spp. and rabbits *Oryctolagus cuniculus* (Tubbs 1974; Swann & Etheridge 1995; Reif *et al.* 2001; Rooney & Montgomery 2013), although red grouse *Lagopus lagopus scotica* will feature in buzzard diet if they are locally available (Graham *et al.* 1995). Red grouse are an economically important gamebird in parts of upland Britain (Hudson 1992), and so understanding predatory mechanisms is an important aspect of reaching conservation and economic objectives (Kenward 1999).

The most scientifically rigorous approach to investigating predator impact on prey is experimental, whereby predators are removed from areas and the prey response compared to similar areas where predators remain, before reversing treatments (Newton 1998). However, when this is not possible due to logistics, lack of spatial and temporal replication or reversal of treatments, or legal/conservation status of predators, a correlative approach looking at relationships between predator and prey can provide useful insights (Newton *et al.* 1997; Thomson *et al.* 1998; Amar *et al.* 2008, 2010; Chamberlain *et al.* 2008).

In this study I explore the key factors determining spatial and temporal variation in the distribution of foraging buzzards on an area of heather moorland in south-west Scotland. I explore the aggregative response of buzzards by investigating annual variation in buzzard foraging patterns in relation to fluctuations in the main prey base, and spatial variation of buzzards in relation to prey and habitat composition. I then use a correlative approach to explore relationships between indices of red grouse mortality and foraging patterns of buzzards – alone and as a constituent of the large raptor community.

4.3 Methods

4.3.1 Study area

The study was conducted over three years, incorporating three summers (2012 – 2014) and three winters (2011/12 – 2013/14) on 114km^2 of Langholm Moor in south-west Scotland. The study site was incorporated by the Langholm Moor Demonstration Project (LMDP) and included the Langholm and Newcastleton Hills SSSI and SPA. Moorland management, including predator control and heather management was undertaken by a team of five gamekeepers to benefit red grouse. The site primarily consists of a mosaic of acidic grassland and ericaceous heather moorland (Redpath & Thirgood 1997; Chapter 1). All data were collected within the LMDP area (Figure 1.1, Chapter 1).

4.3.2 Raptor foraging patterns

Observations of raptors were conducted from fixed vantage points overlooking a total of twelve blocks of approximately 2 km^2 (mean = 2.1 km^2, range = 1.79 km^2 – 2.34 km^2). Summer observations were conducted on ten blocks in 2012 and on twelve blocks in 2013 and 2014 which were added to increase coverage of the study site. During the 2011/12 winter, heavy snow prevented access to one of the ten original blocks and so nine blocks were observed this year, although all twelve blocks were observed in the winters of 2012/13 and 2013/14.

During summer, the mean observation period was 2.6 hours (± 0.1 *s.e.*) and the mean period that each block was observed in total was 46 hours (± 1.5 *s.e.*). Each block was observed twice per month between May and July inclusive in each year giving a total of 552 hours of observation. During winter, the mean observation period was 2.8 hours (± 0.1 *s.e.*), and the mean period that each block was observed in total was 55.1 hours (± 3.7 *s.e.*). Each block was observed once per month between October and March inclusive, giving a total of 661 hours of observation in winter.

During observations, blocks were scanned at two minute intervals with binoculars and the presence and behaviour of all raptors recorded. Observations were not conducted during rain, heavy wind or when visibility dropped below 2 km. I made an attempt to distinguish between hunting and non-hunting behaviour of raptors: quartering, soaring and hovering were considered as hunting behaviour; whilst calling in flight, territorial defence, displaying, and calling or preening while perched were all considered non-hunting behaviour (Thirgood *et al.* 2003). Sightings of non-hunting raptors were excluded from analysis.

Raptors present on Langholm Moor and sighted during observations included buzzard, hen harrier *Circus cyaenus*, peregrine *Falco peregrinus*, goshawk *Accipiter gentilis*, kestrel *Falco tinnunculus*, merlin *Falco columbarius*, and short-eared owl *Asio flammeus.* Barn owl *Tyto alba,* tawny owl *Strix aluco* and long-eared owl *Asio otus* were also present but were rarely seen during daylight. Sightings of sparrowhawk *Accipiter nisus*, hobby *Falco subbuteo,* red kite *Milvus milvus* and red-footed falcon *Falco vespertinus* were very rare during this study. For this study I consider the foraging distributions of the large bird-eating raptors most likely to predate red grouse; these being buzzard, hen harrier, peregrine and goshawk (Linden & Wikman 1983; Graham *et al.* 1995; Redpath & Thirgood 1997; Thirgood & Redpath 1997; Thirgood *et al.* 2003; Park *et al.* 2005; Kenward 2006), hereby termed ‘large raptors’. All other species were excluded from analysis.

4.3.3 Habitat and prey indices

The habitat composition of each of the twelve raptor observation blocks was calculated using data from the Land Cover Map 2007 dataset (LCM 2007) (Morton *et al.* 2011). These data consist of a 25 × 25 metre grid with each square categorized by its dominant vegetation class. Data were incorporated into ArcGIS version 10.2.1 and each raptor observation block mapped in order to calculate the habitat proportions of each. Grass (rough, neutral and acidic grassland) and heather moorland (dwarf shrub heathland, heather-grass mix and ericaceous bog) together comprised more than 90% of the habitat composition in each of the twelve raptor observation blocks. Therefore, a habitat composition index was calculated by log-transforming the ratio of heather moorland to grassland.

Small mammals and lagomorphs are important components of buzzard diet, with passerines and larger birds such as pheasants and red grouse featuring where they are available as alternative prey (Swann & Etheridge 1995; Graham *et al.* 1995; Rooney & Montgomery 2013, Chapter 3). Lagomorphs and pheasants were rare within the raptor observation areas (Thirgood *et al.* 2003), so here I consider indices of small mammals, red grouse and passerines as potential predictors of buzzard foraging patterns.

Small mammals were trapped in late March in all study years on twelve lines of 50 un-baited traps set for two nights. This gave a total of 1,200 trap nights per year, which has been shown to be sufficient at providing an accurate index of vole abundance (Redpath *et al.* 1995). Previous monitoring at Langholm Moor suggests that vole abundance cycles over a three – four year period (Redpath & Thirgood 1999; Chapter 3). Traps were checked each day and captures of small mammals recorded. Field voles *Microtus agrestis* comprised 83% of all small mammals trapped over all years, so the number of voles caught per 100 trap nights was used as an index of vole abundance at each of the twelve trap lines.

The availability of voles to foraging raptors is dependent on both vole abundance and habitat structure, the latter of which affects the ease with which raptors can capture voles (Preston 1990). Vole availability in each of the twelve raptor foraging blocks was calculated following the approach of Preston (1990) as:

$$Vole\ availability = Mean\ vole\ abundance \times \frac{1}{Mean\ vegetation\ height}$$

Mean vole abundance of each of the twelve raptor foraging blocks in each year was assigned using trapping data from the nearest trap line, which were all either within or less than 500 metres from each block. Mean vegetation heights of the twelve raptor observation blocks were calculated using data from surveys in each block conducted during April 2012 using a ‘sward stick’ method (see Calladine *et al.* 2002). At 50 metre intervals along ten 500 metre long transects spaced 100 metres apart, sward height was measured to the nearest five centimetres using a gradated cane. This gave a total of 100 points per block for which mean vegetation height could be calculated.

Red grouse were counted in spring and July each year on ten 0.5 km^2 blocks within ten of the raptor observation blocks. Transects 1 km long and spaced 150 metres apart were walked through each block with a pointer dog quartering 100 metres either side of the transect. All grouse flushed by the dog were counted and recorded to calculate densities in each block (Thirgood *et al.* 2000c). Grouse were not counted in the remaining two raptor observation blocks because these contained very low densities of grouse. For the purposes of assessing the influence of grouse densities on buzzard foraging patterns, I assumed these two blocks contained no grouse, which was confirmed by breeding bird surveys in these blocks which recorded no red grouse in each year. This assumption was tested in the analysis by including these two blocks and then by excluding them and noting any differences in model outputs. There were no differences in conclusions drawn from models with or without the data from these two blocks.

Passerines were counted on each of the twelve raptor observation areas using a modified version of the Breeding Bird Survey (BBS) method used by Thirgood, Leckie & Redpath (1995). Two parallel 1 km transects were walked once in April/early May and again in May/early June and the number of passerines detected were recorded. Meadow pipits *Anthus pratensis* were the dominant species on surveys and comprised 71% of the total number of passerines detected on surveys. Therefore, an index of meadow pipit abundance was derived by taking a mean of the total number of meadow pipits counted in the two surveys in each year (Baines *et al.* 2008).

4.3.4 Red grouse mortality

Indices of red grouse mortality were calculated for each of the ten blocks in which red grouse were counted. This was achieved by log-transforming the number of July grouse ÷ spring grouse, termed 'summer change' here, and by log-transforming the number of spring grouse / previous July grouse, termed 'winter change' here. Juvenile grouse in July were excluded when calculating summer change, but included when calculating winter change. I assumed that immigration to, and emigration from, the study site was negligible because the moor was surrounded by largely unsuitable habitat for red grouse. However, movement within the site between count blocks was likely and indices will include these movements (Redpath & Thirgood 1997).

Winter mortality indices were also derived from data obtained by searching for grouse carcasses using a method described in Thirgood *et al.* (1998). Systematic searches were conducted on nine of the 0.5 km^2 blocks used for grouse counts and raptor observations (the remaining three raptor observation blocks contained low grouse densities and were not searched). Searches were conducted on each block monthly from October to February. Searching was conducted from transects spaced 50 metres apart in October, acting as a 'clear-up round', and 85 metres apart in all other months. During searches, the ground was searched for red grouse carcasses or signs of kills. Every 100 meters the block was also scanned with binoculars for signs of grouse kills. A carcass was recorded if bones, flesh or numerous primary feathers were found. An area of 25 meters around any remains was searched and all remains collected for analysis and to prevent double counting in subsequent searches. Grouse were assumed to have been predated by raptors from the presence of a plucking mound, plucked feathers, notched sternum, and/or presence of raptor pellets nearby, although it was not possible to assign these carcasses to predation by individual raptor species (Moss *et al.* 2000; Watson *et al.* 2007; Park *et al.* 2008). Mammalian predation was assumed from the presence of bitten feathers, crunched bones or the presence of mammalian scats, although again it was not possible to identify mammal species (Hudson *et al.* 1997; Watson *et al.* 2007). Searches were only conducted when snow cover was minimal. Due to snow cover in 2011/2012, data were only available for five blocks in this year.

4.3.5 Statistical analysis

Statistical analyses aimed to explore: (i) the key factors influencing the foraging distribution of buzzards on Langholm Moor in summer and winter, and their relative influence between years, and (ii) relationships in summer and winter between grouse mortality indices and the foraging distributions of buzzards and all large bird-eating raptors (which included buzzards, hen harriers, peregrines and goshawks).

I explored annual variation in prey abundances to compare with any temporal variation in buzzard foraging. Vole data were expressed as 'voles / 100 trap nights' and so I arcsine transformed the vole data to achieve normality before analysing with one-way ANOVA.

To examine which explanatory variables significantly affected buzzard foraging distribution, I used General Linear Mixed Models (GLMMs) with Poisson errors and log-link functions. To account for pseudoreplication between data points collected from the same areas in successive years, I fitted 'block' as a random factor. The number of buzzards seen during vantage point watches was fitted as the response variable with 'number of scans' fitted as an offset term. 'Year' was fitted as a factor, and densities of grouse and meadow pipits, availability of voles, and the ratio of heather:grass all fitted as covariates. I also tested the effect of grouse on buzzard foraging patterns by excluding the two blocks in which I assumed there to be no grouse and examining for any differences this caused to model outputs and conclusions drawn. I examined how relationships between buzzard foraging and prey and habitat variables differed between years by including interactions between each covariate and year. Separate models were constructed to explore buzzard foraging patterns in summer and winter. Indices of meadow pipit abundance were excluded from winter models because pipits largely vacate the uplands in winter (Thirgood *et al.* 1995b).

To explore the relationships between buzzard foraging patterns and indices of grouse mortality, I fitted Linear Mixed Models (LMMs) with normal error, identity-link functions and 'block' as a random factor. For summer data I fitted the log-transformed summer change in grouse as the response variable, which I weighted by grouse density in spring to account for the effect of small changes at low grouse densities. 'Year' was fitted as a factor, and 'summer buzzard sightings / 100 scans' fitted as a covariate. To explore whether the effect of buzzards varied between years, I included a buzzard × year interaction term. I explored relationships in winter using the same method, exchanging summer for winter grouse change and buzzard sightings. To explore relationships between grouse mortality and indices of the total large raptor community, I constructed separate models substituting the buzzard index with an index of sightings of buzzards, hen harriers, peregrines and goshawks combined. Indices of buzzards and all large raptors were not included in the same models to avoid collinearity of predictor variables.

I also explored relationships in winter by using data from grouse carcass searches. Any grouse carcasses with signs of mammalian predation, mixed signs of mammalian and raptor predation or unknown causes of death (N = 47) were removed from analyses, so that only confirmed grouse carcasses with raptor predation signs were retained. I fitted GLMMs with Poisson errors, log-link functions and 'block' as a random factor. The number of grouse carcasses found on each block in a year was used as the response variable, with 'total length of transects searched' as an offset term. 'Year' was fitted as a factor and the winter buzzard index as a covariate in the first model, and winter total raptor index in a separate model. Interaction terms between raptors and year were fitted to explore if effects varied with year.

Significance of model terms was tested using parameter removal and log-likelihood tests with χ^2 statistics (Whittingham *et al.* 2006). Significant interaction terms were explored by testing the main effect in each year, with the random 'site' factor removed and all other main effects retained. All interaction terms were removed from models before exploring main effects. Overdispersion of models was tested using the 'gof' function in the r-package 'aods3' (Lesnoff & Lancelot 2014), and where necessary accounted for by including an observation-level random effect (OLRE) (Bates *et al.* 2012). The inclusion of an OLRE entails assigning each row in the dataset a unique level of a random effect to model the extra-Poisson variation present in the data (Harrison 2014). Collinearity of predictor variables was checked and values of $r > 0.7$ assumed to be indicative of a common underlying factor (Dormann *et al.* 2013). In all models, no two variables were found to be correlated at $r > 0.45$. Model assumptions were checked using procedures outlined in Crawley (2007) by examining plots of residuals. All analyses were conducted in 'R' version 3.2.0.

4.4 Results

4.4.1 Prey abundances

Prey abundances were compared between years to provide a context for any temporal variation in raptor foraging distribution. Field voles, a key prey for buzzards, varied significantly in density between years over all trap lines ($F_{2,33}$ = 15.49, p < 0.001). Vole abundance crashed in 2013 and peaked in 2014. There were no differences between years in the densities of meadow pipits ($F_{2,33}$ = 0.47, p = 0.63), spring grouse ($F_{2,33}$ = 0.67, p = 0.52) or July grouse ($F_{2,33}$ = 0.93, p = 0.41) (Table 4.1).

Table 4.1. Mean ± *s.e.* (range of data in brackets) of abundances of key buzzard prey groups at Langholm Moor (2012 – 2014). N = 12 in each year for each prey survey. Note that prey densities are presented in different units. Significant variations between years (p < 0.05) highlighted in bold (see text for statistics).

	Voles / 100 trap nights	Meadow pipits / km^2	Spring grouse / 0.5km^2	July grouse / 0.5km^2
2012	**3.6 ± 0.7** **(1.0 – 7.8)**	27.6 ± 3.8 (11.0 – 51.0)	12.9 ± 3.0 (0 – 35.1)	24.4 ± 4.9 (0 – 61.5)
2013	**0.6 ± 0.3** **(0 – 3.1)**	30.4 ± 7.5 (19.0 – 42.5)	13.2 ± 2.3 (0 – 23.4)	34.3 ± 7.3 (0 – 87.8)
2014	**5.5 ± 0.8** **(4.1 – 9.4)**	26.3 ± 10.1 (12.0 – 45.0)	17.0 ± 3.0 (0 – 30.0)	36.6 ± 7.7 (0 – 87.8)

4.4.2 Raptor foraging patterns

During summer, buzzards comprised between 72% and 93% of the mean number of sightings of large-raptors engaged in hunting behaviour on raptor observation blocks, with variation between years (Table 4.2). The index of buzzards was highest in summer 2014, when vole densities were highest, and was 183% higher than the buzzard index in 2013 when vole abundance crashed. The index of hen harriers and peregrines were also greatest in 2014: sightings of hunting hen harriers were 102% higher, and peregrines 39% higher compared to 2013.

Winter vantage points revealed that the mean index of foraging buzzards comprised between 82% and 95% of the mean index of all foraging large-raptors, with variation between years (Table 4.2). The buzzard index was highest during the 2013/14 winter and was more than nine times higher than during the 2012/13 winter. Indices of hen harriers, peregrines and goshawks were all highest during the 2013/14 winter.

Table 4.2. Indices of four raptor species during three summers and three winters on Langholm Moor. Data are mean sightings of raptors engaged in hunting behaviour per 100 scans ± standard errors. Summer observations were conducted on ten blocks in 2012 and twelve sites in 2013 and 2014. Winter observations were conducted on nine blocks in 2011/12 and twelve blocks in 2012/13 and 2013/14.

Summer	2012	2013	2014
Buzzard	7.89 ± 2.02	5.55 ± 2.00	15.69 ± 3.86
Hen harrier	0.26 ± 0.11	1.71 ± 0.70	3.46 ± 0.92
Peregrine	0.36 ± 0.29	0.28 ± 0.25	0.39 ± 0.12
Goshawk	0.00 ± 0.00	0.16 ± 0.09	0.00 ± 0.00
Winter	**2011/12**	**2012/13**	**2013/14**
Buzzards	7.18 ± 2.06	1.01 ± 0.29	9.29 ± 1.41
Hen harrier	0.04 ± 0.03	0.02 ± 0.02	1.57 ± 0.59
Peregrine	0.30 ± 0.20	0.03 ± 0.02	0.38 ± 0.09
Goshawk	0.03 ± 0.03	0.00 ± 0.00	0.07 ± 0.06

4.4.3 Factors affecting buzzard foraging patterns

There was a significant interaction between year and the heather:grass ratio on summer buzzard foraging patterns (GLMM: $\chi^2 = 6.57$, d.f = 2, $p = 0.04$). Sub-setting data by year to explore the effect of the heather:grass ratio in each year showed that buzzards avoided heather-dominated blocks in 2012 (GLMM: $\chi^2 = 4.88$, d.f. = 1, $p = 0.03$) and 2013 (GLMM: $\chi^2 = 12.65$, d.f. = 1, $p < 0.001$), but not in 2014 – the peak vole abundance year, when buzzard foraging was unrelated to the heather:grass ratio ($\chi^2 = 0.81$, d.f. = 1, $p = 0.37$; Table 4.A1). This apparent temporal shift in habitat preference of buzzards during summer was mapped in ArcGIS with kriging analysis to produce density contour maps (Figure 4.1). After removing interaction terms, models revealed significant temporal variation in observations of foraging buzzards (GLMM: $\chi^2 = 8.33$, d.f. = 2, $p = 0.02$; Figure 4.3), which varied in line with annual variations in vole abundance. Densities of grouse in July, meadow pipits, and availability of voles were not related to summer buzzard foraging patterns (Table 4.A1). The absence of a relationship between summer foraging patterns and the spatial distribution of voles was confirmed by exchanging the vole availability index for the index of vole abundance from trapping, which similarly showed no relationship (GLMM: $\chi^2 = 0.002$, d.f. = 1, $p = 0.96$, parameter estimate = -0.003 ± 0.07 *s.e.*, ΔAIC = 2.00). July grouse density was also confirmed to have no effect on buzzard foraging by excluding the two blocks in which I assumed there to be no grouse from models (GLMM: $\chi^2 = 0.35$, d.f. = 1, $p = 0.55$, estimate = -0.004 ± 0.007 *s.e.*, ΔAIC = 1.65).

During winter, there was also a significant interaction between year and the heather:grass ratio (GLMM: $\chi^2 = 7.06$, d.f. = 2, $p = 0.03$). Exploring effects in each year revealed that buzzards avoided heather dominated blocks in 2011/12 (GLMM: $\chi^2 = 12.91$, d.f. = 1, $p < 0.001$) and 2012/13 (GLMM: $\chi^2 = 10.78$, d.f. = 1, $p = 0.001$), but not in 2013/14 – the peak vole abundance year, when buzzard foraging was unrelated to the heather:grass ratio (GLMM: $\chi^2 = 0.81$, d.f. = 1, $p = 0.37$; Table 4.A2; density contour maps shown in Figure 4.2). After removing interaction terms, there was significant temporal variation in observations of foraging buzzards (GLMM: $\chi^2 = 18.88$, d.f. = 2, $p < 0.001$; Figure 4.4), which again varied in line with annual variations in vole abundance. There was also a modest positive relationship between the number of buzzards seen hunting and spring grouse density (GLMM: $\chi^2 = 4.83$, d.f. = 1, $p = 0.03$, parameter estimate = 0.05

± 0.02; Figure 4.5); which held when the two blocks in which I assumed there to be no grouse were excluded from models (GLMM: χ^2 = 4.07, d.f. = 1, *p* = 0.04, parameter estimate = 0.06 ± 0.03 *s.e.*, ΔAIC = 2.07). Spatial variation in vole availability had no significant effect on buzzard winter foraging patterns (Table 4.A2), and similar to summer models, vole abundance from trapping was also not significantly related to buzzard foraging patterns in winter (GLMM: χ^2 = 1.59, d.f. = 1, *p* = 0.21, estimate = 0.08 ± 0.06 *s.e.*, ΔAIC = 0.39).

4.4.4 Relationships between raptor foraging and indices of grouse mortality

Summer change in grouse numbers were not significantly related to the index of buzzards, or to the index of all large raptors and did not vary between years. Summer change in grouse numbers were negatively related to spring grouse density (GLMM: χ^2 = 12.04, d.f. = 1, *p* = 0.001) (Table 4.A3). Winter change in grouse numbers were not significantly related to the index of buzzards, or to the index of all large-raptors and did not vary between years. Winter change in grouse was significantly negatively related to grouse density in the previous July (χ^2 = 11.73, d.f. =1, *p* = 0.001) (Table 4.A4). No interaction terms in either the summer or the winter models were significant.

During the same three winters, systematic searches yielded 162 red grouse carcasses. Of these, 115 (71.0%) were attributed to predation by raptors (Figure 4.6). Signs of mammalian predation were found on 18 (11.1%) grouse carcasses, and mixed mammal / raptor signs were also found on 18 (11.1%) of carcasses. It was not possible to reliably distinguish between predation by different species of raptors or mammals (Thirgood *et al.* 1998). We could not reliably assign a cause of death for ten grouse carcasses (6.2%) and one carcass was attributed to a fence collision (0.6%). The mean number of raptor attributed grouse kills found per km of transect searched was 2.45 ± 0.67 in 2011/12; 2.11 ± 0.38 in 2012/13; and 3.32 ± 0.39 in 2013/14. This number of grouse carcasses did not vary between years, nor with variations in buzzard, large-raptor, or grouse density indices (Table 4.A5). There was no correlation between the two indices of winter grouse losses (from count data and from carcass searches) (r = 0.05, n = 23, p = 0.84) (Figure 4.A1).

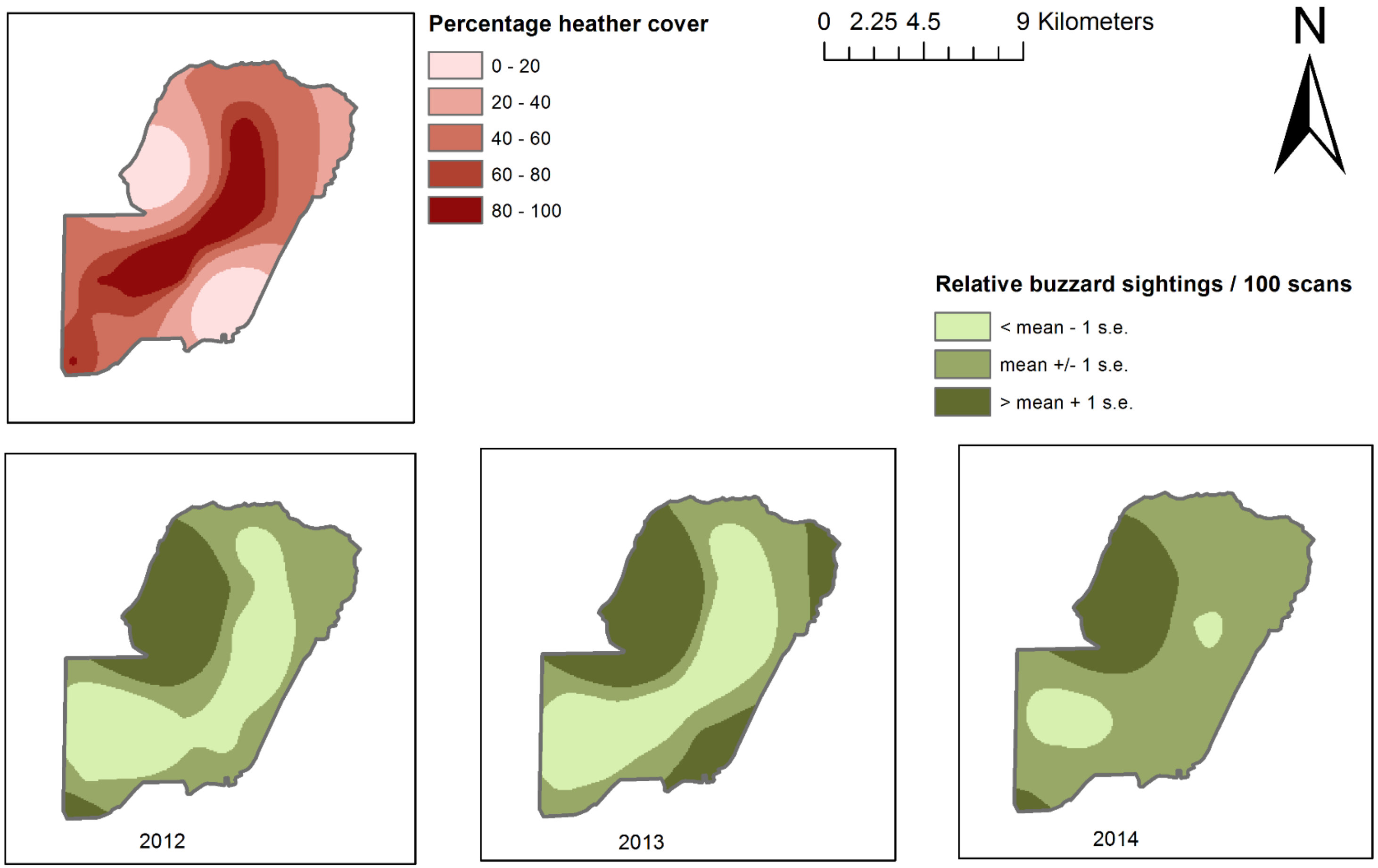

Figure 4.1. Relationship between buzzard foraging patterns in three summers (2012 - 2014) and the distribution of heather dominated vegetation at Langholm Moor.

Distribution of heather dominated vegetation at Langholm Moor from Land Cover Map 2007 data (top).

Relative densities of foraging buzzards in three summers (bottom). Pale shading indicates areas where buzzard sightings were fewer than 1 standard error below the mean for each year, dark shading indicates areas where buzzard sightings were greater than 1 standard error above the mean for each year.

Models indicated that buzzards significantly avoided hunting in the heather dominated areas in 2012 and 2013 when vole abundances were low,
but that there was no significant avoidance of heather in 2014 when vole abundance peaked.

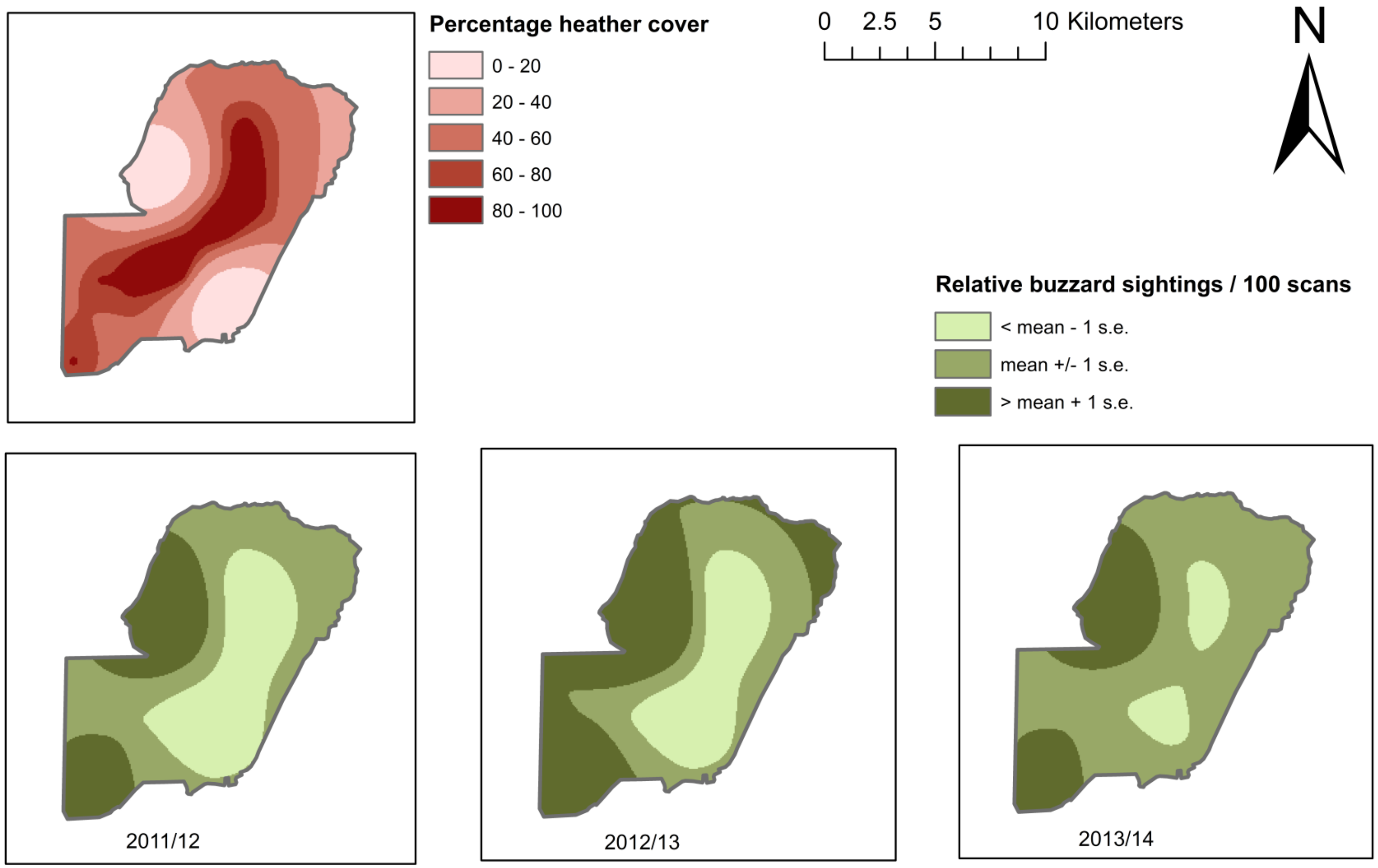

Figure 4.2. Relationship between buzzard foraging patterns in three winters (2011/12 - 2013/14) and the distribution of heather dominated vegetation at Langholm Moor.

Distribution of heather dominated vegetation at Langholm Moor from Land Cover Map 2007 data (top).

Relative densities of foraging buzzards in three winters (bottom). Pale shading indicates areas where buzzard sightings were fewer than 1 standard error below the mean for each year, dark shading indicates areas where buzzard sightings were greater than 1 standard error above the mean for each year.

Models indicated that buzzards significantly avoided hunting in the heather dominated areas in 2011/12 and 2012/13 when vole abundances were low, but that there was no significant avoidance of heather in 2013/14 when vole abundance peaked.

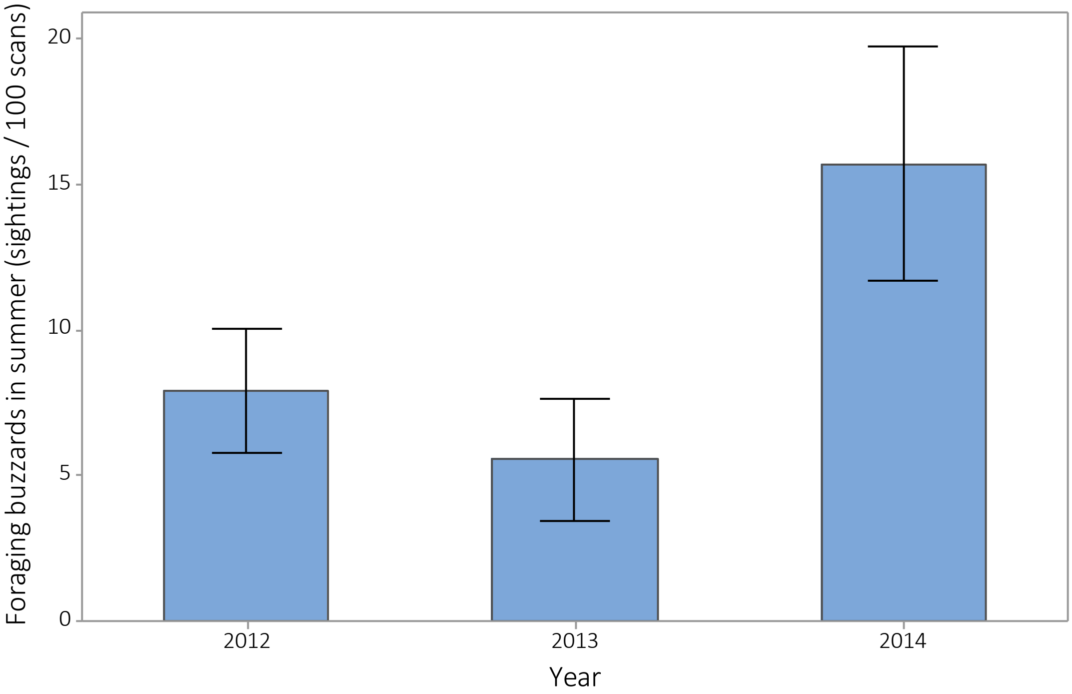

Figure 4.3. Mean (± 1 *s.e.*) index of foraging buzzards during three summers on Langholm Moor. Models indicated that the index of foraging buzzards varied significantly between summers. During the study, 2014 was a peak year in the vole abundance cycle, and 2013 was a crash year.

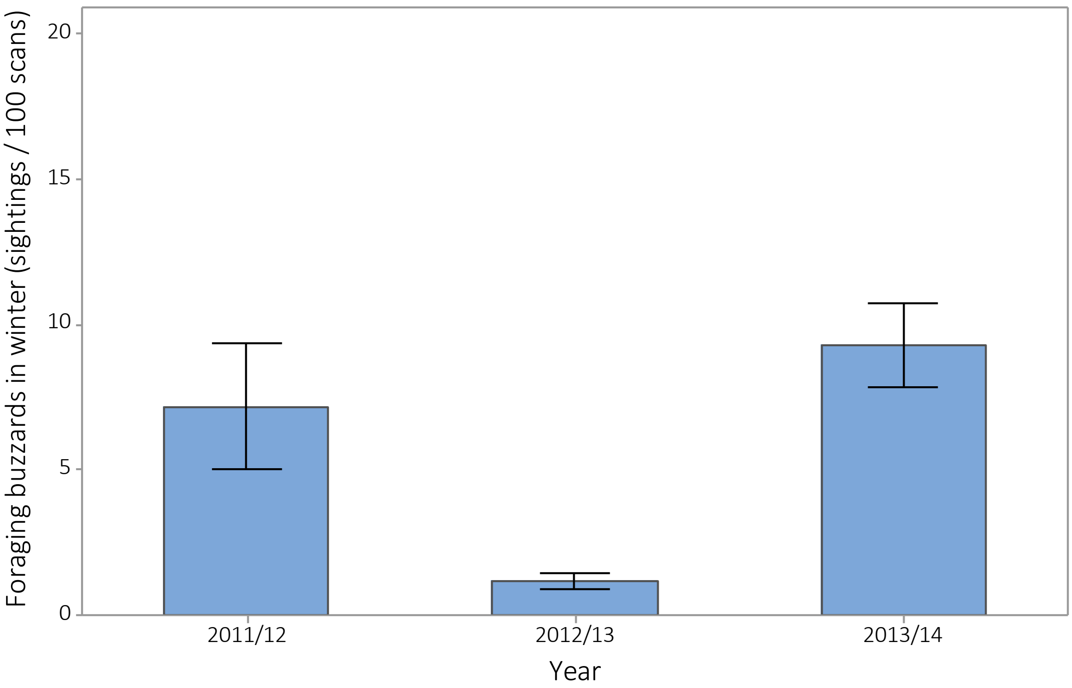

Figure 4.4. Mean (± 1 *s.e.*) index of foraging buzzards during three winters on Langholm Moor. Models indicated that the index of foraging buzzards varied significantly between winters. 2013/14 was a peak year in the vole abundance cycle, and 2012/13 was a crash year.

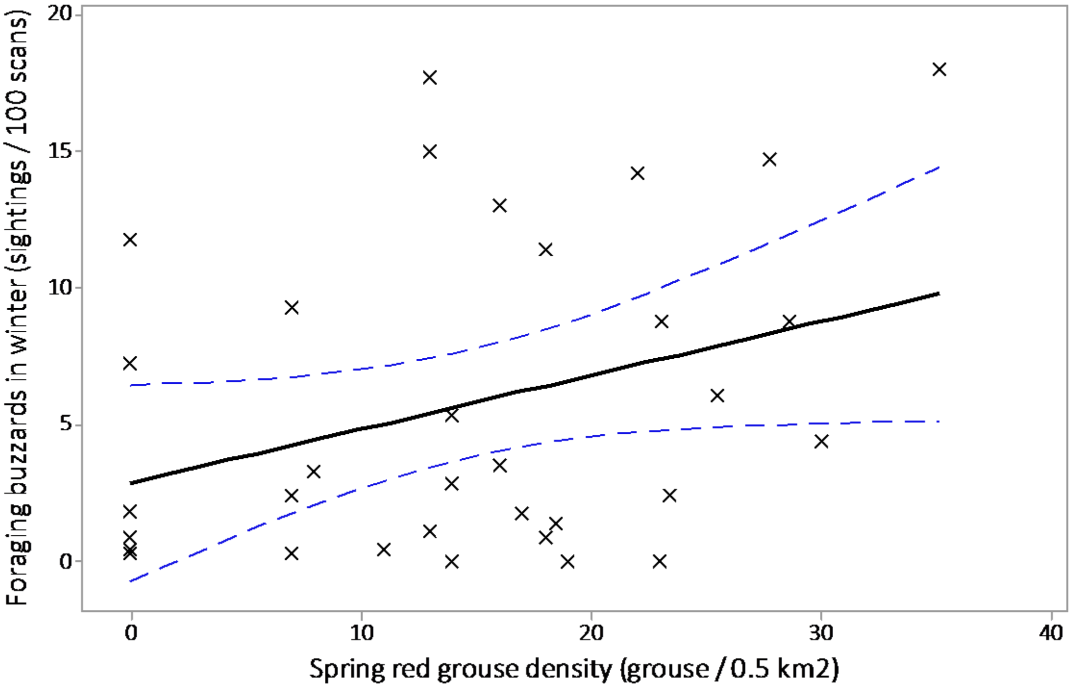

Figure 4.5. Foraging index of buzzards in relation to red grouse density on 33 blocks (2011/12: 9, 2012/13: 12, 2013/14: 12) in three winters on Langholm Moor. Line shows regression fit, with dashed lines showing 95% confidence intervals. Models indicated that, during the winter, buzzards were significantly more likely to hunt in blocks with a higher red grouse density from counts in the following March.

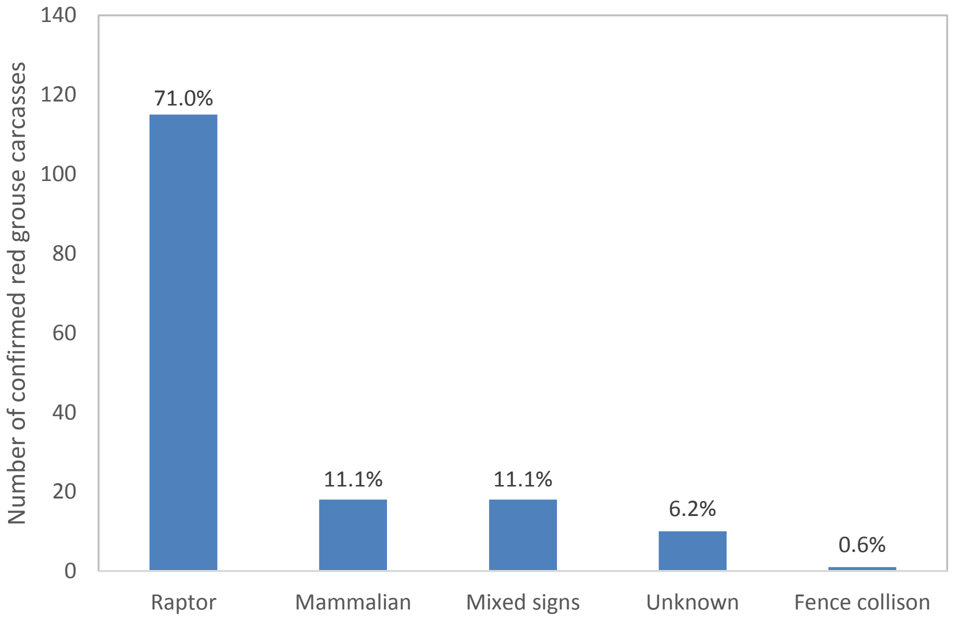

Figure 4.6. Proximate causes of mortality of 162 red grouse found dead over three winters during systematic carcass searches on 0.5km^2 blocks (2011/12: n = 5; 2012/13 & 2013/14: n=9).

4.5 Discussion

Results demonstrated an aggregative numerical response of common buzzards whereby foraging intensity varied between years in line with vole abundance. Voles are an important prey group for buzzards (Swann & Etheridge 1995; Graham *et al.* 1995; Reif & Tornberg 2006), although a recent study at Langholm Moor found no temporal variation in buzzard breeding density or success in relation to variations in vole abundance (Chapter 3). Observations of foraging buzzards in summer included both breeding and non-breeding individuals. Therefore, the response demonstrated here could be due to either more non-breeders attracted onto Langholm Moor, or via breeders spending longer hunting observation areas. Aggregative responses can occur via both mechanisms (Smout *et al.* 2010; Mckinnon *et al.* 2013), although disentangling the two would require breeders to be recognisable from non-breeders, and this was not possible in this study.

Previous studies of *Buteo* species have shown foraging intensity to be greater in areas where vole abundance and availability are higher (Baker & Brooks 1981; Preston 1990). In this study, I found that foraging patterns were not significantly influenced by the spatial variation in vole availability, and this was confirmed by looking for an effect of vole abundance in place of the availability index. However, it should be noted that the inclusion of the heather:grass ratio variable is likely to be at least partially accounting for spatial variation in voles, since voles are both more abundant and more available to be caught in grassier habitat (Thirgood *et al.* 2003; Wheeler 2008). Therefore, I can conclude that by controlling for relative availability due to variation in habitat composition, there was no additional effect of vole abundance or availability as measured in this study. This lack of any relationship above that included in the habitat variable could be explained by the scale at which I assessed buzzard foraging (on observation blocks) being too coarse to detect spatial responses of buzzards to variation in vole availability, which may occur at scales of 1 ha or less (Thirgood *et al.* 2003).

I observed that buzzards hunted in areas with higher red grouse abundance in the winter. Buzzards are opportunistic, generalist predators with a wide dietary breadth (Graham *et al.* 1995; Rooney & Montgomery 2013; Tubbs 1974; Chapter 3). However, many prey groups important to buzzards vacate the uplands of northern Britain in winter, or become relatively less available (Thirgood *et al.* 1995b). Therefore, it could be that grouse increase in importance to buzzards during the winter period as other prey resources become scarce.

Understanding the relative habitat preferences of predators is an important aspect of managing populations of both predators and their prey (Morrison *et al.* 2012). However, only a minority of previous studies have considered how habitat preferences can vary between years (Lõhmus 2003). Buzzards at Langholm Moor have previously been shown to have a tendency to avoid areas with more heather cover (Thirgood *et al.* 2003). Here I found that in both summer and winter periods, buzzards avoided areas with more heather cover during years of low and intermediate vole abundance, but showed no significant habitat preference during the peak vole year. This may reflect a functional response by buzzards as they hunt for alternative prey away from the heather moorland in years when vole abundance on the moor is low (Chapter 3). Rabbits, moles, corvids and pigeons are all important alternative prey for buzzards (Graham *et al.* 1995; Rooney & Montgomery 2013) and occur at greater densities in farmland habitats (Glue 1967; Swann & Etheridge 1995) which are separated from the heather moorland on Langholm Moor (Redpath & Thirgood 1997). During years of low vole abundance, the heather – grass mosaic at Langholm Moor is likely to be a relatively less profitable habitat for buzzards to hunt compared to years of peak vole abundance (Wheeler 2008). This may result in buzzards avoiding heather moorland in years when vole abundances are low. This observation has potential implications for the management of red grouse. In systems involving mobile, generalist raptors and heterogeneous habitats that support numerous prey resources, such as Langholm Moor, the manner in which raptors respond to variations in prey can influence predation rates on all prey (Preston 1990; Mckinnon *et al.* 2013). Buzzards are known to predate red grouse alongside their preferred prey (Graham *et al.* 1995), and recent evidence from Langholm Moor suggests that red grouse are an incidental prey resource for buzzards which may increase in importance in when vole abundance is high (Chapter 3). Evidence from the current study supports this by showing that buzzard foraging intensity was higher in the heather dominated grouse habitats when vole abundances were high. It seems that incidental predation of red grouse by buzzards hunting for voles could increase in years of high vole abundance.

As noted above, aggregative responses can occur when breeding individuals spend longer hunting in particular areas, and/or when more non-breeders are attracted to given areas (Smout *et al.* 2010; Mckinnon *et al.* 2013). In this study, I was unable to distinguish between breeding and non-breeding buzzards, and so understanding the relative effects of each was not possible. Thirgood *et al.* (2003) were able to conclude that responses by hen harriers were due to the habits of breeding individuals because very few non-breeding individuals were seen during their study. However, this would not be the case for buzzards (Kenward *et al.* 2000) in this study, and unlike Thirgood *et al.* (2003), the duration of buzzard hunting activity was not recorded and so cannot be compared to breeding pair density to infer responses by breeding status. A more focussed study whereby breeding individuals are recognisable from non-breeding individuals (e.g. by applying markings such as wing tags to all breeding individuals), or by conducting focussed watches of individuals and timing the duration of their hunting, could both begin to disentangle these processes.

The most scientifically rigorous approach to studying predator impact is by means of predator removal experiments (Newton 1998). However, when predator removal is impractical or unacceptable due to conservation status or protection, correlative approaches can provide useful circumstantial evidence of the impact of predation, although causal relationships and the mechanism behind any impact cannot be reliably derived (Redpath & Thirgood 1997; Park *et al.* 2008). In this study, I explored spatial correlations between indices of foraging raptors and indices of red grouse mortality. I found no evidence that change in grouse numbers, over both summer and winter, were significantly related to indices of either buzzards or all large-raptors seen foraging in the grouse count blocks. One possible reason for this is that the grouse mortality index includes movement of grouse between grouse count blocks, which may have been considerable. Indeed, I found that grouse numbers tended to decline most where the original grouse densities were highest. This may be indicative of emigration from the most densely populated blocks into the more sparsely populated ones. Quantifying these movements would require further intensive study of the red grouse at Langholm Moor through monitoring movements using radio-collars (Redpath & Thirgood 1997). Correlative analysis was also unable to control for confounding factors which may have influenced levels of grouse mortality and movement between blocks. Besides the presence of foraging raptors, micro-habitat conditions and changes, as well as disease may all have been having a large and unmeasured influence on results (Hudson *et al.* 1992; Whittingham & Evans 2004; Park *et al.* 2008).

Systematic searches for grouse carcasses revealed that raptor predation was the most important proximate cause of grouse mortality across all three winters. This was also found during the Joint Raptor Study (JRS) over four winters (Redpath & Thirgood 1997; Thirgood *et al.* 1998). In fact, my estimates of raptors being responsible for 71% of the grouse found dead overwinter is very similar to the 70% found during the JRS. Although, it should be noted that the chief mammalian predators of red grouse (fox and mustelids) were controlled on Langholm Moor during both this study and the JRS. I found no evidence that the number of grouse carcasses found during systematic searches varied temporally, or with indices of foraging raptors or grouse density. Interestingly, there was no correlation between the two indices of winter mortality from counts and from carcass searches. There are a number of possible explanations for this. The first could be that the count data were greatly affected by immigration between count areas as discussed above. In fact, the lack of correlation between winter indices suggests that the summer index (which came from count data only) is likely to have been affected by immigration. There is also the possibility that the carcass search data are subject to their own biases. Although I removed grouse carcasses with signs of mammalian or unknown causes of death before analysis, I cannot be sure that all carcasses assigned to raptor predation were in fact killed by raptors, and this may have affected results. Buzzards are known to scavenge carcasses (Tubbs 1974) and signs left on dead grouse by scavenging buzzards may have been wrongly assigned to the 'raptor predated' category (Kenward *et al.* 2001). It is also unlikely that all carcasses of deceased grouse were found. Mammalian predators may bury prey whilst raptors may carry prey away (Watson *et al.* 2007). The occurrence rates of these processes and their relative effects on results are currently unknown.

Improving our understanding of the raptor-grouse system will require making several improvements to the accuracy of the current study. Firstly, my finding that habitat preferences varied between years should be tested over multiple years and prey abundance cycles to explore the existence of any response found here as well as its underlying mechanism (Salamolard *et al.* 2000; Reif *et al.* 2004). Secondly, I did not consider the effect of inter-specific competition from other raptors on foraging patterns of buzzards. However, since larger species such as golden eagles *Aquila chrysaetos* were absent from Langholm Moor during this study, and other raptors are less likely to affect buzzard foraging habits (Thirgood *et al.* 2003), this omission is unlikely to have affected results to any great extent. Finally, it is important to remember that this study was only conducted in one area of upland moorland, which may not be typical of moorland systems elsewhere (Redpath & Thirgood 1997). The heather-grass mosaic at Langholm Moor is likely to favour high vole densities (Redpath & Thirgood 1997; Wheeler 2008), which may influence the response documented here. Improving our understanding of the responses demonstrated here and their possible impact on red grouse will rely on further study at other sites with different habitat compositions and prey resources.

In conclusion, I found that the foraging distribution of buzzards varied temporally in line with vole abundance. The spatial distribution of red grouse did not significantly affect buzzard foraging in summer, but buzzards hunted where there were more grouse in winter, possibly as grouse became a more important food resource at this time of year. Buzzards avoided heather dominated habitats when vole abundances were low or intermediate, but showed no such avoidance when vole abundances were high. This could potentially increase incidental predation of red grouse by buzzards hunting for voles. I found no evidence that grouse losses were related to indices of raptors in winter and summer. Disentangling the impact of buzzards from other raptors and other causes of grouse mortality will require further data collection on diet and foraging habits of all raptors and the movements and causes of mortality of grouse, or most accurately by experimental study with sufficient replication and control of confounding factors (Newton 1998). Whilst a correlative study such as this cannot prove causation, I have demonstrated some important responses by buzzards, most likely due to fluctuations in their main vole prey, which could influence incidental predation of red grouse by buzzards. These observations could provide a useful framework for further study of buzzard impact on economically important or threatened prey.

4.6 Appendix

Table 4.A1. Factors affecting the foraging distribution of buzzards in summer over three years on Langholm Moor. Effects of July grouse density, meadow pipit density, vole density and habitat composition were tested across three years, or in separate years when there was a significant interaction with year. Main effects were tested with interaction terms excluded. Parameter estimates are taken from a full model. Models were GLMMs with Poisson errors, log-link functions and survey area as random effect. Chi-square statistics, *p*-values ΔAIC values are derived from comparisons between the full model and a reduced model with the parameter removed. Significant values at $p < 0.05$ are shown in bold.

	Summer buzzards								
	Interaction with year				Parameter estimate				
	X^2_2	*p*	ΔAIC		Slope + SE	X^2	*d.f.*	*p*	ΔAIC
Year	-	-	-		-	**8.33**	**2**	**0.02**	**4.33**
July grouse density	2.40	0.30	1.60		0.007 ± 0.007	0.10	1	0.32	1.00
Meadow pipits	0.37	0.83	3.63		0.004 ± 0.01	0.14	1	0.70	1.86
Vole availability	1.76	0.42	2.24		0.91 ± 1.68	0.29	1	0.59	1.71
Heather:Grass	**6.57**	**0.04**	**2.57**	2012	-0.14 ± 0.05	**4.88**	**1**	**0.03**	**2.88**
				2013	-0.25 ± 0.06	**12.65**	**1**	**<0.001**	**10.65**
				2014	-0.01 ± 0.11	0.81	1	0.37	1.19

Table 4.A2. Factors affecting the foraging distribution of buzzards in winter over three years on Langholm Moor. Effects of spring grouse density, vole density and habitat composition were tested across three years, or in separate years when there was a significant interaction with year. Main effects were tested with interaction terms excluded. Parameter estimates are taken from a full model. Models were GLMMs with Poisson errors, log-link functions and survey area as random effect. Chi-square statistics, *p*-values ΔAIC values are derived from comparisons between the full model and a reduced model with the parameter removed. Significant values at $p < 0.05$ are shown in bold.

				Winter buzzards					
	Interaction with year				Parameter estimate				
	X^2_2	*p*	ΔAIC		Slope ± SE	X^2	*d.f.*	*p*	ΔAIC
Year	-	-	-		-	**18.88**	**2**	**<0.001**	**14.88**
Spring grouse density	1.74	0.42	2.26		0.05 ± 0.02	**4.83**	**1**	**0.03**	**2.83**
Vole availability	2.20	0.33	1.80		1.63 ± 1.98	0.65	1	0.42	1.35
Heather:Grass	**7.06**	**0.03**	**3.06**	2011/12	-0.53 ± 0.11	**12.91**	**1**	**<0.001**	**10.91**
				2012/13	-0.25 ± 0.07	**10.78**	**1**	**0.001**	**8.78**
				2013/14	0.05 ± 0.05	0.81	1	0.37	1.19

Table 4.A3. Relationships between the index of change in red grouse numbers over summer and summer indices of buzzards, raptors and red grouse density in spring. Effects were tested across three years, or in separate years when there was a significant interaction with year. Main effects were tested with interaction terms excluded. Indices of buzzards and all raptors were tested in separate models. Parameter estimates are taken from a full model. Models were LMMs with normal errors, identity-link functions and survey area as random effect. Chi-square statistics, *p*-values ΔAIC values are derived from comparisons between the full model and a reduced model with the parameter removed. Significant values at $p < 0.05$ are shown in bold.

	Summer grouse change							
	Interaction with year			Parameter estimate				
	X^2_2	*p*	ΔAIC	Slope + SE	X^2	*d.f.*	*p*	ΔAIC
Year	-	-		-	2.04	2	0.36	1.96
Summer buzzard index	3.18	0.20	0.82	-0.13 ± 0.18	2.37	1	0.12	0.37
Summer raptor index	4.03	0.13	0.03	-0.08 ± 0.01	2.04	1	0.15	0.04
Spring grouse density	1.48	0.48	2.52	-0.81 ± 0.23	**12.04**	**1**	**0.001**	**10.04**

Table 4.A4. Relationships between the index of change in red grouse numbers over winter and winter indices of buzzards, total raptors and red grouse density in July. Effects were tested across three years, or in separate years when there was a significant interaction with year. Main effects were tested with interaction terms excluded. Indices of buzzards and all raptors were tested in separate models. Parameter estimates are taken from a full model. Models were LMMs with normal errors, identity-link functions and survey area as random effect. Chi-square statistics, *p*-values ΔAIC values are derived from comparisons between the full model and a reduced model with the parameter removed. Significant values at $p < 0.05$ are shown in bold.

	Winter grouse change							
	Interaction with year			Parameter estimate				
	X^2_2	*p*	ΔAIC	Slope + SE	X^2	*d.f.*	*p*	ΔAIC
Year	-	-	-	-	0.40	2	0.82	3.60
Winter buzzard index	3.37	0.19	0.63	0.01 ± 0.02	1.33	1	0.25	0.67
Winter raptor index	3.59	0.16	0.06	0.007 + 0.02	1.17	1	0.28	0.83
July grouse density	0.46	0.80	3.54	-0.02 + 0.004	**11.73**	**1**	**0.001**	**9.73**

Table 4.A5. Relationships between the index of red grouse carcasses found during searches in three years and indices of buzzards, total raptors and red grouse density in July. Effects were tested across three years, or in separate years when there was a significant interaction with year. Main effects were tested with interaction terms excluded. Indices of buzzards and all raptors were tested in separate models. Parameter estimates are taken from a full model. Models were GLMMs with Poisson errors, log-link functions and survey area as random effect. Chi-square statistics, *p*-values ΔAIC values are derived from comparisons between the full model and a reduced model with the parameter removed.

	Carcass searches							
	Interaction with year			Parameter estimate				
	X^2_2	*p*	ΔAIC	Slope + SE	X^2	*d.f.*	*p*	ΔAIC
Year	-	-	-	-	1.41	2	0.49	2.59
Winter buzzard index	1.49	0.47	2.50	0.04 ± 0.02	2.76	1	0.10	0.76
Winter raptor index	3.39	0.18	0.60	0.03 ± 0.02	2.03	1	0.15	0.03
July grouse density	2.61	0.27	0.52	0.002 ± 0.007	0.06	1	0.80	1.94

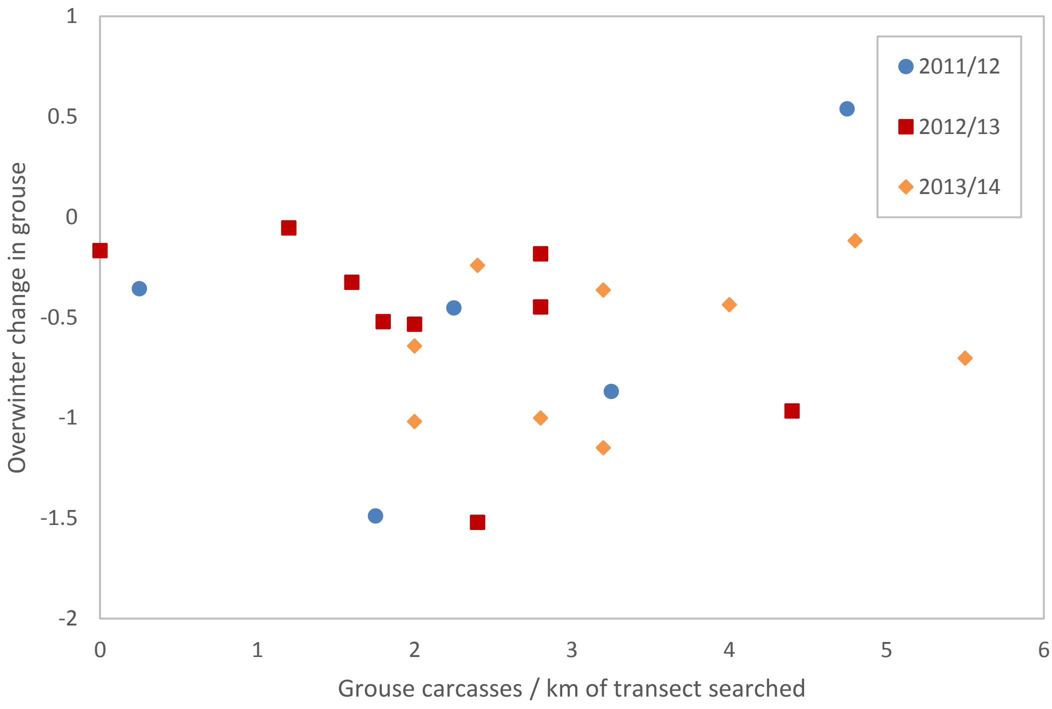

Figure 4.A1. Relationship between the index of overwinter change in grouse (log spring grouse ÷ previous July grouse) and the index of grouse carcasses found during systematic searches. Across all years, there was no correlation between the two indices (r = 0.05, n = 23, p = 0.84).

Chapter 5. Winter diet and home ranges of common buzzards on Langholm Moor: factors influencing predation on red grouse

5.1 Abstract

Investigating the impact of raptors on gamebirds depends on having objective and current information about raptor dietary composition. Raptor diet can vary between seasons, yet relatively few studies have assessed the diet of raptors during the winter, especially in relation to predation of gamebirds. In this study, I demonstrate the use of remote tracking techniques (satellite and radio tags) to locate roost sites of buzzards *Buteo buteo* wintering on an area of heather moorland managed for red grouse *Lagopus lagopus scotica*. Regurgitated pellets were collected from these roost sites and analysed to obtain information on buzzard diet composition during one winter. Buzzard diet was dominated numerically by small mammals which were identified in 88% of pellets and comprised 67% of all prey items, while lagomorphs were most important in terms of total biomass of all prey. After applying correction factors to account for underestimation in pellet analysis, red grouse were estimated to appear in 6% of pellets, form 1% of all prey and constitute 7% of buzzard diet by biomass. Radio and satellite tags also provided home range sizes to inform analysis of the factors leading to variations in the proportion of red grouse remains in buzzard pellets. The proportion of grassland habitat surrounding each roost site was found to be the most important factor influencing the presence of red grouse in buzzard pellets. Buzzards consumed fewer red grouse when roosting in areas with more grassland presumably because grassland habitats contained higher densities of preferred small mammal and lagomorph prey. The amount of heather moorland around roost sites, which was not correlated to the amount of grassland, was not a significant predictor of presence of red grouse in buzzard pellets. I suggest that this shows a spatial response of buzzards to the availability of alternative (non-grouse) prey which may reduce predation of red grouse. Maintenance of grassland habitats rich in alternative, non-grouse prey that are spatially separated from red grouse habitats may reduce predation of grouse by buzzards, although longer-term data are needed to validate results.

5.2 Introduction

The impact of raptors on gamebirds is a contentious and topical issue (Thirgood *et al.* 2000b). Obtaining current information on the extent of raptor predation on gamebirds is required to improve management of all organisms involved (Kenward *et al.* 2001). The common buzzard *Buteo buteo* (hereafter 'buzzard') has undergone an 81% increase in range in Britain over the last 40 years (Balmer *et al.* 2014) and is the most abundant diurnal raptor in Britain (Clements 2002) with a recent population estimate of 56-77,000 breeding pairs (Musgrove *et al.* 2013). In some cases, this population increase and range expansion has reignited conflict with game managers and shooting interests (Lees *et al.* 2013; Parrott 2015). The impact of hen harrier *Circus cyaneus* and peregrine *Falco peregrinus* predation on red grouse *Lagopus lagopus scotica* has been well studied (Redpath & Thirgood 1997). However, the impact of buzzard predation has been less well studied, which is pertinent considering expanding buzzard populations and the associated increase in concern about potential impact.

Assessment of raptor diet is an important component of many studies investigating impact on gamebirds (Redpath *et al.* 2001a; Amar *et al.* 2004; Park *et al.* 2008). To date, the majority of raptor diet studies have been conducted during the raptor breeding season, partly owing to the ease at which data can be collected from nests where activity is centred (Lewis *et al.* 2004). However, diet composition of predatory birds varies between seasons (Marquiss & Booth 1986; Mañosa & Cordero 1992; Amar *et al.* 2003) and impact from raptors on gamebirds can occur year round (Redpath & Thirgood 1999). Assessing raptor diet during the winter is therefore necessary when investigating the impact of predation on gamebirds.

The reduced territorial behaviour and lack of a conspicuous nest outside the breeding season presents a problem for researchers interested in raptor diet during the winter. The winter diet of raptors has been studied by conducting concentrated searches for carcasses to obtain predation rates (e.g. Eng & Gullion 1962; Watson *et al.* 2007); analysing stomach contents (e.g. Mañosa & Cordero 1992); and by intensive radio-tracking combined with searches for evidence of predation events (Kenward *et al.* 1981a, 2001; Widén 1987; Tornberg & Colpaert 2001). The collection and analysis of regurgitated pellets provides an efficient and frequently used method of obtaining data on raptor diet in the breeding season (Redpath *et al.* 2001a; Rexer-Huber & Bildstein 2012; Rooney & Montgomery 2013). However, locating roost sites to collect pellets outside the breeding season can be challenging unless roost sites are obvious, which is why this method has been most successful for communally roosting species (Marquiss & Booth 1986; Clarke *et al.* 2008; Rexer-Huber & Bildstein 2012).

Recent advancements in the technology of satellite- and radio-telemetry equipment have widened the scope of raptor biology studies. Remote tracking of raptors has been employed to investigate ecological processes such as dispersal, breeding rates, dietary composition, migration and mortality (Kenward *et al.* 2001; Walls *et al.* 2005; Rutz *et al.* 2006; Penteriani *et al.* 2013; Hays 2014; Klaassen *et al.* 2014; Limiñana *et al.* 2014). Remote tracking can also be used to investigate avian home range size (Haworth *et al.* 2006; Soanes *et al.* 2013) which can be important for assessments of population density, resource use and foraging patterns (Anderson 1982). However, its use as a method of locating winter roost sites of raptors to collect regurgitated pellets has not been tested in Britain before.

In this study I employed remote tracking technology, supplemented with observations, to locate roost sites of buzzards wintering on and around an area of upland heather moorland managed for red grouse. The aim was to recover regurgitated pellets from these roost sites which could be analysed for dietary composition of buzzards in winter. In particular, I was interested in exploring the factors influencing the presence of red grouse in the diet of wintering buzzards.

5.3 Methods

5.3.1 Study site

The study was carried out at Langholm Moor (55.1 – 55.3°N, 3.0 – 2.8°W) in south-west Scotland on land owned by Buccleuch Estates. The study site encompasses 221 km^2 of the Dumfries and Galloway and Scottish Borders regions, which includes 76 km^2 designated as the Langholm – Newcastleton SSSI and SPA. The study site was chosen to include the 114 km^2 of land managed under the Langholm Moor Demonstration Project (LMDP) plus a 2 km buffer zone (Fig. 5.1). The 2 km buffer zone was chosen in an attempt to include roost sites of buzzards likely to hunt on the LMDP site using estimates of buzzard home ranges at Langholm (Graham, Redpath & Thirgood 1995; Chapter 3). Moorland management, including predator control and heather management, is undertaken by a team of five gamekeepers for the benefit of red grouse within the LMDP area (for more information on the study site see Chapter 1 section 1.5.1).

5.3.2 Buzzard tagging and roost sites

As part of the management for red grouse on Langholm moor, live-catching crow-cage traps (a.k.a. ladder-traps) are operated for the control of carrion crows *Corvus corone*. Traps usually contained carcasses of pheasants *Phasianus colchicus* as bait for crows. Between October 2013 and January 2014, nine buzzards entered these traps as non-target species. Five of these were fitted with satellite (GPS) tags (model: Ecotone SAKER-4 GPS/GSM): three immature two/three year olds (two males and one female); and two juveniles (one male and one female). The other four were fitted with radio (VHF) tags (model: Biotrack TW-3 2/3AA): three immature females and one juvenile male. Buzzards were trapped and released the same day. Traps were checked at least three times a day by field workers and gamekeepers.

Data from tags were collected after a period of at least 4 days which allowed tagged individuals to resume normal behaviour (Kenward 2001). Data from GPS tags were sent via the GSM (mobile telecommunication) network to an online server before downloading. The recording schedule of GPS tags was set to record locations four times per day, although no data were sent during days when low light levels reaching the solar charging panel caused the batteries to drop below operating voltage. Data from VHF tags were obtained by triangulation using a three-element hand-held Yagi antenna. Three bearings were taken from within 1 – 2 km of the tagged individual, and positions were plotted on a map to an accuracy of ca. 100m. Any positions with an error greater than 100m (n = 9, 5.7% of all positions) were excluded from analysis (Kenward 2001). When an intermittent signal from VHF tags indicative of flight was received, an attempt to observe the buzzard was made and this position at time of first observation recorded. Three to four positions per VHF-tagged individual were obtained each week during calm weather to facilitate triangulation. A minimum of 30 positions were collected throughout the study period for each VHF tagged individual: a minimum for calculating standard home ranges (Kenward 2001). To reduce the risk of autocorrelation of positions, no two positions were obtained within three hours of each other for either GPS or VHF tags. Roost sites of the nine tagged individuals were located from locations of GPS tags and by triangulation of VHF tags at dawn and dusk. Repeated fixes obtained at three to five day intervals confirmed the continued usage of roost sites by tagged buzzards.

Initial locations of GPS and VHF tagged individuals suggested that buzzards roosted each night on coniferous plantation edges and in gullies containing deciduous trees. To increase the sample of roost sites, vantage point watches were conducted at dawn and dusk overlooking apparently suitable sites, and at locations where incidental sightings of buzzards had been made. In this way, an additional 14 roost sites were found within the study site, bringing the total number of roost sites used in this study to 23 (Figure 5.1). The continued usage of roost sites by buzzards was confirmed at least weekly by direct observations of a buzzard at the roost site.

5.3.3 Pellet collection and analysis

Roost sites identified by tracking tagged individuals were searched for signs of regular use. Active roosts were identified from the presence of faecal droppings, freshly moulted feathers and down, and fresh pellets (Hardey *et al.* 2009). Roosts were searched fortnightly and all pellets were recovered between October 2013 and March

2014. Any pellets found under trees at which a buzzard had not been seen were not collected since they may have been produced by other *Accipitriformes* or *Strigiformes* roosting close by.

Pellets were frozen and dried prior to dissection and analysis. Remains were identified to the lowest possible taxonomic level. Mammal hairs and bones were identified using Teerink (1991) and Yalden & Morris (2009). Feathers and feather fragments were identified using Brown *et al.* (2003) and matched against reference samples. The minimum number of individual prey items present in a pellet was recorded to reduce overestimation.

All prey identified in pellets were assigned to one of the following six prey groups:

- Small mammals (field vole *Microtus agrestis;* common mole *Talpa europaea;* common shrew *Sorex araneus* and unidentified small mammals).
- *Lagomorph spp.* (European rabbit *Oryctolagus cuniculus;* brown hare *Lepus europaeus*. Separation of these two species is reliable only at the microstructural level (Wolfe & Long 1997) so these two species are not distinguished here).
- Invertebrates (beetles *Coleoptera spp.* (largely *Carabidae spp.* and *Scarabidae spp.*)*;* earthworms *Megadrilacea spp.*).
- Pheasant *Phasianus colchicus.*
- Red grouse *Lagopus lagopus scotica.*
- Other birds (*Passeriformes spp.*; *Corvidae spp.; Columbidae spp.* Unidentified bird remains).

Since pellets usually contained more than one prey item (mean 2.7 ± 0.4 *s.e.* items), two measures of prey frequency data from pellet analysis were derived using previous methods (Redpath *et al.* 2001a):

1. Pellet frequency. The percentage of pellets containing a given prey type (irrespective of amount in each pellet).
2. Pellet relative frequency. Occurrences of a particular prey type as a percentage of all identified items in pellets.

Summary data are expressed using each of these measures. Additionally, pellet relative frequency data were used to calculate the proportion of total biomass of all prey that each of the six prey groups constituted. There is no equivalent measure of biomass for pellet frequency data.

When calculating proportions of diet by biomass, weights of mammals were derived from values for adult individuals in Aulagnier *et al.* (2009) and Salamolard *et al.* (2000). Bird weights were taken from Snow & Perrins (1998) and Robinson (2005). Averages of sexes were used for prey items where the sex could not be reliably determined. The weight of a field vole was used for small mammals unidentified to species level, European rabbit was used for *Lagomorph spp.* unidentified to species, and meadow pipit was used for passerines unidentified to species because these were all the most common species on surveys for these groups (Chapter 3). Weights of invertebrates, amphibians and reptiles were taken from Salamolard *et al.* (2000), Rooney & Montgomery (2013) and ARKive [www.arkive.org].

Pellet analysis is known to carry inherent bias in the estimation of diet composition (Simmons *et al.* 1991; Redpath *et al.* 2001a; Lewis *et al.* 2004; Chapter 2). To reduce the bias that pellet analysis had on results, correction factors were applied to results. Correction factors were derived from a controlled feeding experiment involving captive buzzards conducted in 2014. This experiment found that red grouse were detectable in 52% of buzzard pellets produced following a grouse meal when analysed with conventional analysis techniques described in Yalden & Morris (2009). The experiment also found that small mammals were detectable in 99% of pellets produced following a small mammal meal although the number of small mammal individuals detected was 53% of the number eaten by the buzzard prior to pellet production (Stickler *et al.* unpublished data – see Thesis Appendix, section A1). Using these detectability values, I corrected numbers and presence of prey identified in pellets prior to analysis. All birds identified to species were assumed to have the same detectability rates in pellets as grouse, whereas bird remains that were unidentifiable to species were assumed to have detectability rates of 94% as per values from the experiment. Detectability rates of lagomorphs and invertebrates were unknown and were unchanged.

5.3.4 Buzzard home ranges

Home ranges of tagged buzzards were calculated to inform subsequent analyses of factors influencing buzzard diet, which were considered with an average defined home range size of each buzzard roost site. Home range sizes were calculated using kernel density estimation (KDE). KDEs estimate the likelihood, or probability, of an individual being found within a given region in which it has been recorded (Worton 1989). KDE produces a utilisation distribution, which allows for multiple centres of activity based on probability of occurrence. In this respect, KDE is little affected by infrequent but long-range 'excursion trips' which buzzards are known to take (Walls & Kenward 1998), and which are not directly linked to resource use within the home range. These can exaggerate home range size when simple range outline techniques such as Minimum Convex Polygons (MCP) are used. KDE instead produces probability contours, or isopleths, within which a given probability of occurrence is estimated. The 50% isopleth represents a 'core range' where the animal is expected to occur 50% of the time (Anderson 1982; Haworth *et al.* 2006), and these were calculated in this study to derive average core range sizes of buzzards. KDEs were produced in ArcGIS version 10.2. Cell size was set at 100 metres with Gaussian kernels and likelihood cross-validation smoothing parameter (Horne & Garton 2006). Core range sizes were averaged and used in subsequent analyses to explore possible factors influencing the presence of red grouse in buzzard diet (see below).

5.3.5 Factors influencing red grouse in buzzard diet

Analyses aimed to explore the relative influence of key factors which may explain variation in the occurrence of red grouse in pellets collected from each roost site.

The generalist and opportunistic nature of buzzards (Tubbs 1974) can result in large variations in dietary composition depending on the availability of different habitats and their associated prey resources (Swann & Etheridge 1995; Graham *et al.* 1995; Rooney & Montgomery 2013). Therefore, the effect of habitat composition within an area equal to the average core range size around each roost site was considered as a factor determining the presence of red grouse in the pellets found at each roost site. Selection of habitat variables for analysis is outlined in Table 5.1.

Hunting efficiency is known to increase with age in raptors (Newton *et al.* 1981; Kruger 2005) which can also influence prey choice (Rutz *et al.* 2006; Penteriani *et al.* 2013). Therefore, during observations of buzzards at roosts conducted at least fortnightly, the age of the buzzard seen using the roost site was noted from plumage patterns on the breast, tail and greater coverts (Hardey *et al.* 2009; Svensson *et al.* 2009). Buzzards were categorised as either 'adult' (individuals over 3 years); 'immature and juvenile' (individuals less than 3 years); or 'unknown age' if the individual could not reliably assigned to one of these two categories. Buzzards tagged with GPS or VHF tags were already assigned an age class. The effect of buzzard age class on the occurrence of red grouse in pellets was therefore also examined. Data from GPS and VHF tags suggested that buzzards were largely faithful to one roost site (mean percentage of recorded locations of tagged individuals in the same roost site at dusk = 89%, range = 74% – 100%). Observations of plumage patterns of buzzards at roost sites at dusk suggested this was also the case for non-tagged individuals. Therefore, for the purposes of analyses, it was assumed that pellets collected from each of the 23 roost sites came from a different individual.

General linear models (GLMs) with binomial error structure and 'logit' link functions were constructed to explore factors influencing the occurrence of red grouse in buzzard diet. The response variable was the occurrence of red grouse as a proportion of total prey items identified in pellets from each roost site (n=23) using pellet relative frequency data. Variables outlined in Table 5.1 were included as main effects. Only uncorrelated covariates were included in models, assuming that Pearson correlation coefficients of $r \geq 0.7$ were indicative of a common underlying factor (Dormann *et al.* 2013). No two variables were found to be correlated in models ($r \leq 0.35$, $p \geq 0.1$ in all cases).

An information theoretic (IT) approach was taken to explore the factors influencing the proportion of red grouse in buzzard diet. This approach to inference of biological mechanisms contrasts to the traditional null hypothesis significance testing (NHST) approach in that it recognises that data rarely provide absolute support for a single hypothesis. Instead the extent to which given predictors support an explanation (relative to others) is the basic aim of the IT approach used here (Richards *et al.* 2010). Furthermore, this method reduces biases in parameter estimation, multiple hypothesis testing and inappropriately relying on a single 'best' model associated with the use of stepwise regression (Whittingham *et al.* 2006).

Candidate models were compared using a method similar to that described in Whittingham *et al.* (2005) whereby corrected Akaike's Information Criterion (AICc) were calculated for candidate models using the 'dredge' function of the MuMIn package in R version 3.1.1 (Barton 2013). Comparisons were made between models within the 95% confidence set, which is the smallest subset of candidate models where the combined model weights (ωi) sum to 0.95. These represent a set of models, within which there is 95% confidence that the best approximating model to the true model is contained. The relative importance of variables was compared using model-averaged parameter estimates and the cumulative sum of Akaike weights ($\Sigma\omega i$), which is a summed weight of all models in which the variable appears. To overcome the problem of poor predictors being assigned unrealistically high selection probabilities (Burnham & Anderson 2002), a single randomly generated variable with values between 0 and 1 was added to the set of variables. Generating 100 of these data sets allowed summed Akaike weights to be averaged for this null variable, which allows comparison with existing variables (Whittingham *et al.* 2005). Model fit was tested using diagnostic plots of residuals versus fitted values and Q-Q plots. The distance to heather variable was log-transformed to reduce heteroscedasticity in residuals. All statistical analyses were carried out in 'R' statistical software version 3.1.1.

5.3.6 Testing key assumptions

It was necessary to make various assumptions about the area and habitat composition of buzzard home ranges in analyses. One of these assumptions concerns the consideration of habitat composition around all buzzard roost sites within an area equal to the average core range size. Whilst 23 roost sites were identified in total, I was only able to measure core home ranges for the sub-sample of nine tagged buzzards. As outline above, my approach was to consider habitat composition around all 23 roost sites within a circle of area equal to the core range of the nine tagged buzzards. These circles were centred on each of the 23 roost sites, which assumes that roost sites are centrally situated within the core range. To test this assumption of roost site centrality, I plotted the geometric centre of each of the nine polygons representing the core ranges of the tagged buzzards in ArcGIS. For core ranges that were a single polygon, this was the geometric centre of those polygons, but this approach also allowed the identification of a single geometric centre for core ranges which were in the form of more than one polygon (see Fig. 5.A1 & 5.A2). Although geometric centres may not be the same as activity centres (Kenward 2001), they are suitable for the purpose of testing this assumption that roost sites are located at the centre of a core range area. The straight line distance between these geometric core range centres and the relevant roost sites was then measured. These distances were compared in relation to the span of the core range (distance between the furthest points of the core range). If the geometric centre to roost site distance was a small fraction of the span, I could have some confidence in using roost sites of all buzzards as an estimated core range centre.

The assumption of roost site centrality is important because it may affect the measurement of habitat surrounding each roost site. By assigning circular core ranges centred on all roost sites, I have assumed that the habitat composition of these areas is similar to the habitat composition of the true core range. To test this assumption, I compared the habitat compositions of the core ranges of the nine tagged buzzards to the habitat compositions of a circle centred on the corresponding roost site equal in area to the core range. If these compositions were similar, I could have some confidence that the habitat compositions of the roost-centred home ranges of the 14 untagged buzzards were not greatly dissimilar than their (unknown) true core ranges. Data from the Land Cover 2007 dataset (Morton *et al.* 2011) were used to compare habitat compositions of the nine core ranges and their corresponding roost-centred ranges. Across all nine core range areas, heather moorland (heather moorland, heather/grass mix and ericaceous bog classes), grassland (rough, acidic and improved grassland) and forest (conifer plantation and mixed deciduous woodland) comprised between 97.2% and 99.9% of total habitat composition of all core range areas. A fourth group, ‘other’, was considered so that the habitat compositions of all areas totalled 100%. To test the null hypothesis that there was no difference in habitat compositions between the nine measured core ranges and the nine circles centred on the roost sites, compositional analysis was used (Aebischer *et al*. 1993), since habitat types could not be considered independent of each other. I transformed data to log-ratios using ‘other’ as the denominator. Differences in habitat composition between measured core ranges and roost-centred circles were tested using MANOVA applied to the log-ratios (see Chapter 2 and Aebischer *et al*. (1993) for more details on statistical method).

Table 5.1. Parameters used as explanatory factors in models exploring variation in the proportion of red grouse as prey in buzzard diet from pellets collected around 23 roost sites on and around Langholm Moor.

Predictor	Description	Justification
Buzzard age	Three-level factor – Adult (n = 8); Immature/juvenile (n = 8); birds of unknown age (n = 7).	Hunting efficiency increases with age in raptors (Newton *et al.* 1981; Kruger 2005) which may affect prey choice (Rutz *et al.* 2006; Penteriani *et al.* 2013).
Heather moorland*	Proportion of habitat in a core range around the roost site consisting of heather moorland* from Landcover Map 2007 data (LCM 2007)†	A measure of the extent of habitat favoured by red grouse, and therefore a proxy of red grouse abundance (Thirgood *et al.* 2000b).
Grassland*	Proportion of habitat around the roost site consisting of grassland habitat* from LCM 2007 data†	A measure of the extent of habitat favoured by voles and lagomorphs (Redpath & Thirgood 1997; Thirgood *et al.* 2003), and therefore a proxy of abundance of alternative prey favoured by buzzards (Graham *et al.* 1995).
Distance to heather	Distance in metres from the roost site to the nearest patch of heather moorland* from LCM 2007 data†	A key determinant of resource use according to central foraging theory which may affect the use of red grouse habitat by buzzards (Arroyo *et al.* 2009)

* No variable pairs were correlated ($r < 0.35$, $p > 0.1$ in all cases).

†’Heather moorland’ cover was created by combining heather moorland, heather/grass mix and ericaceous bog classes; ‘grassland’ cover was created by combining rough and improved grassland classes from LCM 2007.

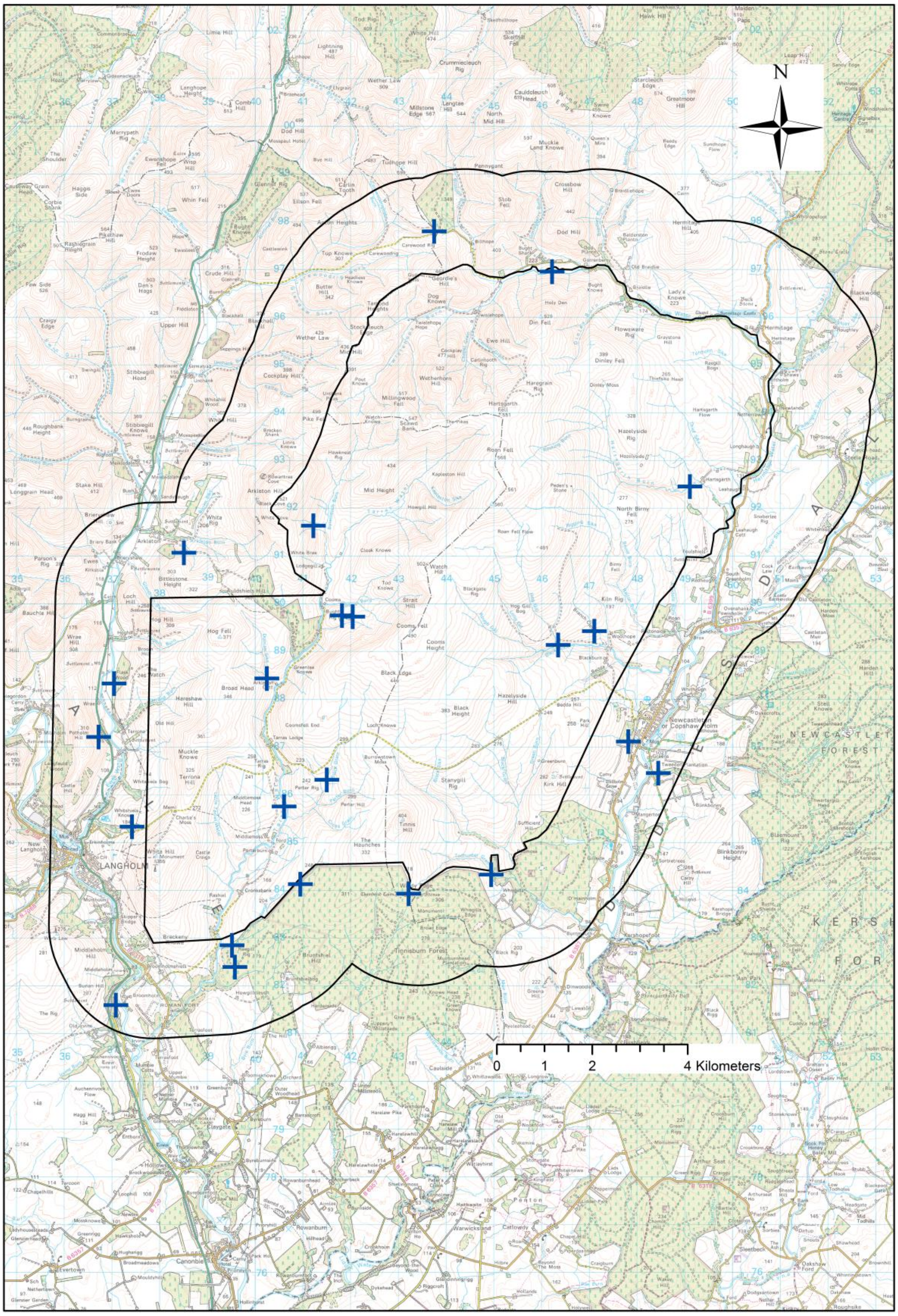

Figure 5.1. Locations of 23 buzzard roost sites (blue crosses) found within the LMDP area (inner black line) plus a 2 km buffer zone (outer black line) during the winter of 2013/14.

5.4 Results

5.4.1 Roost sites and pellets

Between October 2013 and January 2014, 23 active roost sites were identified on and around Langholm Moor (Fig. 5.1). Searches of these roost sites between October 2013 and March 2014 yielded 409 pellets (mean pellets per roost site = 17.8, range = 12 – 32). Categorising roost sites by age of occupying buzzard gave 203 pellets collected from eight roost sites of immature/juvenile buzzards, 117 pellets collected from eight roost sites of adult buzzards, and the remaining 89 pellets collected from seven sites used by buzzards of an unknown age.

Analysis of pellets yielded a total of 1,107 individual prey items with a mean of 2.7 (*s.e.* ± 0.4) prey items in each pellet. Data from initial pellet analysis are given in Table 5.2, and data following the application of correction factors are given in Table 5.3 and shown in Fig. 5.2.

After correction factors were applied to initial pellet analysis data, both measures of prey frequency showed small mammals to be the dominant prey group. Small mammal remains were estimated to be present in 89.4% of all pellets and comprise 76.5% of total prey items. Numerically, invertebrates were the second most important group, estimated to occur in 34.7% of pellets and comprise 11.4% of all prey items. Results by biomass showed that *Lagomorph spp.* were estimated to comprise the biggest portion of buzzard diet (44.4%). Unlike pellets collected during the breeding season (Chapter 3) no pellets contained remains of *Amphibia or Reptilia*.

Red grouse occurred in 2.9% (n = 12) of all pellets (corrected to 5.6%, n = 23) and comprised 1.1% (n = 12) of all prey items (corrected to 1.3%, n = 23), equivalent to 4.8% of the total biomass of all prey (corrected to 6.9%).

Table 5.2. Number and percentage of pellets (n = 409) containing a given prey type (pellet frequency) and prey items identified in pellets (n = 1,107) (pellet relative frequency) from buzzard roost sites (n = 23) on Langholm Moor between October 2013 and March 2014. Data are pooled over all roost sites, with range of percentages between roost sites given. Since pellets often contained more than one item, pellet frequency sums to > 100%.

	Pellet frequency			Pellet relative frequency			Total biomass	
Prey group	N	%	Range	N	%	Range	%	Range
Small mammals	361	88.3	61.5 – 100	739	66.8	51.3 – 82.2	14.9	8.0 – 37.0
Lagomorph spp.	89	21.8	6.5 – 46.2	89	8.0	2.2 – 16.7	59.7	21.3 – 88.7
Invertebrates	142	34.7	14.3 – 53.9	207	18.7	5.9 – 33.3	0.1	0 – 0.4
Pheasant	22	5.4	0 – 25.0	22	2.0	0 – 8.1	17.6	0 – 53.6
Red grouse	12	2.9	0 – 14.3	12	1.1	0 – 6.0	4.8	0 – 25.6
Other birds	38	9.3	0 – 33.3	38	3.4	0 – 11.8	2.8	0 – 18.1

Table 5.3. Pellet analysis data from Table 5.2, with correction factors applied using results from a buzzard feeding experiment (Stickler *et al.* - Thesis Appendix, section A1). Pellet frequencies were corrected assuming detectability rates of 99% for small mammals, and 52% for identified birds (94% for unidentified birds). Pellet relative frequencies were corrected assuming detectability rates of 53% for small mammals and 52% for identified birds (94% for unidentified birds). Values for lagomorphs and invertebrates were unchanged. Corrected biomass values were calculated from corrected pellet relative frequencies.

	Pellet frequency			Pellet relative frequency			Total biomass	
Prey group	N	%	Range	N	%	Range	%	Range
Small mammals	365	89.4	62.2 – 100	1394	76.5	63.9 – 86.6	20.9	11.9 – 51.8
Lagomorph spp.	89	21.8	6.5 – 46.2	89	4.9	1.3 – 10.1	44.4	12.7 – 80.7
Invertebrates	142	34.7	14.3 – 53.8	207	11.4	3.2 – 22.3	0.1	0 – 0.3
Pheasant	42	10.3	0 – 48.1	42	2.3	0 – 9.0	25.1	0 – 62.7
Red grouse	23	5.6	0 – 27.5	23	1.3	0 – 6.8	6.9	0 – 31.4
Other birds	73	17.9	0 – 64.1	73	3.7	0 – 12.8	3.4	0 – 19.1

5.4.2 Buzzard home ranges

A mean of 40 points were obtained from the four VHF tags (range: 33 – 48) and a mean of 146 points were obtained from the five GPS tags (range: 66 – 260). Kernel Density Estimates revealed that the mean core range (50% isopleth) of all tagged buzzards was $2.1 km^2$ (± 0.7 *s.e.*) (Figures 5.A1 & 5.A2, Chapter Appendix). Estimates of mean core range did not differ between GPS and VHF tags (two sample t-test with equal variances: $t = 0.12$, d.f. = 7, $p = 0.91$). The habitat variables in Table 5.1 were therefore considered in a $2.1 km^2$ area centred on each roost site when exploring variation in red grouse remains identified in pellets between buzzard roost sites.

5.4.3 Red grouse in buzzard diet

The factors influencing the occurrence of red grouse as a proportion of all prey items identified in pellets from all 23 roost sites were explored by comparing candidate models within the 95% confidence set (Table 5.4). Examination of candidate models showed that all models contained the 'grassland' variable (the proportion of grassland in a $2.1 km^2$ around the roost site). The top ranking model contained only this variable, and the Akaike weight of this model showed that it was 1.8 times likelier than the next-ranking model ($\omega = 0.33$ versus 0.18). Model averaging produced summed Akaike weights (i.e. selection probabilities, $\Sigma\omega i$) for the four predictor variables which could be ranked in the order of: grassland > heather distance > age > heather. Summed Akaike weights for heather distance, age and heather were much lower than that of grassland and well within the range of the null variable. The binomial logistic regression model showed that the proportion of grassland habitat around each roost site had a significant negative effect on the proportion of red grouse in buzzard pellets (Figure 5.3; $R^2 = 0.51$; $\chi^2_1 = 31.72$; $p < 0.001$), and the model averaged parameter estimate for this relationship was -7.69 ± 2.53 SE.

5.4.4 Testing key assumptions

The mean distance between roost sites and the geometric centre of core ranges was 484.8 metres (± 140.6 *se*). As a percentage of home range span, this roost-to-range-centre distance averaged 24.3% (± 7.2 *se;* range = 7.6% - 81.6%). The average habitat composition of the nine measured core ranges was 11.3% heather moorland, 68.2% grassland, 20.0% forest and 0.6% other. The average habitat composition of the nine corresponding circles centred on roost sites was 9.4% heather moorland, 65.2% grassland, 23.4% forest and 1.0% other. Habitat composition did not differ significantly between the measured core ranges and the roost centred circles ($\Lambda = 0.63$, $p = 0.13$).

Table 5.4. Candidate models for explaining variation in the proportion of red grouse found in buzzard pellets collected from 23 roost sites on and around Langholm Moor during winter 2013-14. The variables given in Table 5.1 were all included as main effects. Models shown represent the 95% confidence set. The table indicates which variables were included in each model (indicated with a '1'); corrected AIC (AICc); change in AIC from the best fitting model (ΔAICc); and Akaike weight (a measure of model selection probability; *ωi*). Model-averaged parameter estimates (β) and their standard errors (*s.e.*) weighted by *ωi* are presented for each variable, along with cumulative sums of Akaike weights (Σ*ωi*) for models including the variable for the 95% confidence set and all models. Σ*ωi* provides a measure of relative importance of each variable, and has also been calculated for 100 null variables for which the mean and range of model weights are given.

Variable	Age	Heather distance	Grassland	Heather	AICc	ΔAIC	*ωi*
			1		36.84	0.00	0.33
	1		1		38.04	1.20	0.18
		1	1		38.05	1.22	0.18
			1	1	39.07	2.23	0.11
		1	1	1	39.72	2.88	0.08
	1	1	1		39.94	3.10	0.07
β	-	1.94e-04	-7.69	1.86			
s.e. of β	-	3.84e-04	2.99	5.62			
Σ*ωi* (95% conf. set)	0.25	0.33	0.95	0.19			
Σ*ωi* (all models)	0.30	0.33	>0.99	0.24			
Null variable							
Mean Σ*ωi*	0.29						
Σ*ωi* range	0.16 - 0.61						

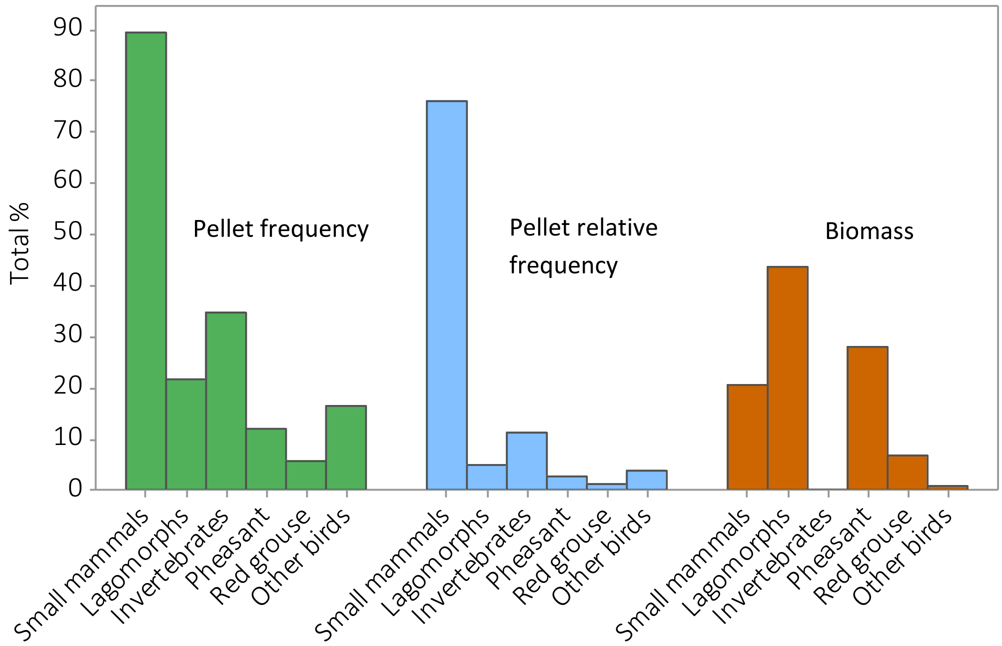

Figure 5.2. Percentages of three measures derived from analysis of 409 pellets collected at 23 buzzard roosts between October 2013 and March 2014. Correction factors were applied to data (see text). Pellets usually contained more than one item so pellet frequency sums to > 100%. Biomass measures are derived from corrected pellet relative frequency data.

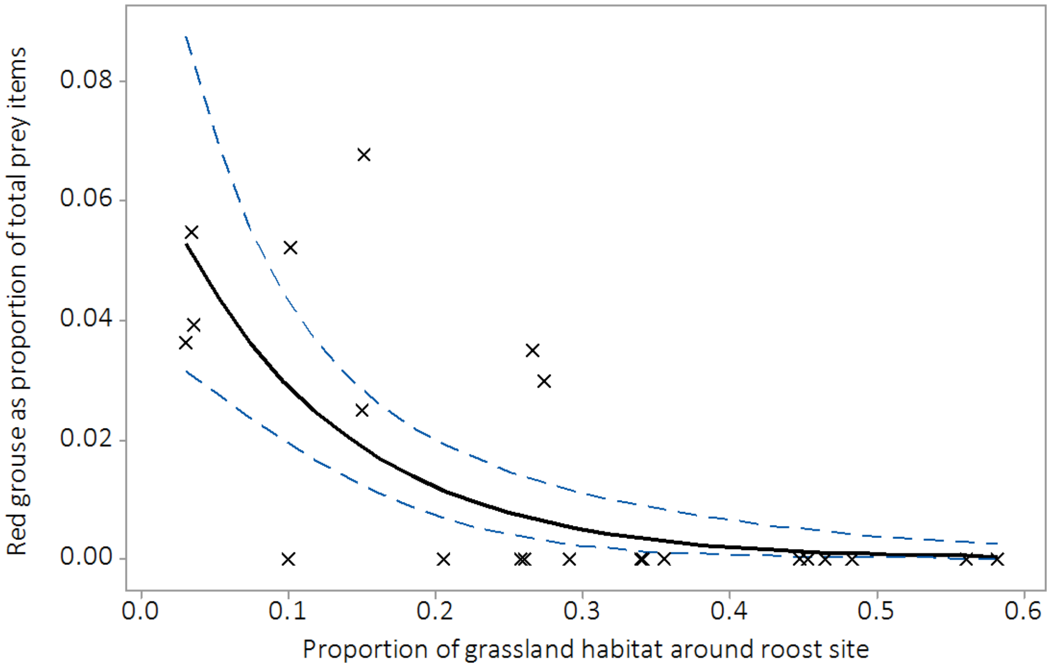

Figure 5.3. Binomial logistic regression relationship between red grouse as a proportion of prey identified in buzzard pellets and the proportion of grassland around 23 buzzard roost sites on Langholm Moor during the 2013/14 winter. Correction factors were applied to pellet data (see text). Solid line shows model fit, dashed line shows 95% confidence intervals.

5.5 Discussion

Objective assessment of predation on gamebirds can aid in finding solutions to minimise conflict (Kenward 1999). Assessing dietary composition forms the basis of many studies investigating the impact of raptor predation on gamebirds (Park *et al.* 2008). The majority of these studies are conducted during the raptor breeding season (Lewis *et al.* 2004) yet raptor diet can vary between seasons (Mañosa & Cordero 1992; Amar *et al.* 2003) and impact on gamebirds can occur year round (Redpath & Thirgood 1999). This study is the first to assess the winter diet of buzzards roosting on land managed for red grouse shooting in Britain. This study demonstrated, perhaps also for the first time in Britain, the effectiveness of using remote tracking technologies in locating winter roost sites where buzzard pellets could be collected and analysed to obtain dietary composition data.

The favoured prey of buzzards wintering on and around Langholm Moor was small mammals. This supports previous studies of buzzard diet in Britain during the breeding season (Swann & Etheridge 1995; Graham, Redpath & Thirgood 1995; Chapter 3) and buzzard diet in Europe during the winter (Mañosa & Cordero 1992). Invertebrates were also an important prey resource numerically, which may reflect the increased consumption of invertebrates by buzzards in winter (Tubbs 1974; Wuczyński 2005). In terms of total biomass of prey identified, lagomorphs were the principal prey resource for buzzards, a finding also supported by other buzzard diet studies (Swann & Etheridge 1995; Graham *et al.* 1995; Rooney & Montgomery 2013). Unlike pellets collected from nests during the breeding season (Chapter 3), no remains of herpetofauna were found in pellets collected during this study. This may reflect a decreasing availability of these prey outside of summer (Selås 2001) or an underestimation of their importance when using pellet analysis (Selås, Tveiten & Aanonsen 2007; Chapter 2). Following the application of correction factors to account for bias in pellet analyses, red grouse were estimated to occur in 6% of pellets and form 1% of the total number of prey items identified, equivalent to 7% of the biomass of all prey in winter buzzard diet. It should be noted that presence of a prey species in the diet of a predator says very little in itself about impact on prey which would require, in part, information on predation rates and the degree to which predation was additive to other causes of mortality (Newton 1998;

Thirgood *et al.* 2000c). Nevertheless, the methods demonstrated in this study could prove useful in future investigations of raptor diet and impact on prey during the winter months.

In this study, red grouse were less frequent in pellets collected from roost sites surrounded by more grassland, and this was the most important factor determining variation in proportion of red grouse in buzzard pellets. The amount of heather moorland, used as a proxy for red grouse density here (Thirgood *et al.* 2000b), was not a significant predictor of red grouse in buzzard pellets and was not correlated to the amount of grassland around buzzard roosts. Grassland habitats contain higher densities of voles and lagomorphs (Thirgood, Redpath & Graham 2003; Chapter 3; Chapter 4), which are important prey groups to buzzards in upland Britain (Swann & Etheridge 1995; Graham, Redpath & Thirgood 1995; Chapter 3). Buzzards at Langholm Moor have also previously been shown to preferentially hunt in grassier areas (Thirgood *et al.* 2003), particularly during years when vole abundance on the heather-dominated moorland is low (Chapter 4), presumably in response to the greater abundances of small mammals and lagomorphs in grassland habitats. The result of the current study, whereby buzzards were less likely to eat red grouse as the proportion of grassland increased around the roost site, may reflect a spatial response of buzzards to greater abundances of alternative (i.e. non-grouse) prey, resulting in less opportunistic predation of red grouse. This has potential implications for the management of raptors alongside red grouse, because it may show that availability of alternative prey in habitats spatially separated from red grouse habitats can reduce predation pressure on red grouse. However, further study over a longer time period and in other locations is needed to confirm these results.

The diet of generalist predators such as buzzards can vary over time in relation to natural prey fluctuations, which is termed the functional response (Korpimaki & Norrdahl 1991; Redpath & Thirgood 1999; Salamolard *et al.* 2000; Reif *et al.* 2004; Chapter 3). To better understand the functional responses of buzzards on Langholm Moor and their impacts on red grouse, it will be necessary to repeat this study over successive winters alongside prey abundance monitoring. It would also be beneficial to explore these results over multiple study sites, with greater variation in habitat composition, to further disentangle habitat effects on buzzard prey choice (Kenward *et al.* 2001).

Analysis of regurgitated pellets provides a time efficient and widely used method of analysing raptor diet (Tornberg & Reif 2007). However, pellets have been shown to underestimate avian remains relative to mammalian remains (Redpath *et al.* 2001; Chapter 2). In this study, an attempt was made to reduce some of these biases using data from a recent study of pellets from captive buzzards with a manipulated diet (Stickler *et al.* unpublished data – see Thesis Appendix section A1). Nevertheless, this experiment may contain its own sources of inaccuracy and so biases may still remain in the present assessment of buzzard diet. Further collection of buzzard diet data during the winter, coupled with continued exploration of methodological biases, would improve the accuracy of present estimates.

In this study I considered the effects of habitat composition within a circular area surrounding all roost sites equal in area to a measured core range of a sub-sample of nine tagged buzzards. I tested the assumptions that roost sites were centrally located and that habitat compositions were similar between measured core ranges and the roost-centred-circles. Analysis suggested that roost sites were situated at a distance from the centre which was on average equivalent to approximately a quarter of the total core range span. This suggests that buzzards tended not to roost in the centre of their home ranges, and that there was a violation of the centrality of roosts assumption. This is perhaps not surprising considering that buzzards tend to roost on forest edges and wooded gullies (Tubbs 1974; *pers. obs.*), while primarily being hunters of open country and forests with open canopies (Tubbs 1974; Kenward *et al.* 2001), whilst dense coniferous plantations dominated the woodland cover at Langholm Moor. However, whilst this assumption was seemingly violated by my analysis approach, it would be an unacceptable leap of faith to assign core ranges to untagged buzzards in the absence of data on the true shape of their core ranges. Furthermore, analysis showed that there was no significant difference in the broad habitat compositions of the nine measured core ranges and the corresponding nine roost-centred circular areas. Therefore, it is likely that the use of circular core ranges for all buzzard roosts had only a small effect on my analysis of habitat and its effect on the occurrence of red grouse in buzzard pellets. This may not be the same for any future studies in areas with different habitat composition, or even for studies of other raptor species, and these assumptions, as well as any others, should be tested on a case-by-case basis.

Results of the present study may have also been affected by the tendency for juvenile and sub-adult buzzards to enter traps prior to tagging. Young raptors are known to range further than adults, a reflection of inexperience in hunting or mate searching (Newton 1979; Penteriani *et al.* 2013). It was not possible to predict the degree to which estimates of home range size used as the basis for analysis in this study would have differed had all tagged individuals been adults. However, the effect of long range excursions was minimised by considering core ranges, and in the absence of alternative data it is the most appropriate estimate available. A greater sample size of tagged individuals, including buzzards of varying ages, studied over a longer time period would improve the reliability of home range size estimates, as well as diet variation between age classes. In this study, tagged buzzards appeared to be largely faithful to one roost site, having been recorded at one roost at 89% of locations at dusk. However, confirming this level of faithfulness to one roost site would require a greater sample of tagged individuals.

In conclusion, this study has demonstrated the use of remote tracking as a method of investigating raptor diet during the winter, which to date has been understudied especially in relation to exploring impact on gamebirds. This is pertinent considering the increased interest in this subject, and the occurrence of seasonal variability in raptor diet composition. Although conclusive causal relationships could not be proven, results highlight that the availability of alternative prey resources, spatially separated from red grouse habitats, may reduce buzzard predation pressure on red grouse. Provision and conservation of areas of alternative foraging habitat could be a useful avenue for further research into reducing conflict between raptors and gamebirds.

5.6 Appendix

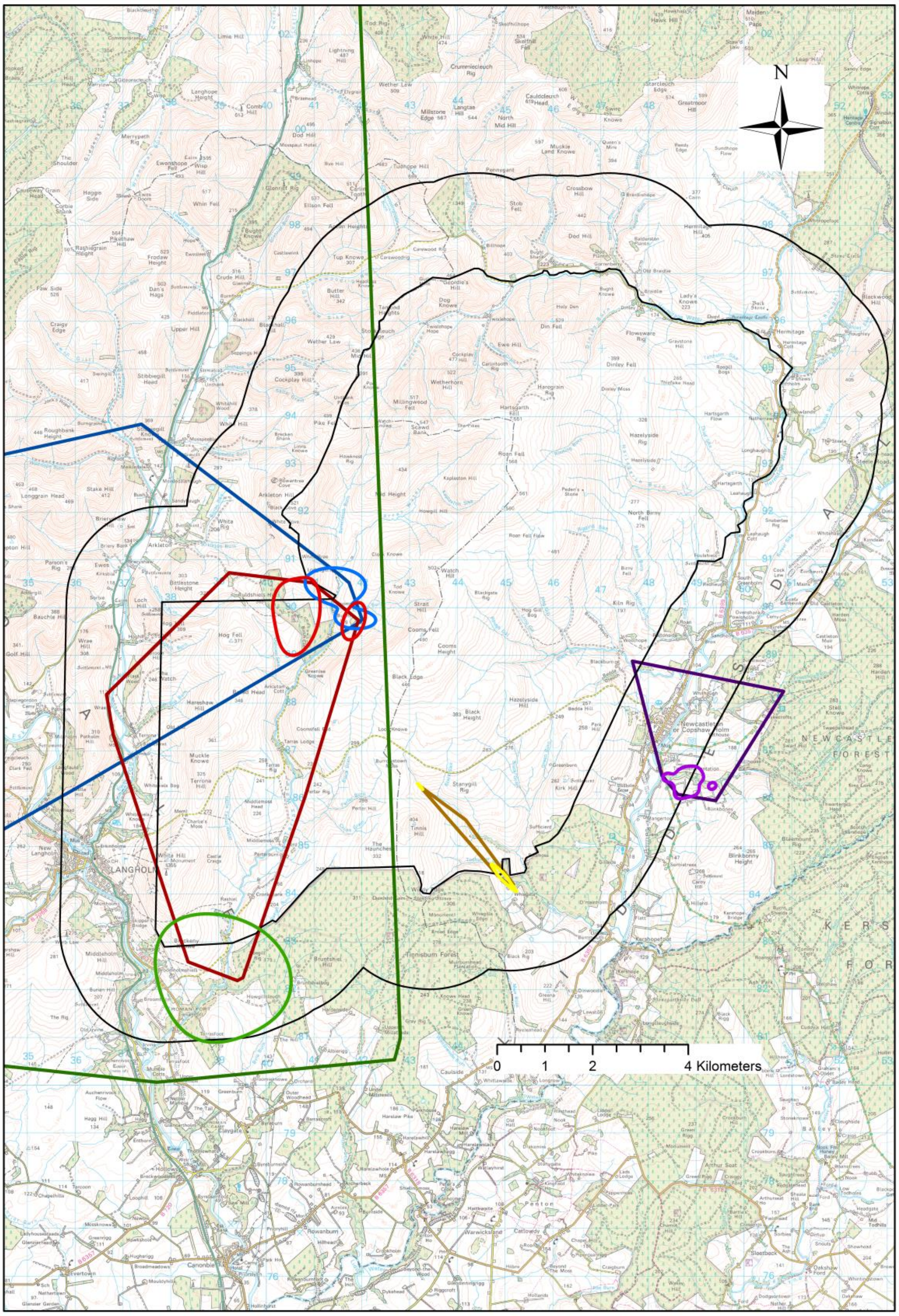

Figure 5.A1. Home ranges of five buzzards fitted with **GPS tags** during the winter of 2013/14. A different colour is used for each individual. Inner smoothed lines show core ranges (50% KDE isopleth) used in analysis, outer straight lines show 100% MCPs for illustrative purposes. Inner black line delimits the LMDP area, outer black line is the 2 km buffer zone used for this study.

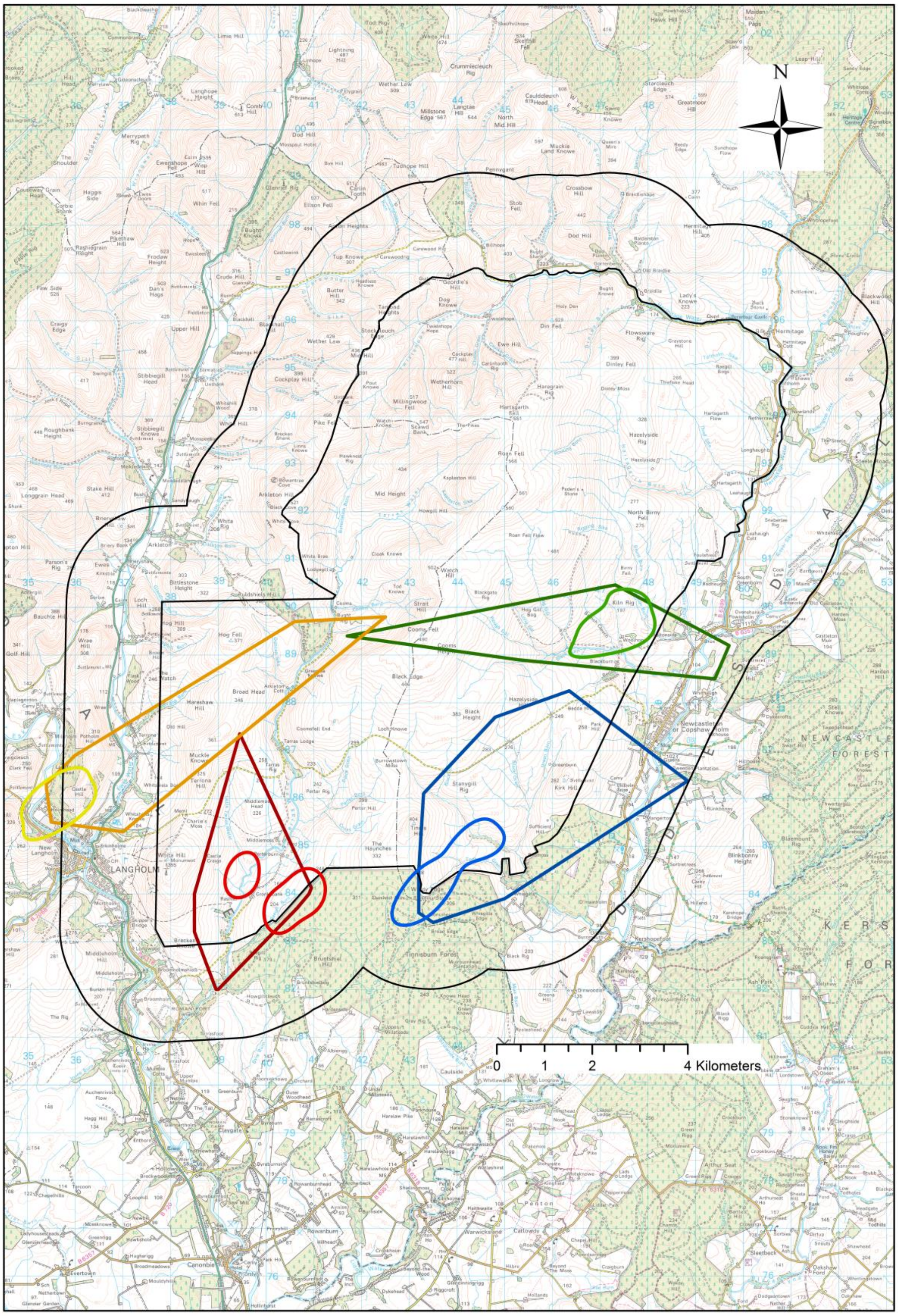

Figure 5.A2. Home ranges of four buzzards fitted with **VHF tags** during the winter of 2013/14. A different colour is used for each individual. Inner smoothed lines show core ranges (50% KDE isopleth) used in analysis, outer straight lines show 100% MCPs for illustrative purposes. Inner black line delimits the LMDP area, outer black line is the 2 km buffer zone used for this study.

Chapter 6: Estimating the impact of common buzzard predation on red grouse: a bioenergetics modelling approach

6.1 Abstract

Human-wildlife conflict can arise when predation is perceived to affect human activity. There is a continuing need to estimate the impact of recovering raptor populations in the UK on economically important gamebirds, to ensure that any management decisions are based upon current and accurate data. Common buzzards have increased in population and range in Britain and this has brought them into conflict with gamebird managers. Here I develop bioenergetics and consumption models to estimate the potential consumption of red grouse by buzzards during three summers and one winter. Data were collected on an area of moorland in south-west Scotland managed to restore red grouse shooting. Buzzard population size on Langholm Moor was estimated at 125 individuals during the summer (including non-breeding and breeding individuals and their young) and 53 individuals during the winter. Models estimated that the energetic requirement of this population was 1.5×10^7 kJ, equivalent to 2.8×10^6g of food for each 122 day summer period, and 1.4×10^7kJ, or 2.6×10^6g of food for a 243 day winter period. Camera images in one year recorded no red grouse delivered to buzzard nests, and so consumption models based on these data estimated that no grouse were eaten in this year. In other years and with other diet methods, grouse consumption models estimated that the total buzzard population ate between 64 and 318 adult red grouse during one summer (variation between year and method). These estimates of grouse consumption by buzzards were equivalent to buzzards eating between 5% and 26% of all adult red grouse present in spring. Additionally, models estimated that buzzards ate between 96 and 380 grouse chicks during one summer, again with variation between year and method. During one winter, models estimated that buzzards ate 384 grouse, equivalent to 11% of the total grouse present in autumn and 31% of the total number estimated to die overwinter. Results suggest that while consumption of grouse by individual buzzards is low, total levels of consumption could be considerable if buzzard population size is large enough, assuming additive mortality. Further research is needed to address the assumptions, uncertainty and limitations here, and to test potential mitigation techniques. This approach could be a useful tool for managers interested in measuring the impacts of predation on economically important or threatened prey.

6.2 Introduction

Understanding the impact of predation on prey populations is a complex and controversial issue in applied ecology (Ormerod 2002). Accurate quantification of impact is important when designing management solutions and attempting to reach economic and conservation objectives (Reynolds & Tapper 1996; Kenward 1999; Thirgood *et al.* 2000a; Roby & Lyons 2003). Generalist predators can drive prey population dynamics through their ability to switch between available prey resources (Korpimäki & Norrdahl 1991; Redpath & Thirgood 1999; Reif *et al.* 2004; Mckinnon *et al.* 2013). Quantifying the impact of predation by generalist predators on their main and alternative prey requires current and spatially relevant data.

In Britain, the predation of gamebirds by raptors is a particularly contentious issue (Thirgood *et al.* 2000a; Kenward *et al.* 2001; Park *et al.* 2008). The partial recovery of many raptor species in the UK (Greenwood *et al.* 2003) has reignited and intensified concern over their impact on gamebirds (Amar *et al.* 2008; Lees *et al.* 2013). The common buzzard *Buteo buteo* (herein 'buzzard') is a generalist raptor whose preferred prey are voles *Microtus* spp. and European rabbits *Oryctolagus cuniculus*, but they will also predate gamebirds when available (Tubbs 1974; Swann & Etheridge 1995; Graham *et al.* 1995; Kenward *et al.* 2001). Buzzards have greatly increased in abundance and range in Britain since the 1970's (Musgrove *et al.* 2013; Balmer *et al.* 2014), and have been the most common diurnal raptor for over a decade (Clements 2002; Musgrove *et al.* 2013). Whilst the impact of buzzards on released pheasants *Phasianus colchicus* has been studied (e.g. Kenward *et al.* 2001; Parrott 2015), their potential impact on red grouse *Lagopus lagopus scotica* is not well understood. Assessing impact from recovering buzzard populations will be key to informing debate and management.

Red grouse are an economically important game bird in parts of upland Britain (Hudson 1992). Long-term declines in red grouse numbers are principally associated with declines in heather-dominated moorland, changes in management including reductions in gamekeeper density and increasing populations of several generalist predators including red fox *Vulpes vulpes* and corvids *Corvus spp*. (Hudson 1992; Thompson *et al.* 1995; Thirgood *et al.* 2000b). However, on local and short-term scales the impact of raptor predation on red grouse can be significant. Between 1992 and 1996, the Joint Raptor Study (JRS) assessed the extent to which raptor predation from hen harrier *Circus cyaenus* and peregrine *Falco peregrinus* limited red grouse numbers on Langholm Moor in south-west Scotland (Redpath & Thirgood 1997). Results from the JRS showed that predation of red grouse by raptors can limit grouse abundance and reduce hunting revenues (Redpath & Thirgood 1997; Thirgood & Redpath 2008). Since 2007, Langholm Moor has been the site of the Langholm Moor Demonstration Project (LMDP) which seeks to reconcile red grouse shooting with raptor conservation (Langholm Moor Demonstration Project 2007). Recent data from Langholm suggest that the numbers of buzzards recorded during systematic vantage point watches are now approximately three times higher than the JRS during summer, and marginally higher during winter (Chapter 4; LMDP 2014b), and that red grouse feature in buzzard diet during summer (Chapter 3) and winter (Chapter 5). Here, I attempt to assess the impact of buzzard predation on red grouse at Langholm Moor to help inform any future management decisions.

The most scientifically rigorous approach to studying predator impact is to experimentally remove the predator from an area and study the response of the prey compared to a similar area, before reversing the treatment (Newton 1998). When predator removal is impractical or unacceptable due to conservation status or protection, estimates of prey consumption can provide useful initial information. Bioenergetics models have previously been used to estimate consumption of prey by predatory birds (Phillips *et al.* 1999; Gremillet *et al.* 2003; Roby & Lyons 2003; Votier *et al.* 2004a). These models use estimates of the energy requirements of predators together with estimates of prey energy content and predator population size to calculate the total amount of energy required to sustain a population over a given time period. Combining bioenergetics calculations with estimates of diet composition allows the total number of prey items consumed to be estimated. This approach avoids some of the potential problems associated with using food capture rates (Roby & Lyons 2003), which can be biased by selection of observation period or foraging site (Redpath & Thirgood 2003).

Here I develop bioenergetics and consumption models using data recently collected at Langholm Moor to estimate the number of red grouse consumed by buzzards. I compare these estimates to estimates of red grouse population size at Langholm Moor to consider the potential impact on red grouse by buzzards. Any estimate of grouse loss to raptor predation requires a number of assumptions to be made (Redpath & Thirgood 2003). Here I state key assumptions and, where possible, use recently collected or published data to test these. I also analyse the sensitivity of models to input parameters, and produce minimum and maximum estimates as confidence limits, in order to highlight areas of uncertainty and hence direct future research.

6.3 Methods

6.3.1 Study site

The study was conducted during 2011 – 2014 on Langholm Moor in south-west Scotland (for more details of the study site see Chapter 1). The study site encompassed 168 km^2 of land owned by Buccleuch Estates and was chosen to include the 114 km^2 covered by the Langholm Moor Demonstration Project (LMDP) plus a 1 km buffer zone.

Moorland management to benefit red grouse was undertaken by a team of five gamekeepers within the LMDP area and included rotational burning and cutting of heather, and control of crows, foxes and mustelids. All raptors were strictly protected. Buzzards nested and roosted in trees and wooded gullies within the LMDP area and in the mixed and coniferous forests on the project periphery (Graham *et al.* 1995; Chapter 3, Chapter 5). Buzzards hunted the moor where red grouse were resident year round (Thirgood *et al.* 2003; Chapter 4).

6.3.2 Buzzard diet composition

During three summers (May – July inclusive) between 2011 and 2013, 32 successful buzzard nests were studied, defined as those fledging at least one chick. These were nests which were discovered close to hatching, thereby allowing assessment of diet composition throughout the nestling period (2011 = 11, 2012 = 10, 2013 = 11). Motion triggered cameras, fitted to oversee these nests, captured video clips of one – five minutes duration. Six high-definition video recording units (model: Mini HDVR LS-H720) were rotated systematically between nests. Recording units were deployed at each nest for a minimum of three days during each of the following periods: the first week post-hatching, between one and four weeks post-hatching and from four weeks post-hatching until young had fledged and ceased to be fed at the nest (mean nestling period of 32 nests = 50 days, *s.e.* = 0.74). Collected footage was analysed and prey delivered to nests identified. Prey were recorded as 'unknown' if they were obscured and couldn't be identified.

Concurrent to cameras recording prey deliveries, searches for prey remains and regurgitated pellets were conducted at the same 32 nests. Searches were conducted within a 50 metre radius of the nest five times during the nestling period: when hatching was confirmed, during each of the three recording unit rotation periods, and during the first week post-fledging. Searches within the nest itself were conducted when cameras were installed, when chicks were ringed, and when cameras were removed during the first week post-fledging. Recorded prey remains were removed to prevent double counting. Pellets were frozen and dried prior to dissection and analysis. Prey were identified using Teerink (1991), Brown (2003) and Yalden (2009). Prey were identified to the lowest possible taxonomic level, and were assumed to represent one individual prey item, unless it was obvious that more than one individual was present. All diet data were collected between late-April and early-August in each year, depending on hatching and fledging dates at each nest studied.

All methods of assessing raptor diet carry inherent sources of bias. Indirect methods (e.g. analysis of prey remains or regurgitated pellets) can overestimate larger prey items, whilst direct observations can underestimate prey diversity indices (Redpath *et al.* 2001; Lewis, Fuller & Titus 2004; Tornberg & Reif 2007; Chapter 2). These biases can also differ between years as raptors respond functionally to variations in local prey abundances (Chapter 2). In recognition of this, data from all three methods of assessing buzzard diet during the summer are used here to create separate estimates of red grouse consumption by buzzards (red grouse are henceforth referred to as 'grouse'. Whilst black grouse *Tetrao tetrix* are present on Langholm Moor, none were recorded in buzzard diet).

During the winter of 2013/14 (October – February inclusive), buzzard diet was estimated from regurgitated pellets found at roost sites. Roost sites were located from radio- and GPS-tracking of nine buzzards at dusk and dawn, and from vantage point observations combined with searches of suitable roosting areas, i.e. wooded gullies and woodland (see Chapter 5 for more details on methods). To retain comparability and consistency with summer models, only roost sites within the LMDP area plus the 1 km buffer zone were considered (n = 20). It was not possible to collect either direct video images or sufficient numbers of prey remains during the winter months due to the absence of a focal nest. Therefore, estimates of grouse consumption by buzzards during the winter were based on assessment of buzzard diet using pellet analysis only.

Pellet analysis carries inherent bias in the estimation of diet composition (Simmons *et al.* 1991; Redpath *et al.* 2001; Lewis *et al.* 2004; Chapter 2). To quantify any bias in the detection of grouse remains in pellets, a controlled feeding experiment involving captive buzzards was conducted in 2014 in collaboration with this study. This experiment found that grouse were detectable in 52% of buzzard pellets produced following a grouse meal, when analysed with conventional techniques described in Yalden & Morris (2009). The experiment also found that small mammals were detectable in 99% of pellets produced following a small mammal meal although the number of small mammal individuals detected was 53% of the number eaten by the buzzard prior to pellet production (Stickler *et al.* unpublished data – see Thesis Appendix, section A1 for more details). Using these detectability values, I corrected the numbers of prey identified in pellets prior to inputting values in models. This was done for both summer and winter pellet data. Detectability rates of lagomorphs and invertebrates were unknown and were unchanged.

Buzzard diet in summer and winter was converted to percentages of total biomass of prey at each nest or roost site. Weights of mammals were derived from values for adult individuals in Aulagnier *et al.* (2009) and Salamolard *et al.* (2000), unless it was obvious that the prey item was a young individual, in which case these were halved (Rooney & Montgomery 2013). Bird weights were taken from Snow & Perrins (1998) and Robinson (2005). Averages of sexes were used for prey items where the sex could not be reliably determined. The weight of a field vole *Microtus aegrestis* was used for small mammals unidentified to species level, European rabbit was used for *Lagomorph spp.* unidentified to species, and meadow pipit *Antus pratensis* was used for passerines unidentified to species because these were all the most common species on surveys for these groups (Chapter 3). Weights of invertebrates, amphibians and reptiles were taken from Salamolard *et al.* (2000), Rooney & Montgomery (2013) and ARKive [www.arkive.org]. Grouse as a mean percentage of total biomass in buzzard diet was used in bioenergetics and consumption models. During summer, means were calculated for each year, adult grouse and grouse chicks and for each method (cameras, prey remains and pellets) to produce consumption estimates in three years based on each method. During winter, mean biomass was calculated using data from pellet analysis for adult grouse only. Winter data were only available for one year (2013/14) and so estimates here are produced for just that season.

6.3.3 Buzzard population estimation

The size of the buzzard population was estimated within the same area as diet data were collected. The number of breeding pairs was estimated by counting the number of active nests on the study site during the summers between 2011 and 2013. Nests were considered active if they were freshly lined, had fresh prey remains and pellets nearby, or if territorial adults were heard calling (Tubbs 1974; Hardey *et al.* 2009). It was assumed that all nests within the LMDP area were located as this was systematically and thoroughly searched in each year. However it is possible that some nests within the 1 km buffer zone were not identified in some years. To account for this, it is assumed that the same density of nests occurred in the buffer zone as in the LMDP area, and by extrapolation the number of nests in the entire study site could be estimated. Extrapolation was felt to be justified because median nearest neighbour distances (NND) of nests were similar on the LMDP site and in the buffer zone in each year (Mann-Whitney Tests: 2011 W = 82.5, p = 0.81; 2012 W = 58.0, p = 0.35; 2013 W = 129.0, p = 0.60).

The number of chicks present in nests was estimated during two sub-periods of the nestling period in order to account for brood size decline: hatching – 25 days, and 26 days to fledging at 50 days which was the mean nestling period at Langholm Moor in three years and for buzzards in Britain (Dare 1961; Hardey *et al.* 2009). Counts of chicks were made from video footage or during visits to search for prey remains at the 32 studied nests. Mean brood sizes for the first nestling sub-period were calculated from counts of chicks made between 8 and 18 days post-hatching, and for the second nestling sub-period between 32 and 45 days post-hatching. The number of chicks in each nestling sub-period did not vary between years (Kruskal-Wallis Test: hatching – 25 days, H = 2.18, d.f. = 2, $p = 0.34$; 26 days – fledging, H = 1.96, d.f. = 2, $p = 0.38$), and so the mean number of chicks across all years was used in models for each sub-period.

When estimating predator impact it is important to include the non-breeding component of the population (Kenward *et al.* 2000; Valkama *et al.* 2005). Non-breeding individuals consist of juveniles and adults without breeding territories, the latter also referred to as 'floaters' (Penteriani *et al.* 2011). The occurrence of non-breeders in raptor populations have been experimentally confirmed in over 40 species (Newton 1992) and can make up a considerable proportion of a population (Newton 1979), including that of buzzards (Kenward *et al.* 2000). Breeding rates (the proportion of the total population breeding) are difficult to investigate without experimentation and can vary between species, habitat and stability of populations (Newton 1979; Penteriani *et al.* 2011). Ringing data for buzzards in Britain has shown that breeding birds comprise between 33 and 38% of the total spring population (i.e. before young have fledged) (Kenward *et al.* 2000). In the absence of any estimates from Langholm Moor, I assume a breeding rate of buzzards at Langholm Moor of 35.5%, being the mid-point of the 33 – 38% estimation from ringing data for Britain as a whole.

The winter buzzard population at Langholm Moor was estimated using a mark – re-sighting method. Between June 2012 and November 2013, individually numbered patagial wing tags were fitted to 33 nestlings, and to 13 juveniles and sub-adults caught in live catch crow-cage traps (a.k.a. ladder-traps) intended for the control of carrion crows *Corvus corone* on the LMDP site. Vantage point surveys lasting approximately three hours each conducted throughout October 2013 on twelve sites and incidental sightings of buzzards across the site revealed that ten marked individuals remained on the study site by November 2013. Between November 2013 and March 2014, these twelve vantage point surveys were conducted once per month (see Chapter 4 for more details). When buzzards were seen during these vantage point surveys and incidentally whilst conducting fieldwork on Langholm Moor, whether or not the individual was wing tagged was recorded. Population size was estimated using a Lincoln-Petersen Index of the ratio of tagged to un-tagged birds from the re-sighting data. To reduce the effect of movements on and off the site on population estimation in non-closed systems, I estimated population using a monthly pair approach (Minta & Mangel 1989). This involved considering the number of tagged birds assumed to be present on the site in a given month and then using sightings data in the following month to estimate population size. This had the effect of reducing the period between release (or confirming continued presence of tagged individuals) and collection of sighting data, and therefore reducing the effect of movements on and off the site. This approach was repeated three times throughout the winter (November & December; December & January; January & February) and a mean population estimate taken from the three estimates.

Most studies of sex ratios in raptor nestlings have found no significant deviation from a 1:1 ratio (Newton 1979; Newton *et al.* 1981), and I have no reason to consider that there was differential post-fledging mortality between sexes, therefore I assumed a 1:1 sex ratio of all buzzard ages in both summer and winter.

6.3.4 Bioenergetics and grouse consumption models

Bioenergetics and prey consumption models were constructed to estimate the number of grouse consumed by buzzards at Langholm during three summers and one winter. Models utilised average values from buzzard diet and population data from Langholm Moor, and other parameters and sources from published literature (Table 6.1).

The ‘Field Metabolic Rate’ (FMR) measures the energy requirement of a free-living animal behaving normally in its natural habitat (Nagy 1987). Estimations of FMR are derived from doubly-labelled water (DLW) techniques which measure CO_2 production following water labelling (Lifson & McClintock 1966; Masman *et al.* 1988). FMR is principally determined by body mass and phylogeny, which together account for 93 – 95% of variation in FMR (Nagy *et al.* 1999). Here, FMR values for buzzards were estimated using allometric equations for 'all birds' in Nagy *et al.* (1999), and estimated for breeding adults, non-breeding adults and chicks separately.

The FMR of non-breeding adults were calculated as follows:

Equation 1 $$FMR = 10.5 \times M^{0.68}$$

where M is mass in grams, and FMR is measured in kJ/day.

FMR calculations for breeding adults during incubation and chick rearing periods were as follows:

Equation 2 $$FMR(incubating\ female) = 12.9 \times M^{0.61}$$

Equation 3 $$FMR\ (chick\ rearing) = 13.8 \times M^{0.65}$$

Breeding male buzzards provision their incubating female mate (Hardey *et al.* 2009), and so equation 3 was used for breeding males during both incubation and chick rearing periods. Since adult buzzards display reversed size sexual dimorphism whereby adult females are approximately 20% heavier than males, FMR was calculated separately for adult males and females. Body masses for adults were taken from Robinson (2005).

FMR of nestlings was calculated as:

Equation 4 $$FMR\ (nestlings) = 4.58 \times M^{0.76}$$

Nestling mass was calculated using growth curves produced from measurements of 58 nestlings at Langholm between 2012 and 2014 (Figure 6.1). Nestling age was estimated from measurements of the fifth primary, which is related to the age of nestling buzzards (Austin & Houston 1997) using:

Equation 5 $$A = 12.75 + 0.125 \times P5$$

where A is age in days, and P5 is the length of the fifth primary in mm.

Weight was measured to the nearest 10 grams for the same 58 nestlings. Fullness of the nestling's crop was estimated as empty, ¼, ½, ¾ or full, with 10 grams weight deducted for each increment on this scale (Hardey *et al.* 2009). Estimated nestling age was then plotted against weight to create growth curves of nestlings at Langholm (Figure 6.1). No data were available on wing length or mass of nestlings before approximately 15 days of age, and so weight at 15 days was used prior to this. Equations derived from growth curves were used to estimate change in nestling weight with age. A logarithmic relationship best fitted the data ($R^2 = 0.72$), whereby:

Equation 6 $$M = 568.44 \times \log(A) - 1300.5$$

where M is mass in grams, and A is estimated age in days.

Daily and total FMR for nestlings could then be calculated as for adults. Newton (1978) showed that heavier female sparrowhawk nestlings did not consume more than their male siblings. Considering this and in the absence of data on differences in weight between male and female nestlings, nestlings were not separated by sex. Chicks were considered fully grown at fledging (Tubbs 1974; Hardey *et al.* 2009).

FMR values for all individuals were used to estimate Daily Food Requirements (DFR) depending on age, sex (of adults) and breeding status. DFR was calculated using Crocker *et al.* (2002) whereby:

Equation 7 $$DFR = \frac{FMR}{Energy\ content\ of\ food \times (1 - moisture\ content) \times Assimilation\ efficiency}$$

where DFR is in grams; energy content of food is in kJ/g, and moisture content and assimilation efficiency are proportions between 0 and 1.

Energy and moisture content were taken from values for vertebrate prey in Crocker *et al.* (2002) and assimilation efficiency from Bairlene (1999) for *Accipitriformes*.

In order to estimate the total number of grouse consumed by an individual buzzard of a given DFR, the following equation was adapted from Korpimäki and Norrdahl (1991):

Equation 8 $$Individual\ red\ grouse\ eaten = \frac{TFR \times PB}{MMP \times 100}$$

where TFR is total food requirement in grams (DFR × time in days); PB is percentage biomass in buzzard diet consisting of grouse; and MMP is mean mass of prey (grouse) in grams.

The mass of adult grouse was assumed to be 600g, which is a mean of male and female adult grouse (Snow & Perrins 1998). Masses of males and females were not separated because there were no data on the sex bias of predation rates on grouse at Langholm Moor.

The proportion of a prey item that consists of indigestible parts increases with increasing prey size (Slagsvold *et al.* 2010). Kenward *et al.* (1981a) estimated that 75% of the body mass of a pheasant was eaten by goshawks *Accipiter gentilis*, and this figure was also used by Tornberg *et al.* (2012) when estimating consumption of black grouse by buzzards. Therefore, here it was assumed that the consumed mass of an adult grouse was 75% of 600g (i.e. 450g). Grouse chick mass was assumed to be 61.3g, which was the mean weight of chicks at 15 days old at Langholm Moor (LMDP, *unpublished data),* chosen as an estimated average age of grouse chicks observed being delivered to buzzard nests in this study (Chapter 3). Grouse chick weight was not adjusted for indigestible parts because the indigestible portion of a grouse chick would be small (Slagsvold *et al.* 2010), and on one occasion grouse chicks were observed to be swallowed whole by buzzards on camera footage, as were other similar sized prey.

The number of grouse consumed by buzzards was calculated separately for non-breeding adults (separated by sex); incubating females; chick rearing females; chick and mate provisioning males; chicks; and fledglings. This estimate was then multiplied by estimates of population, before summing to create estimates of total consumption in the summer and winter. Estimates were created based on summer diet data from each year separately to explore variation between years, and for each diet assessment method to highlight methodological differences.

The number of grouse eaten by buzzards was estimated during the periods between the twice annual grouse counts at Langholm Moor. This allowed for comparisons between consumption estimates and estimates of total grouse populations from counts. At Langholm Moor, red grouse are counted twice a year on 28 transects using pointer dogs, first in late-March/early-April (spring) to estimate pre-breeding densities and again in late-July to estimate post-breeding densities (Thirgood *et al.* 2000c). Distance sampling corrections were applied to these data, which corrected for differences in counting efficiency between observers, dogs and grouse densities. This entailed recording the perpendicular distance from the transect line to the position at which each grouse was recorded, before calculating an effective strip using the program DISTANCE (Thomas & Buckland 2010). Grouse density was then calculated as:

Equation 9

$$Grouse\ density = \frac{Total\ grouse\ counted}{Transect\ length \times (effective\ strip\ width \times 2)}$$

Analysis of aerial photography data collected at Langholm recorded a core grouse habitat area of 30 km^2 (Langholm Moor Demonstration Project 2014). I therefore multiplied grouse density estimates (in birds / km^2) by 30 to create estimates of total grouse population on Langholm Moor in each period (Table 6.A1 – Chapter Appendix). For each period, I assumed zero grouse emigration from or immigration to the moor, since Langholm Moor is essentially an island moor surrounded by habitat unsuitable to red grouse (Redpath & Thirgood 1997).

There are caveats associated with comparing estimates of consumption with estimates of grouse population. The density of grouse on Langholm Moor will vary between the start and the end of the grouse breeding season. During this period, a number of adult grouse will die, and grouse chicks will fledge. While the first grouse counts in spring will only include adult grouse, the July counts will include both adults and fledged chicks. However, the July counts were unable to distinguish between adult and young grouse on some occasions, so the adult to young ratio is unknown in July from count data alone, although July counts do provide a reasonable estimate of total grouse density and hence population. Therefore, I only compared the estimates of adult grouse consumed by buzzards to estimates of adult grouse population in spring, and I did not compare estimates of grouse chick consumption to any population estimate, since the total number of grouse chicks is unknown as many of those hatched will have already died before the July counts and because not all grouse were identified to age in July.

The period between the spring and July counts averaged 122 days at Langholm. This period included the buzzard incubation period (35 days) which begins in early April (Tubbs 1974), the nestling period (50 days) (Hardey *et al.* 2009, *pers. obs.*) and a 37 day period during which all fledglings were assumed to remain on Langholm Moor (Walls & Kenward 1998). The period between the July and the subsequent spring grouse counts averaged 243 days, during which time all buzzards were considered as non-breeding adults for the purposes of calculations.

6.3.5 Sensitivity analysis

To assess the relative importance of variation in model input parameters, a sensitivity analysis was conducted following the approach of previous bioenergetics and consumption studies (Phillips, Thompson & Hamer 1999; Gremillet *et al.* 2003; Roby & Lyons 2003; Votier *et al.* 2004). The value of each input parameter was increased by 1% of the original value and changes in output value (total number of grouse estimated to have been consumed) were recorded for each change in input value. Additionally, the value for each input parameter was raised and lowered to extreme maximum and minimum values considered reasonable from data gathered at Langholm Moor when available, or from values in published literature (Table 6.4). The effects on model output of inputting each of these extreme values were also recorded in an attempt to highlight variables which would most benefit from further data to improve model accuracy. Variation in breeding rates; breeding period length; FMR; ingestion rate; assimilation efficiency; and mass, energy and moisture contents of grouse prey were all taken from published literature (see Table 6.4 for sources). Following the approach of Phillips, Thompson & Hamer (1999), Gremillet *et al.* (2003) and Votier *et al.* (2004), variation in the proportion of total biomass of summer buzzard diet consisting of grouse was taken as ± 1 *s.e.* of the proportion at all 32 nests. Data from prey remains were used for this purpose because these contained the greatest degree of variation between nests. Number of breeding pairs was adjusted by ± 25%, which encompasses yearly variation of breeding density of buzzards at Langholm since 2008 (LMDP, *unpublished data*) and buzzard populations elsewhere in Britain (Kenward *et al.* 2000; Swann & Etheridge 1995). Brood sizes were varied by ± 1 *s.e.* of broods counted at Langholm for each of the two nestling sub-periods. Variation in winter population was adjusted by ± 1 *s.e.* of the estimates of winter population size over the three monthly pairs from which estimates were made. Variation in the proportion of total biomass of winter buzzard diet consisting of grouse was taken as ± 1 *s.e.* of the mean proportion from pellets collected from all roost sites. Variation in buzzard mass was adjusted by ± 1 *s.e.* of weights of 37 juveniles/sub-adults and 58 nestlings weighed at Langholm between 2012 and 2014.

6.3.6 Variability in estimates

To assess the maximum variability, and hence uncertainty, around the estimates of grouse consumption by buzzards, I also re-ran models by altering all input parameters to their extreme values (Table 6.4), in order to produce maximum and minimum estimates of total grouse consumption, following the approach of Gremillet *et al.* (2003). These estimates provided confidence limits, within which the total number of grouse consumed by buzzards at Langholm Moor are likely to vary according to variation and uncertainty in my estimates of local biotic and abiotic conditions.

Table 6.1. Parameters used in bioenergetics and consumption models to produce average estimates of consumption.

		Source
Breeding pairs	17.6	This study
Breeding rate	35.5%	Kenward *et al.* 2000
Brood size (0 - 25 days)	1.7	This study
Brood size (26 - 50 days)	1.6	This study
Incubation period	35 days	Tubbs 1974
Nestling period	50 days	Hardey *et al.* 2009; this study
Post-fledging period	37 days	This study
Winter population	53.2	This study
Total summer period	122 days	This study
Total winter period	243 days	This study
Adult female buzzard mass	1000 grams	Robinson 2005
Adult male buzzard mass	780 grams	Robinson 2005
Buzzard chick mass	Adjusted for age*	This study
Adult red grouse mass (mean of sexes)	600 grams	Snow & Perrins 1998
Red grouse chick mass	61.3 grams	LMDP (*unpubl. data*)
Ingestion rate	75%	Kenward *et al.* 1981
Food assimilation efficiency	82%	Bairlein 1999
Food moisture content	72%	Barton & Houston 1993
Food energy content	23.2 kJ/gram	Barton & Houston 1993

* Buzzard chicks mass calculated using growth curves (Figure 6.1)

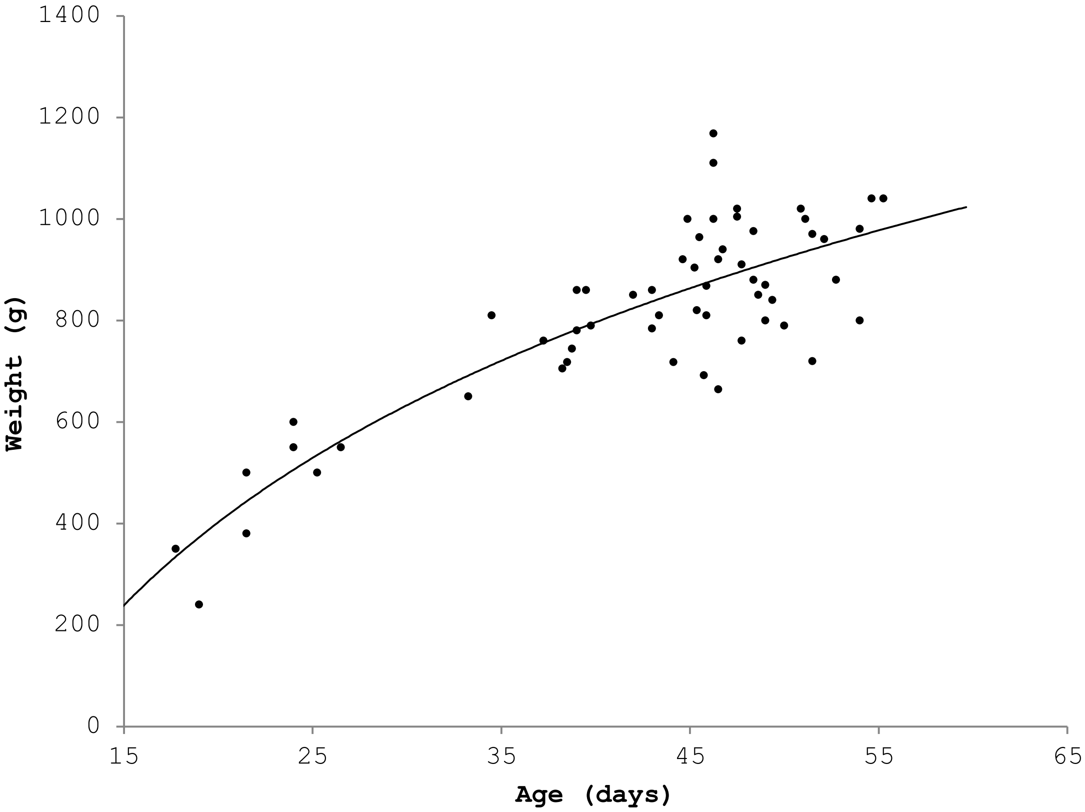

Figure 6.1. Growth curves produced for 58 buzzard nestlings at Langholm between 2011 and 2013. Weight was measured to the nearest 10g, and adjusted for fullness of crops (see text). Age was calculated using: Age (in days) = 12.75 + 0.125 × fifth primary length (Austin & Houston 1997).

6.4 Results

6.4.1 Diet composition

During the three summers, a total of 2,320 hours of footage were collected from the 32 nest cameras, and analysis of footage yielded 1,005 prey deliveries. From searches inside and around the same 32 nests, 486 prey remains and 217 pellets were recovered. Analysis of pellets collected in summer produced 476 prey items (see Chapters 2 & 3 for more details on these results). During the 2013/14 winter, 358 pellets were collected from 20 buzzard roost sites; yielding 952 prey items (see Chapter 5 for more details on these results). Correction factors were applied to pellet data (Stickler *et al.* unpublished data - see methods and Thesis Appendix section A1).

Using camera image data, adult grouse averaged between 0% (in 2011 when no grouse were seen on camera footage) and 2.6% of total biomass of prey, and chicks averaged between 0% (2011, no records) and 0.4%. Using prey remains data, adult grouse averaged between 1.7% and 5.1%, with grouse chicks averaging between 0.3% and 0.8%. Using pellet data, adult grouse averaged between 2.1% and 4.2%, and grouse chicks between 0.2% and 0.8%. Analysis of the winter pellets collected from 20 roost sites during the 2013/14 winter revealed that grouse comprised an average of 6.6% of total biomass of identified prey (Table 6.2).

6.4.2 Population estimation

In each year (2011 – 2013), 12 active buzzard nests were located within the LMDP site. At this density (0.11 nests / km^2) an additional 5.6 nests were assumed to occur in the 1 km buffer zone in each year. This estimated number of nests gave population estimates of 17.6 breeding males and 17.6 breeding females. Buzzard brood counts during the first half of the nestling period gave an average brood size of all nests of 1.7 chicks, and counts during the second half of the nestling period gave an average brood size of 1.6. Chicks per nest did not vary between years in either of the two nestling sub-periods (Kruskal-Wallis ANOVA: First half, H = 5.01, d.f. = 2, *p* = 0.08; second half, H = 3.25, d.f. = 2, *p* = 0.20). Assuming a breeding rate of 35.5%, 32 non-breeding males and 32 non-breeding females were assumed to be present on Langholm Moor and a 1 km buffer zone in addition to the breeding pairs. During the 2013/14 winter, a total of 196 individual buzzard sightings were made between December 2013 and February 2014. Of these sightings, 38 were of individuals fitted with patagial wing-tags. Sub-setting the data into pairs of months gave population estimates of 70.0 in December, 38.7 in January and 50.8 in February. An average of these estimates (mean ± *s.e.* = 53.2 ± 7.4) was used as a population estimate in grouse consumption estimation models.

6.4.3 Bioenergetics modelling

Bioenergetics modelling estimated that average daily Field Metabolic Rates (FMRs) for adult buzzards (calculated using average input values given in Table 6.1) varied between 874.2 kJ / day for an incubating female and 1,229.9 kJ / day for a female during chick rearing. These FMR estimations were equivalent to Daily Food Requirements (DFRs) of between 166.8g / day for an incubating female and 234.7g / day for a chick rearing female. Average FMRs for chicks in the nest were 356.3 kJ / day during the first half of the nestling period and 706 kJ / day for the second half. These were equivalent to DFRs of 68g / day and 134.7g / day respectively.

Combining individual FMR and DFR estimations for all buzzard age classes with population size estimates gave a total energy requirement during a summer period (122 days) for buzzards at Langholm Moor of 1.5×10^7 kJ. This is the equivalent of 2.8×10^6 grams of food required to support the estimated buzzard population at Langholm for one summer period. Chick rearing females had a 6.8% higher FMR and DFR than non-breeding females, and chick rearing was 40.7% more energetically costly than incubation for females. An adult male provisioning for his mate and chicks had a 7.6% higher FMR and DFR than a non-breeding male. Average FMR and DFR values for chicks were 98.2% higher in the second half of the nestling period than in the first half as chicks grew. Requirements of nestlings formed 5.1% of the total food requirement of all buzzards at Langholm Moor during the summer (Table 6.3; Figure 6.2). During the winter period (243 days) the total energy requirement for the estimated winter buzzard population was 1.4×10^7 kJ; the equivalent of 2.6×10^6 grams of food. Over a 365 day year these estimates equate to a total energy requirement of 2.8×10^7 kJ, equivalent to 5.4×10^6

grams of food required to sustain the estimated buzzard population at Langholm Moor over one year (Table 6.3).

6.4.4 Grouse consumption modelling

Average energy and food requirement estimates from bioenergetics models were combined with diet data to estimate the average number of grouse the total estimated buzzard population at Langholm Moor would eat during summer and winter. During summer, estimates of consumption of adult and grouse chicks were produced separately, and for each of the three diet assessment methods in each of the three study years. Winter estimates were for adult grouse only, and data were only available for pellets collected during one winter. Using the average input values (see Table 6.1), average output estimates could be produced for buzzards of each age and sex category, and these are given in Tables 6.A2 – 6.A4 in the Chapter Appendix. Totals for the average estimates in each period and for each diet assessment method are given in Table 6.5, along with minimum and maximum estimates provided as confidence limits.

Using camera image data from three summers, models estimated that the total buzzard population at Langholm Moor ate, on average, 163.4 adult grouse in 2012 and 63.6 in 2013. Comparing these consumption estimates to estimates of total grouse population at Langholm Moor (Table 6.A1 in Chapter Appendix) showed that buzzards consumed on average the equivalent of 12.5% of all adult grouse present on the moor in spring 2012 and 4.6% in 2013. Models also estimated that buzzards ate 201.5 grouse chicks in 2012 and 105.3 in 2013. Models estimated that buzzards ate no grouse, adults or chicks, in 2011 owing to no grouse being recorded on nest camera footage that year.

Using prey remains data from the same three summers, models estimated that buzzards ate on average 318.1 adult grouse in 2011; 238.9 in 2012; and 104.2 in 2013. These estimates are equivalent to buzzards eating an average of 26% of all adult grouse present in spring 2011; 18.3% of adult grouse in 2012 and 7.5% of adult grouse in 2013. Models also estimated that buzzards ate 380 grouse chicks in 2011; 233.5 in 2012; and 146.5 in 2013.

Using pellet data from the same three summers, corrected for underestimation of grouse, models estimated that buzzards ate on average 262.6 adult grouse in 2011; 177.7 adult grouse in 2012; and 128.5 adult grouse in 2013. These estimates are equivalent to buzzards eating an average of 21.5% of all adult grouse present in spring 2011; 13.6% of adult grouse in 2012 and 9.2% of adult grouse in 2013. Models also estimated that buzzards ate 366.3 grouse chicks in 2011; 265.5 in 2012 and 96.1 in 2013.

Based on data from analysis of pellets collected during winter 2013/14, models estimated that buzzards consumed on average 384.2 grouse during the 243 day winter period on Langholm Moor (Table 6.5). This is equivalent to buzzards eating an average of 10.5% of the total grouse population estimated to be present at Langholm Moor in July 2013, also equivalent to 31.2% of the total number of grouse estimated to have died over the same winter (from the difference between the July 2013 and spring 2014 estimates – see Table 6.A1 in Chapter Appendix).

6.4.5 Estimates by breeding status

Models assumed that the size of the non-breeding population was constant between years (using a breeding rate of 35.5% from Kenward *et al.* (2000)), and that non-breeder diet, in terms of the proportion of grouse in the diet measured by each method, was the same as that measured for breeding individuals (these assumptions are discussed later). Therefore, the proportion of the total estimated grouse losses to all buzzards attributed to non-breeding individuals was consistent between years within each method of diet analysis. For all methods and years, the non-breeding individuals were estimated to consume 56.4% of the total estimates of grouse consumption (outlined above and given in Tables 6.A2 – 6.A4) over the entire 122 day summer period, whereas chicks and breeding adults during the nestling period and subsequent post-fledging period were estimated to consume the other 43.6% of the total grouse estimated to be consumed. Chicks in the nest (50 day period) were estimated to consume 5.1% of the total grouse consumed in each year and for each method. If we were to assume that no buzzards were breeding on Langholm Moor during any summer period, the food requirements for breeding activities (incubation and chick and mate provisioning) could be estimated. The requirements of chicks and breeding activities accounted for 12.5% of the total requirements of the whole estimated population in each year.

6.4.6 Sensitivity analysis

By changing the value of the input parameters of the grouse consumption model by 1% of their original value, the total estimated number of grouse consumed by buzzards was affected by 1% or less for all input parameters except food moisture content which altered the estimated number of grouse consumed by 2.7%. By changing the input values of the summer grouse consumption model to those considered to be reasonable extremes, the breeding rate (which affects the size of the non-breeding population) had the greatest effect on the total estimated number of grouse consumed. In fact, by changing the breeding rate to 23% (from the original 35.5%), the estimated total number of grouse consumed was 47.6% higher, whilst changing the breeding rate to 48%, the estimated total number of grouse consumed was 22.8% lower (variation in breeding rate taken from Kenward *et al.* (2000)). After the breeding rate input value, grouse as a proportion of total biomass of buzzard diet had the second greatest effect on the estimated number of grouse consumed. By changing the proportion of grouse in the diet by 1 standard error of the mean proportion measured, the estimated number of adult grouse consumed was ± 35.8% of the original estimate, and ± 39.1% for grouse chicks. By changing the winter population estimate by ± 1 standard error of the measured value, the estimated number of grouse consumed in winter was affected by ± 27.8%, and by ± 31.8% when the proportion of grouse in buzzard diet was changed by ± 1 standard error (Table 6.4).

6.4.7 Confidence limits of estimates

As well as producing average estimates of grouse consumption by buzzards, extreme values of all input variables were also input into models to produce maximum and minimum confidence limits. Average, minimum and maximum estimates are all given in Table 6.5 for both adult red grouse and red grouse chicks and from all three diet assessment methods. For camera image data, the minimum estimate of adult grouse consumed by buzzards was 0 in 2011 and the maximum estimate was 793 consumed in 2012. The equivalent for grouse chicks was a minimum of 0 in 2011 and a maximum of

885 in 2012. Using prey remains data for consumption of adult grouse, the minimum estimate was 13 grouse in 2013 and the maximum was 1,606 in 2011. For grouse chicks the minimum was 31 in 2013 and 1,918 in 2011. Using pellet data, the minimum estimate for consumption of adult grouse was 21 in 2012 and 2013 and the maximum was 1,229 in 2011. For grouse chick, the minimum estimate was 16 in 2013 and the maximum was 1,918 in 2011.

Table 6.2. Mean percentage ± *s.e.* of total biomass of prey in buzzard diet consisting of red grouse adults and chicks. During summer, data were averaged across 11 nests in 2011, 10 nests in 2012 and 11 nests in 2013 using three methods. During the 2013/14 winter, pellet data were averaged across 20 roost sites. Prey weights were adjusted for indigestible parts and for detectability in pellet analysis in both summer and winter (see text). Mean values here were input into grouse consumption estimation models.

	Adult red grouse	Red grouse chicks
Summer		
Camera images		
2011	0 ± 0	0 ± 0
2012	2.6 ± 1.4	0.4 ± 0.2
2013	1.0 ± 0.5	0.2 ± 0.1
Prey remains		
2011	5.1 ± 3.0	0.8 ± 0.5
2012	3.8 ± 2.2	0.5 ± 0.2
2013	1.7 ± 1.1	0.3 ± 0.1
Pellet analysis		
2011	4.2 ± 2.0	0.8 ± 0.5
2012	2.9 ± 1.9	0.6 ± 0.2
2013	2.1 ± 1.1	0.2 ± 0.1
Winter		
Pellet analysis		
2013/14	6.6 ± 2.1	N/A

Table 6.3. Estimated average bioenergetics and food requirements of buzzards at Langholm. Daily field metabolic rate (FMR) and daily food requirement (DFR) are calculated for an individual buzzard depending on age, sex and breeding status using average input values. Total FMR and total food requirement (TFR) are calculated for each buzzard class depending on population estimates and length of period considered.

	FMR (kJ/day/ buzzard)	DFR (g/day/ buzzard)	Period (days)	Population estimate	Total FMR (kJ/ period)	TFR (g)
Summer (122 days)						
Provisioning male	1046.5	199.7	85	17.6	1.6×10^6	3.0×10^5
Incubating female	874.2	166.8	35	17.6	5.4×10^5	1.0×10^5
Chick rearing female	1229.9	234.7	50	17.6	1.1×10^6	2.1×10^5
Chick in the nest (0 - 25 days)*	356.3	68.0	25	29.8	2.7×10^5	5.1×10^4
Chick in the nest (26 - 50 days)*	706.0	134.7	25	27.5	4.9×10^5	9.3×10^4
Non-breeding male	972.3	185.5	85	32.0	2.6×10^6	5.1×10^5
Non-breeding female	1151.3	219.7	85	32.0	3.1×10^6	6.0×10^5
Post fledging period male	972.3	185.5	37	63.4	2.3×10^6	4.4×10^5
Post fledging period female	1151.3	219.7	37	63.4	2.7×10^6	5.2×10^5
Total					$\mathbf{1.5 \times 10^7}$	$\mathbf{2.8 \times 10^6}$
Winter (243 days)						
Non-breeding male	972.3	185.6	243	26.6	6.3×10^6	1.2×10^6
Non-breeding female	1151.3	219.7	243	26.6	7.4×10^6	1.4×10^6
Total				**53.2**	$\mathbf{1.4 \times 10^7}$	$\mathbf{2.6 \times 10^6}$
Total for year					$\mathbf{2.8 \times 10^7}$	$\mathbf{5.4 \times 10^6}$

*Values for chicks were calculated on a daily basis using growth curves (Figure 6.1) and adjusted for average brood size before inputting in models.

Values presented here are averages for each sub-period.

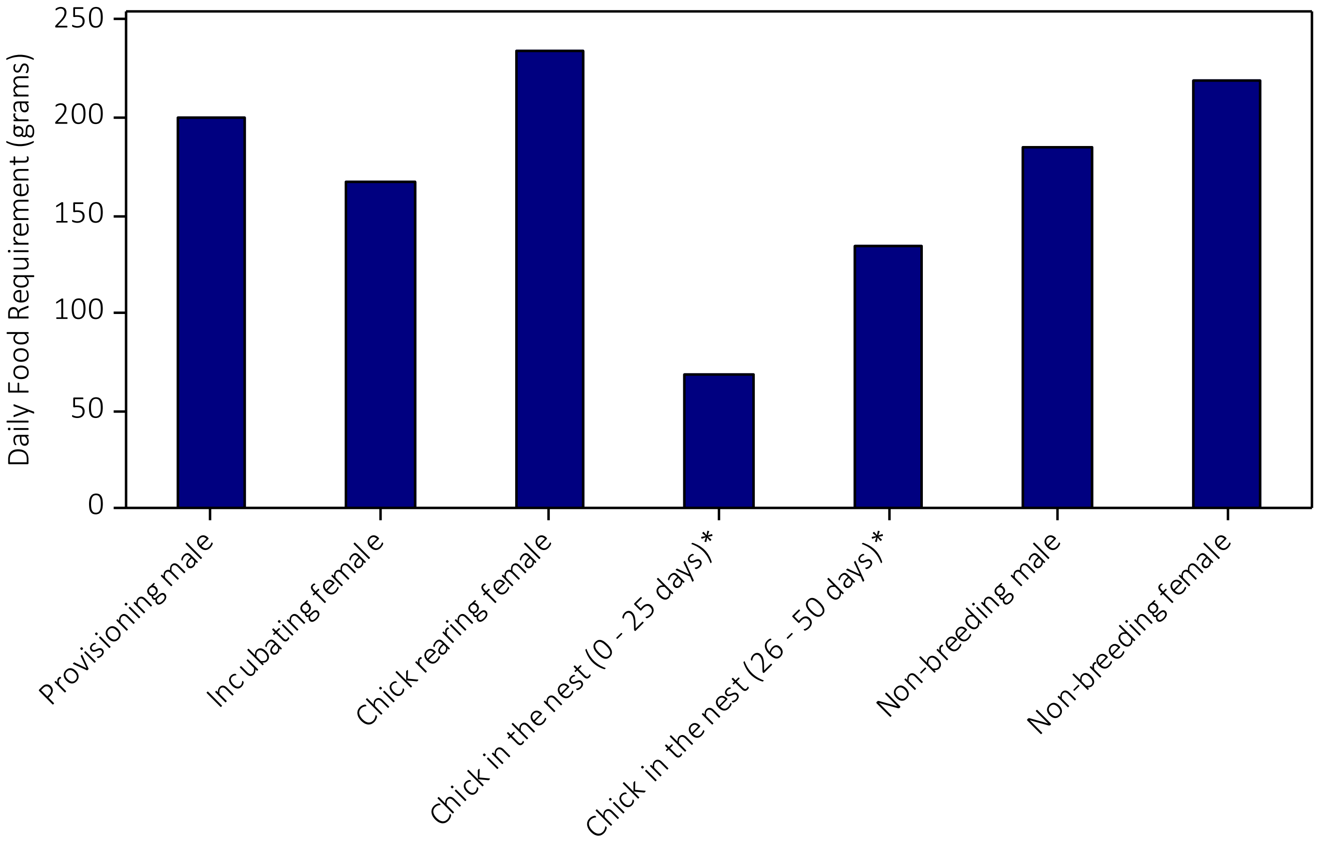

Figure 6.2. Daily Food Requirements of seven buzzard age classes estimated from bioenergetics models.

*Values for chicks were calculated on a daily basis using growth curves (Figure 6.1) and adjusted for average brood size. Values presented here are averages for each sub-period.

Table 6.4. Sensitivity analysis for bioenergetics and consumption models parameters.

Parameter	% change in output for 1% increase	Likely extremes	Source for extreme values	% change in output at extremes
Summer model				
Breeding population	0.44	± 25%	Kenward *et al.* 2000; LMDP 2014; Swann & Etheridge 1995	± 10.9
Breeding rate	0.57	23% / 48%	Kenward *et al.* 2000	+47.6, -22.8
Brood size (< 25 days)	0.02	± 6.7%	This study	± 0.12
Brood size (26 - 50 days)	0.10	± 5.6%	This study	± 0.24
Incubation period	0.08	± 2 days	Robinson 2005	± 0.46
Nestling period	0.19	± 6 days	Robinson 2005	± 2.26
FMR	1.00	± 10%	Nagy *et al.* 1999; Phillips 1999	± 10
Adult buzzard body mass	0.68	± 2%	This study	± 1.3
Buzzard chick mass	0.04	± 3%	This study	± 0.1
Adult red grouse mass	-0.99	± 7%	Schei *et al.* 2005	+7.5, -6.5
Red grouse chick mass	-0.99	± 11%	Park *et al.* 2001	+12.4, -9.9
Ingestion rate	-0.99	± 3%	Slagsvold *et al.* 2010	+4.2, -3.8
Assimilation efficiency	-0.99	± 8%	Nagy *et al.* 1999; Phillips 1999	+8.7, -7.4
Food moisture content	2.69	± 4%	Bairlein 1999	+11.7, -9.5
Food energy content	-0.99	± 10%	Nagy *et al.* 1999; Phillips 1999	+11.1, -9.1
% adult grouse biomass in diet	1.00	± 1.26	This study	± 35.8
% grouse chick biomass in diet	1.00	± 0.19	This study	± 39.1
Winter model				
Winter population	1.00	± 7.4	This study	± 27.8
FMR	1.00	± 10%	Nagy *et al.* 1999; Phillips 1999	± 10
Adult buzzard body mass	0.68	± 2%	This study	± 1.3
Adult red grouse mass	-0.99	± 7%	Schei *et al.* 2005	+ 7.5, -6.5
Ingestion rate	-0.99	± 3%	Slagsvold *et al.* 2010	+4.2, -3.8
Assimilation efficiency	-0.99	± 8%	Nagy *et al.* 1999; Phillips 1999	+8.7, -7.4
Food moisture content	2.69	± 4%	Bairlein 1999	+11.7, -9.5
Food energy content	-0.99	± 10%	Nagy *et al.* 1999; Phillips 1999	+11.1, -9.1
% adult grouse biomass in diet	1.00	± 2.1	This study	± 31.8

Table 6.5. Estimates of buzzard consumption of red grouse at Langholm Moor derived from bioenergetics and prey consumption. Data are total estimated number of grouse consumed for each of three summers using three diet assessment methods and for one winter using pellets from roost sites. Also presented are minimum and maximum estimates for each period and data source, produced by inputting the minimum and maximum values for all parameters into the model and recording the output. All estimates are produced for consumption of adult grouse and grouse chicks separately.

		Adult red grouse			**Red grouse chicks**		
Diet assessment method	Year	Average estimate	Minimum estimate	Maximum estimate	Average estimate	Minimum estimate	Maximum estimate
Camera images (nests)	2011	0.0	0.0	0.0	0.0	0.0	0.0
	2012	163.4	25.5	793.0	201.5	30.9	885.1
	2013	63.6	10.6	297.4	105.3	15.5	442.5
Prey remains (nests)	2011	318.1	44.6	1605.8	380.0	46.5	1917.7
	2012	238.9	34.0	1189.5	233.5	46.5	1032.6
	2013	104.2	12.8	555.1	146.5	30.9	590.1
Pellets (nests)	2011	262.6	46.8	1229.2	366.3	46.5	1917.7
	2012	177.7	21.3	951.6	265.5	61.9	1180.1
	2013	128.5	21.3	634.4	96.1	15.5	442.5
Pellets (winter roosts)	2013/14	384.2	109.5	1138.3			

6.5 Discussion

6.5.1 Accuracy of estimates

Any estimation of prey consumption requires that assumptions be made and will be subject to biases (Phillips *et al.* 1999; Gremillet *et al.* 2003; Redpath & Thirgood 2003; Roby & Lyons 2003; Votier *et al.* 2004a). The accuracy of estimates depends on model structure and quality of input variables, each of which will have specific variability (Boyd 2002). In this study, I have attempted to use the most current data collected at Langholm where possible. Nevertheless, there are a number of assumptions and sources of possible inaccuracy in my estimates.

To acknowledge the uncertainty in my estimates, I produced minimum and maximum estimates to provide confidence limits around the average estimates. These confidence limits were substantial in nearly all instances, and serve to highlight that a measure of uncertainty is introduced by each of the many input values, and this uncertainty becomes multiplied at each stage of the estimation process (Boyd 2002). In fact, the maximum estimates of the number of grouse consumed were so large in some instances as to actually exceed the total number of grouse estimated to be present in spring. This either reflects an underestimation of the total number of grouse to be present, or more likely, an overestimation of the number of grouse consumed by buzzards. This is not to say that the estimates are themselves worthless, just that considerable uncertainty remains, and by highlighting where this uncertainty is introduced, research aimed at improving the robustness of current estimates can be directed, as was a key aim of this study.

Sensitivity analysis indicated that dietary composition estimates had a proportionately large effect on model outputs. In this study I collected data on the presence of red grouse in buzzard diet during three summers and one winter in an attempt to incorporate seasonal variation in diet, known to occur in raptors (Mañosa & Cordero 1992; Amar *et al.* 2003). Summer estimates revealed large annual variations in estimates of grouse consumed by buzzards, in much part owing to variation in buzzard diet composition (Chapter 3). However, I wasn't able to estimate yearly variation in winter buzzard consumption of grouse as only one winter was sampled. Winter buzzard diet composition would benefit from more data, collected over numerous years, to increase consumption estimate accuracy.

While I was able to use diet composition estimates from nest cameras, prey remains and pellets during the breeding season, winter diet data came exclusively from pellet analysis because I was unable to conduct direct observations in the winter. This means that methodological differences could not be explored in terms of their effect on consumption estimates in the same way as breeding season estimates were. Longer-term or more intensive data collection during winter, for example by following individuals with radio-tracking techniques to assess predation rates (Rutz 2003), could improve model accuracy.

An additional assumption made by using data from pellets is that grouse remains in a single pellet represent one grouse eaten. As scavengers, buzzards are known to return to previous kills for additional meals (Tubbs 1974; Barton & Houston 1993; Allen & Feare 2003). If multiple buzzard pellets containing grouse are actually remains of the same individual grouse, models here will have overestimated consumption of grouse, especially during winter when other methods were unavailable. In the future, this could be addressed through conducting a scavenging trial, with the aim of assessing the frequency that wild buzzards return to large kills such as a grouse. Combined with collection and analysis of pellets, this could increase our understanding of this source of bias.

I made an attempt to address detectability bias of pellet analysis with recent data from an experiment with captive buzzards (Stickler *et al.* unpublished data – see Thesis Appendix, section A1), but these detectability values will themselves carry inaccuracy. For example, captive birds may not be representative of natural individuals in their behaviour, energy requirements or prey handling (Dare 1961). However, it is felt that correction was justified considering the low values of detectability highlighted by the captive buzzard experiment. The robustness of correction factors could be improved by validating wild buzzard pellets following known meal compositions, again possibly with intensive observations or remote tracking (Kenward *et al.* 1981a; Rutz 2003).

A further issue with winter diet assessment concerns an uncertainty about the independence of buzzard roost sites. Because buzzards are predominately monogamous (Picozzi & Weir 1974; Tubbs 1974), the number of nests at which data were collected in the summer was likely to be the same as the number of breeding pairs. Yet, whether the 20 winter roost sites at which pellets were collected represented 20 individuals is less certain. However, data from radio and GPS tagging of nine buzzards on Langholm during the same winter showed roost site use was regular by these individuals (see Chapter 5 for details), indicating that it is likely that 20 individuals were sampled. More observations of marked individuals or tracking of radio-/GPS-tagged individuals could improve our knowledge of this in the future.

Assessment of diet during the summer was also not without limitations. All methods of assessing diet carry inherent biases, and there is no method that can provide an absolute measure of dietary composition in raptors (Redpath *et al.* 2001a; Lewis *et al.* 2004; Tornberg & Reif 2007). A number of previous studies have advocated combining estimates across methods (Collopy 1983; Simmons *et al.* 1991; Rooney & Montgomery 2013). However, the effect of combining estimates could vary between species, habitats and years (Redpath *et al.* 2001; Chapter 2) and therefore requires caution. For transparency here the decision was made not to combine estimates from three methods used during the summer, and instead produce consumption based on each method. Using data from prey remains, models produced higher estimates of adult grouse consumption by buzzards in all three years, and higher estimates of consumption of grouse chicks in two out of three years compared to estimates produced with nest camera and pellet analysis data. The overestimation of large birds in prey remains data is well documented in raptor diet studies (Redpath *et al.* 2001; Lewis *et al.* 2004; Chapter 2). Conversely, depending on the sampling regime, direct observations with methods such as nest cameras may miss the relatively few records of large birds delivered to nests. This could have a relatively large effect on model output because large birds, such as grouse, have a proportionately large contribution to total biomass of prey. This is highlighted by results from consumption models produced for 2011 using camera image data, which estimated that no grouse were eaten by buzzards in that year. Evidently, this is certain to not be the case, considering that grouse remains were found at the nests and in the pellets of the same breeding pairs filmed with nest cameras.

Inherent in my estimates of buzzard diet composition, and hence consumption estimates, is the key assumption that data are representative of diet of all buzzards. This means that I assumed that data from the sampled nests and roosts were typical of all nests and roosts. I have reasonable confidence in this assumption because nests and roosts were sampled within the same area of Langholm Moor in each year. Also, sampled nests comprised the majority of the number of nests estimated to be on the study site in each year. In winter, the presence of grouse in pellets was found to be lower in pellets from roosts in grassier areas (Chapter 5) and I attempted to ensure that roosts were sampled in a range of habitats on and around Langholm Moor. Nevertheless, increased sample sizes could still increase the accuracy of estimates.

Similarly, I assumed that diet composition data are representative of the diets of all individuals, whether they were breeders or non-breeders. Sampling nests to estimate diet proportions is a widely used technique for diet assessment of breeding raptors (Lewis *et al.* 2004), yet it is more difficult to assess diet in non-breeders. There is evidence suggesting that hunting efficiency is greater in breeding than non-breeding raptors (Penteriani *et al.* 2013). It is possible therefore that the amount of grouse, which are a large and relatively difficult prey for a buzzard to capture (Tubbs 1974; Graham *et al.* 1995), may be lower in the diet of non-breeding and younger individuals. Thus, the assumption that diet was similar between breeders and non-breeders may have overestimated consumption by non-breeders. Testing this would require additional intensive data collection, such as from radio tracking and observing predation events (Kenward *et al.* 1981a) of non-breeding individuals.

During winter all buzzards were classed as non-breeders in models. Nevertheless, diet choice can change with age as individuals become more efficient hunters (Rutz, Whittingham & Newton 2006). Previous analysis at Langholm suggested that the presence of grouse in buzzard pellets collected at winter roosts was not related to the age of the buzzard observed regularly using the roost site (Chapter 5). Quantification of non-breeding buzzard diet, including age and seasonal variability, could also improve model accuracy.

Sensitivity analysis showed that population estimates also had a relatively large effect on model outputs. The breeding rate during the summer, which affects the estimated number of non-breeders, had the greatest effect on summer model outputs. I assumed a breeding rate of 35.5% which is an average for buzzards in Britain from ringing data (Kenward *et al.* 2000). However these estimates come from data that are now 15 years old, during which time buzzards have increased in population and range throughout Britain (Balmer *et al.* 2014). Models would benefit from recent data on population and breeding rates at Langholm.

During the winter, buzzard population estimation was based on a Lincoln-Petersen Index following a mark, release and resighting approach. This type of index assumes that populations are largely ‘closed’, that is, sedentary with no movement on or off the study site. While individuals were only marked on Langholm Moor, it is likely that some tagged individuals moved off the site while some un-tagged individuals moved on. In both of these cases, the ratio of tagged to un-tagged birds would be lowered and this would inflate estimates. I attempted to minimise this effect by restricting observation periods to a single month and using the number of tagged birds present in the previous month, before taking an average estimate. Sightings were also conducted during the winter which is a period of relative stability for buzzards (Walls & Kenward 1998). However, it would be valuable to understand the degree of stability of the buzzard population at Langholm Moor, and also the extent to which buzzards hunted on the moor relative to the time they spent away from the moor. Improving our understanding of both of these aspects would benefit from more data collected over a number of years using individually marked or remotely tracked individuals.

Bioenergetics models estimated FMR and DFR using published calculations (Nagy *et al.* 1999), which were adjusted to account for differences in buzzard weight and age, using data from Langholm Moor where possible. However, these estimates are based on calculations which will themselves have inherent variability, for example between seasons. It is often assumed that energetic costs may be higher during colder periods due to the extra costs of thermoregulation (Riedstra *et al.* 1998; Phillips *et al.* 1999). However, birds can alter their behaviour during cold periods to conserve energy (Warkentin & West 1990; Gremillet *et al.* 2003), for instance buzzards may increase hunting from the ground (Wuczyński 2005). The effect of this variability on estimates here may therefore be small. Bioenergetics models estimated DFR of adult buzzards to range between 166.8g for an incubating female and 234.7g for a chick rearing female, which are within the range of previous estimates of wild buzzards in the UK gathered from observations (Dare 1961).

6.5.2 Impact on grouse at Langholm Moor

Weir (1978) estimated that a single pair of peregrines with four young would eat 110 red grouse during a single breeding season. Redpath & Thirgood (1999) estimated that on average a pair of peregrines would remove between 12.8 and 34.8 grouse, adults and young, in a breeding season. In comparison, the models in this study estimated that a pair of buzzards with an average brood size for Langholm Moor would remove between 0 and 13.6 grouse including adults and chicks, depending on yearly variation in diet composition and the method of diet assessment. Similarly, Picozzi (1978) estimated that a pair of hen harriers removed 255 grouse chicks from an area of moorland in Scotland, while Redpath & Thirgood (2003) estimated that between 89 and 141 grouse chicks were taken by each hen harrier pair at Langholm. Equivalent figures for buzzards in this study were between 0 and 7.4 grouse chicks per buzzard nest. It seems therefore that impact on grouse at Langholm Moor by the average buzzard pair is low compared to some other raptor species, which is to be expected considering the differences in ecology and the more generalist nature of buzzards compared to hen harriers and peregrines. However, this study has shown that if the buzzard population is large, total impact on grouse populations is potentially considerable.

In this study, models revealed a large yearly variation in the total estimated number of grouse eaten by buzzards during the summer. Using data from both prey remains and pellets, estimates of buzzard consumption on adult grouse declined year-on-year between 2011 and 2013. Using prey remains data, models estimated that buzzards ate approximately half of the number of adult grouse in 2013 that they ate in 2011, and only a third of the grouse chicks in 2013 that were eaten in 2011. Similarly, models using pellet data estimated that only a quarter of the number of adult grouse and two-fifths of the number of grouse chicks eaten in 2011 were eaten in 2013. This is despite grouse density during this study peaking in 2013 (Table 6.A1 – Chapter Appendix). Redpath & Thirgood (1999) showed that yearly variations in estimates of grouse loss to hen harriers and peregrines were due to yearly variation in raptor population size, the number of young raised per pair and variation in provisioning rates of grouse. However, I estimated that the buzzard population size at Langholm was the same between years and found no significant difference in brood sizes between year. This means that yearly variations here were due to differences in the proportion of grouse in buzzard diet. Recent data from Langholm Moor suggest that buzzard predation rates on grouse may be linked to fluctuations in field voles, whereby higher vole densities may encourage foraging on the moor (Chapter 4) and increase incidental predation on grouse (Chapter 3).

Redpath & Thirgood (1999) did not attempt to estimate consumption of grouse by peregrines during winter because of the problems associated with generating feeding rates from pellet analysis. While the estimates here are not free from problems associated with pellet analysis, the bioenergetics approach has produced a ‘current best’ estimate for buzzard predation on grouse in winter. Additional research, focussing on winter diet composition and population estimation, conducted over several years, would be beneficial in increasing the accuracy of estimates.

I was also able to estimate the proportional rates of consumption of grouse by buzzards according to breeding status and age. Estimates suggested that non-breeding individuals contributed 56.4% of the total consumption of grouse, while chicks in the nest contributed just 5.1% of the total consumption of grouse. This is potentially important if considering the potential impact of selective removal of individuals to reduce impact of grouse. In recent years, applications for licenses to remove buzzards (either lethally or not) to reduce impact of predation on gamebirds are being made for breeding individuals only (FERA 2012). My estimates suggest removal of breeders only may have only limited effect (while acknowledging the far greater uncertainty associated with estimates attributed to non-breeders) even when I assume that all records of grouse represent predation rather than scavenging events. Many proposed interventions associated with breeding individuals (e.g. removal of nests or eggs, or removal of territorial adults) are likely to either result in the retention of the territorial adults or their replacement by non-breeding individuals from nearby (Penteriani *et al.* 2011). My estimates of grouse consumption suggest that by removing the food requirements of nestlings and those associated with incubation and chick provisioning (above those required for non-breeders), total grouse losses would still be 87.5% of those currently estimated. This suggests that reduction of losses of grouse to buzzard predation will require a more holistic approach, considering limiting effects from all buzzards irrespective of breeding status.

It cannot be assumed that the same number of grouse consumed by buzzards would persist if buzzards were not present at Langholm. There are a number of reasons for this. Firstly and crucially, I cannot be sure that the grouse recorded in assessments of buzzard diet were actually killed by the buzzard eating them. Although a buzzard is capable of predating prey as large as adult grouse, buzzards are also known to scavenge kills from other predators or following death of prey from other causes of mortality (Tubbs 1974; Barton & Houston 1993; Graham *et al.* 1995; Allen & Feare 2003). A trial assessing scavenging rates of buzzards could improve our understanding of the ratio of killed:scavenged prey in the diet of buzzards.

Secondly, I have not been able to identify the degree to which buzzard predation on grouse is additive to other mortality causes. Compensatory mortality may occur if: (i) buzzards predated non-territorial grouse or ones that would not have bred had they not been predated, (ii) there were sufficient non-territorial grouse to replace the predated territorial birds, or (iii) those grouse that were predated by buzzards would have died from other causes of mortality (Redpath & Thirgood 1997). If compensation is occurring through any or a combination of these scenarios, the estimates of consumption here will not be the same as the number of grouse removed from the moor by buzzards. There were no data on the territorial status of the grouse eaten by buzzards. However, diet analysis showed that as well as eating grouse buzzards ate known predators of grouse and grouse chicks, such as crows, weasels *Mustela nivalis* and stoats *Mustela erminea.*

These are known to feature in buzzard diet elsewhere (Swann & Etheridge 1995; Rooney & Montgomery 2013), and their predation by buzzards may have introduced a degree of compensation of the number of grouse predated by buzzards. For these reasons, estimates of impact here should be treated with caution and as best current estimates only.

When considering estimates of grouse consumption by buzzards in a context of driven grouse shooting, as is the aim of the management at Langholm Moor (Langholm Moor Demonstration Project 2007), it is important to note that not all of the grouse eaten by buzzards would have been available to shoot in the absence of buzzards. The proportion of the total grouse population killed during a season of driven grouse shooting depends on a number of local biotic and abiotic factors specific to the moor being hunted. These include, but are not limited to: the distance and area grouse are driven over, the demographic composition of the grouse population, the skill and accuracy of the shooters, weather conditions, and vegetation length and density (Hudson & Rands 1988; Hudson & Newborn 1995; Bunnefeld *et al.* 2009). Additionally, for the reasons outlined above, many grouse may not have survived in the absence of buzzards as mortality from other causes replaced predation by buzzards.

Although not as powerful as predator removal experiments (Newton 1998), estimating predator consumption can play an important role in understanding the impact of predation on prey groups. The models developed here could be a useful tool for researchers interested in exploring the potential impact of predation on economically important or threatened prey. However, the key assumptions that have been highlighted would need addressing prior to any implementation of management action, as well as social and economic considerations which are beyond the scope of this study.

6.6 Appendix

Table 6.A1 Mean densities and population sizes of red grouse at Langholm Moor derived from distance sampling on 28 grouse count transects in spring and July between 2011 and 2014. Total grouse populations were estimated by multiplying densities by the assumed core grouse habitat area of 30km^2 at Langholm (Langholm Moor Demonstration Project 2014). Total grouse includes all grouse counted, including those of unknown age.

	Adult grouse/ km^2	Grouse chicks/ km^2	Total grouse/ km^2	Adult grouse population	Grouse chick population	Total grouse popn
Spring 2011	40.8	n/a	40.8	1223.8	n/a	1223.8
July 2011	36.5	35.0	73.2	1096.5	1049.5	2196.9
Spring 2012	43.4	n/a	43.4	1303.1	n/a	1303.1
July 2012	36.4	45.4	81.8	1092.6	1362.8	2455.4
Spring 2013	46.4	n/a	46.4	1391.9	n/a	1391.9
July 2013	30.2	76.8	122.5	905.6	2304.0	3675.7
Spring 2014	81.5	n/a	81.5	2445.2	n/a	2445.2

Note: The following three tables (Tables 6.A2 – 6.A4) are produced from bioenergetics and consumption models using average input values given in Table 6.1, and presented for each buzzard age/sex class. For brevity, maximum and minimum confidence limits are not provided for each buzzard age/sex class, but are given for the whole population in Table 6.5.

Table 6.A2. Estimates of buzzard consumption of red grouse at Langholm Moor. Data are grouse consumed per buzzard during periods considered (see Table 6.3) and as totals for each buzzard class. Estimates are derived from bioenergetics and prey consumption models using analysis of **camera images** collected from 32 nests over three summers.

	Adult grouse						Grouse chicks					
	Grouse eaten / buzzard			Total grouse eaten			Grouse eaten / buzzard			Total grouse eaten		
	2011	2012	2013	2011	2012	2013	2011	2012	2013	2011	2012	2013
Summer												
Provisioning male	0.0	1.0	0.4	0.0	17.4	6.8	0.0	1.2	0.6	0.0	21.5	11.2
Incubating female	0.0	0.3	0.1	0.0	6.0	2.3	0.0	0.4	0.2	0.0	7.4	3.9
Chick rearing female	0.0	0.7	0.3	0.0	12.1	4.7	0.0	0.8	0.4	0.0	14.9	7.8
Chick in the nest (0 - 25 days)	0.0	0.1	0.0	0.0	3.0	1.2	0.0	0.1	0.1	0.0	3.6	1.9
Chick in the nest (26 - 50 days)	0.0	0.2	0.1	0.0	5.4	2.1	0.0	0.2	0.1	0.0	6.7	3.5
Non-breeding male	0.0	0.9	0.4	0.0	29.4	11.5	0.0	1.1	0.6	0.0	36.3	19.0
Non-breeding female	0.0	1.1	0.4	0.0	34.8	13.6	0.0	1.3	0.7	0.0	42.9	22.4
Post fledging male	0.0	0.4	0.2	0.0	25.4	9.9	0.0	0.5	0.3	0.0	31.3	16.3
Post fledging female	0.0	0.5	0.2	0.0	30.0	11.7	0.0	0.6	0.3	0.0	37.0	19.3
Total				**0.0**	**163.4**	**63.6**				**0.0**	**201.5**	**105.3**

Table 6.A3. Estimates of buzzard consumption of red grouse at Langholm Moor. Data are grouse consumed per buzzard during periods considered (see Table 6.3) and as totals for each buzzard class. Estimates are derived from bioenergetics and prey consumption models using analysis of **prey remains** collected from 32 nests over three summers.

	Adult grouse						Grouse chicks					
	Grouse eaten / buzzard			Total grouse eaten			Grouse eaten / buzzard			Total grouse eaten		
	2011	2012	2013	2011	2012	2013	2011	2012	2013	2011	2012	2013
Summer												
Provisioning male	1.9	1.4	0.6	33.9	25.5	11.1	2.3	1.4	0.9	40.5	24.9	15.6
Incubating female	0.7	0.5	0.2	11.7	8.8	3.8	0.8	0.5	0.3	13.9	8.6	5.4
Chick rearing female	1.3	1.0	0.4	23.4	17.6	7.7	1.6	1.0	0.6	28.0	17.2	10.8
Chick in the nest (0 - 25 days)	0.2	0.1	0.1	5.7	4.3	1.9	0.2	0.1	0.1	6.9	4.2	2.6
Chick in the nest (26 - 50 days)	0.4	0.3	0.1	10.5	7.9	3.4	0.5	0.3	0.2	12.5	7.7	4.8
Non-breeding male	1.8	1.3	0.6	57.3	43.0	18.7	2.1	1.3	0.8	68.4	42.0	26.4
Non-breeding female	2.1	1.6	0.7	67.8	50.9	22.2	2.5	1.6	1.0	81.0	49.8	31.2
Post fledging male	0.8	0.6	0.3	49.3	37.1	16.2	0.9	0.6	0.4	58.9	36.2	22.7
Post fledging female	0.9	0.7	0.3	58.4	43.9	19.1	1.1	0.7	0.4	69.8	42.9	26.9
Total				**318.1**	**238.9**	**104.2**				**380.0**	**233.5**	**146.5**

Table 6.A4. Estimates of buzzard consumption of red grouse at Langholm Moor. Data are grouse consumed per buzzard during periods considered (see Table 6.3) and as totals for each buzzard class. Estimates are derived from bioenergetics and prey consumption models using analysis of **pellets** collected from 32 nests over three summers and 20 roost sites in one winter.

	Adult grouse						Grouse chicks					
	Grouse eaten / buzzard			Total grouse eaten			Grouse eaten / buzzard			Total grouse eaten		
	2011	2012	2013	2011	2012	2013	2011	2012	2013	2011	2012	2013
Summer												
Provisioning male	1.6	1.1	0.8	28.0	19.0	13.7	2.2	1.6	0.6	39.1	28.3	10.3
Incubating female	0.5	0.4	0.3	9.6	6.5	4.7	0.8	0.6	0.2	13.4	9.7	3.5
Chick rearing female	1.1	0.7	0.5	19.4	13.1	9.5	1.5	1.1	0.4	27.0	19.6	7.1
Chick in the nest (0 - 25 days)	0.2	0.1	0.1	4.7	3.2	2.3	0.2	0.2	0.1	6.6	4.8	1.7
Chick in the nest (26 - 50 days)	0.3	0.2	0.2	8.7	5.9	4.2	0.4	0.3	0.1	12.1	8.8	3.2
Non-breeding male	1.5	1.0	0.7	47.3	32.0	23.1	2.1	1.5	0.5	65.9	47.8	17.3
Non-breeding female	1.7	1.2	0.9	56.0	37.9	27.4	2.4	1.8	0.6	78.1	56.6	20.5
Post fledging male	0.6	0.4	0.3	40.7	27.6	19.9	0.9	0.6	0.2	56.8	41.2	14.9
Post fledging female	0.8	0.5	0.4	48.2	32.6	23.6	1.1	0.8	0.3	67.3	48.8	17.7
Total				**262.6**	**177.7**	**128.5**				**366.3**	**265.5**	**96.1**
Winter												
Non-breeding male			6.6			175.9						
Non-breeding female			7.8			208.3						
Total						**384.2**						

Chapter 7: Discussion

Buzzard 'sitting on the fence' at Langholm Moor [Photo credit: John Wright]

"The management of predation depends on the profound
basic understanding of predators and the systems they occupy."

S. Ormerod
(2002)

7.1 Study context and aims

Human-wildlife conflicts are often contentious and ultimately damaging for both wildlife and the people involved (Madden 2004). In many parts of the world, instances of conflicts are increasing with the expansion of human activities into natural wildlife habitats (Woodroffe *et al.* 2005). Conflicts involving predators can be particularly controversial when predators compete with humans for shared resources, which may be economically important, and when predators are legally protected and admired by the public (Woodroffe *et al.* 2005). When the various and sometimes numerous human interest groups involved in these conflicts have different attitudes and priorities, the conflicts can become highly controversial. It has been frequently recognised by stakeholders, often including those on seemingly opposing sides, that a key part of resolving conflict is open dialogue between these groups (Redpath *et al.* 2013). In order to have any chance of reaching solutions, this dialogue must utilise current ecological knowledge of the systems in question (Lees *et al.* 2013). As I explained at the beginning of this thesis, it was a broad aim of mine to improve our understanding of the predator-prey relationship between buzzards and red grouse, with the hope that this knowledge would facilitate such dialogue and hasten the development of management solutions.

The first step to finding successful solutions to any human-wildlife conflict is to define the conflict itself. Traditionally, human-wildlife conflicts were defined as ‘situations where the actions of humans or wildlife has an adverse effect on the other’ (Conover 2002). However, this definition can portray wildlife as ‘conscious antagonists’, and can therefore ignore the underlying human dimension (Peterson *et al.* 2010). Often, these conflicts are more accurately described as being conflicts between human interest groups over wildlife (Redpath *et al.* 2014). This is the case for the broad context of the current study. Red grouse are an economically important game species in parts of Britain (Sotherton *et al.* 2009), which are prey to a variety of avian and mammalian predators (Hudson & Newborn 1995), one of which is the common buzzard. The recovery of buzzard ranges and populations the effects of persecution, pesticides and reductions in prey (Balmer *et al.* 2014) has created and reignited conflicts with gamebird shooting interests (Harradine *et al.* 1997; Lees *et al.* 2013; Parrott 2015). Explicitly, conflict has arisen between stakeholders chiefly concerned with the maintenance of red grouse management and those more concerned with the conservation of raptors (Thirgood *et al.* 2000a). This conflict has considerable implications for the management of large parts of the British Uplands (Thirgood & Redpath 1999; Gibbons *et al.* 2008). Indeed, the conflict surrounding raptors and red grouse is now one of the most contentious, topical and intractable examples of a conflict involving humans and wildlife in Britain today (Redpath & Thirgood 1997; Thirgood *et al.* 2000a; Ormerod 2002; Woodroffe *et al.* 2005; Sotherton *et al.* 2009; Redpath *et al.* 2014). Once the conflict has been defined, it is important for stakeholders to work together to find mutually acceptable and effective management solutions (Redpath *et al.* 2014). As explained above, it is only with access to sound ecological knowledge of the systems involved that effective management solutions can be found.

Over the last two decades, much of the focus surrounding the raptor-grouse issue has centred around the impact of hen harrier and peregrine predation on red grouse (Redpath & Thirgood 1997; Redpath *et al.* 2010), and this remains an important area of ecological study and debate today (Langholm Moor Demonstration Project 2014; Redpath *et al.* 2014). However, the relationships between other raptor species, including the common buzzard, and red grouse have received less attention. Whilst the relationship between buzzards and pheasants has been studied (Kenward *et al.* 2001; Parrott 2015), there are no published studies that have focussed on examining the potential for buzzards to impact on red grouse. This is despite a widespread and well documented recovery of buzzard population and range during the last 40 years (Clements 2002; Musgrove *et al.* 2013; Balmer *et al.* 2014), and an increasing concern amongst gamekeepers that buzzards are impacting negatively on gamebirds (Harradine *et al.* 1997; FERA 2012; Lees *et al.* 2013).

In this thesis, I have addressed this gap by investigating aspects of diet, foraging behaviour and responses to changing prey abundances of a population of buzzards on Langholm Moor – an upland heather-moor managed for the shooting of red grouse. Langholm Moor has been a key site for studying the raptor-grouse system in Britain for over two decades now, starting as the site of the Joint Raptor Study (JRS) (1992 – 97) and now as the site of the Langholm Moor Demonstration Project (LMDP) (2008 – Present). The active management for the benefit of red grouse alongside strict protection of raptors make this an appropriate study site for exploring how buzzards may impact on a managed population of red grouse.

As I outlined in the introduction, a variety of methods have been used to assess the impact of predation (also see review in Park *et al.* (1995)). These include questionnaires, dietary analysis, correlational studies, survival analyses and experimental manipulation of predator numbers. Probably the most scientifically rigorous way of assessing the impact of a predator on its prey is to conduct predator removal experiments (Newton 1998). However, since most concerns surrounding the impacts of predation on red grouse surround legally protected raptors (Park *et al.* 2008), these experiments have not been conducted in order to study impact on red grouse.

Therefore, in this study I focussed on dietary analysis, foraging patterns and responses to prey abundances in order to explore and predict the potential impacts of buzzards on red grouse. Specifically I aimed to:

1. evaluate the key biases of methods used to assess raptor diet composition (Chapter 2);
2. investigate numerical and functional responses of buzzards during the breeding season (Chapter 3);
3. investigate factors determining buzzard foraging patterns and their relationship with grouse mortality indices (Chapter 4);
4. describe buzzard diet in the winter and explore the factors leading to the presence of red grouse in buzzard diet (Chapter 5);
5. estimate the number of red grouse removed by buzzards from Langholm Moor (Chapter 6).

In this discussion I review how my findings have addressed each of my aims, before attempting to draw links between these findings in order to explore some key themes this study has highlighted. I then discuss the implications for management of red grouse on Langholm Moor and elsewhere. Finally, I identify how we can improve our understanding of this system and review some of the recent management solutions which have been proposed to reduce buzzard impacts on gamebirds, and suggest how my research lends support to the efficacy or otherwise of some of these for mitigating the impacts of buzzards on red grouse.

7.2 Addressing the aims of the thesis

7.2.1 Aim 1: to explore biases of methods for assessing raptor diet

In Chapter 2, I investigated the biases associated with three methods of assessing the composition of raptor diet. The analysis of prey remains and regurgitated pellets collected at nest sites are two commonly utilised sources of data for indirectly describing raptor diet during the breeding season. Recently, the use of remote video technology has become a viable option to collect large amounts of data from direct observations of nests. I collected data on the composition of buzzard diet using these three methods at 32 nests in three years on and around Langholm Moor. I compared data obtained from direct observations using motion-triggered nest cameras with analysis of prey remains and regurgitated pellets collected at the same 32 nests. My results showed that methods can over- and under-estimate particular prey species, which may be useful in understanding the biases and limitations of future raptor diet studies. In addition, I found that biases varied between years, a finding that is possibly unique to this study, which could affect the results of studies interested in temporal variations in raptor diet.

In recognition of these findings from Chapter 2, I utilised all three methods in Chapters 3 & 6 and discussed the conclusions that I would derive had just one method been available. In Chapter 5, when describing the diet of buzzards in winter (Aim 4), only one method (pellet analysis) was available and so I discussed the possible influence this had on the results of that chapter, and also incorporated results from a recent study which aimed to better quantify the biases of pellet analysis (Stickler *et al.* unpublished data – see Thesis Appendix, section A1).

7.2.2 Aim 2: to investigate numerical and functional responses of buzzards during the breeding season

In Chapter 3 I sought to investigate how buzzards responded to annual changes in prey abundance, and in particular how this might affect the impact of buzzards on red grouse.

The abundance of voles, the preferred prey of buzzards at Langholm and elsewhere, declined during the study, whilst red grouse, lagomorph and meadow pipit abundances did not change. Consequently, there appeared to be evidence of a functional response, in terms of changing dietary composition, to these annual changes in vole abundance. As predicted, buzzards ate fewer voles when vole abundance was lower. However, buzzards did not appear to eat more grouse when vole abundance was lower. Instead, evidence from prey remains and pellets showed that buzzards ate fewer red grouse when vole abundance was lower, preferring to eat a wider variety of prey, which included more rabbits, moles, shrews, corvids and pigeons. It appeared that when vole abundance was lower, buzzards selected prey from the grass-dominated farmland periphery of the moor, thus drawing them away from heather-dominated areas of the moor favoured by red grouse. I suggested this showed red grouse to be an incidental prey of buzzards, which they encounter while hunting for voles on the moor.

I found no evidence of a numerical response to annual changes in vole abundance by buzzards in terms of breeding density and breeding success. This highlighted the generalist and opportunistic nature of buzzards which was sufficient to not affect breeding parameters when abundances of their main vole prey decline.

I suggested that the heterogeneous landscape at Langholm Moor where main, alternative and incidental prey of buzzards were distributed in patches was a key driver of these results. These data highlight that knowledge of all available prey resources is important when investigating predator responses.

7.2.3 Aim 3: to investigate factors determining buzzard foraging patterns and their relationship with grouse mortality indices

In Chapter 4 I explored correlates of buzzard foraging patterns on Langholm Moor, in terms of habitat and prey, during both summer and winter. I also explored whether the relative importance of these factors varied between years as prey abundances changed.

Temporally, buzzard hunting intensity varied in line with annual variations in vole abundance, although the spatial distribution of voles did not explain any further variation. This latter result may have reflected a discrepancy between the scales at which I assessed buzzard foraging and vole abundance indices, in that voles may vary at a finer spatial scale than those used for assessing buzzard foraging. Buzzards hunted in areas with more grouse during the winter, which I suggested reflected a greater importance of grouse to buzzards during the winter when other prey were less available. I found that the effect on buzzard foraging patterns of broad habitat composition varied between years: buzzards avoided heather dominated areas in years when vole abundance was low, but not when vole abundances were high. These results supported the findings of Chapter 3, in suggesting that incidental predation of red grouse by buzzards may increase when vole abundances are high thereby promoting buzzard foraging in red grouse habitats. I also used a correlative approach to explore relationships between indices of grouse mortality and foraging patterns of buzzards and of all large bird-eating raptors, although I found no evidence of any relationships.

I suggested that these results gave further evidence for a response by buzzards to vole abundance which could influence incidental predation of grouse, but further work is needed to disentangle the impact of buzzards from other raptors.

7.2.4 Aim 4: to describe buzzard diet in the winter and explore factors leading to buzzards eating grouse

In Chapter 5, I turned my attention exclusively to the winter period in an attempt to describe buzzard diet composition. To date, the vast majority of studies describing the composition of raptor diet have been conducted during the breeding season because the presence of a nest at which activity is centred makes collecting data an easier prospect. During the 2013/14 winter, I conducted a tagging project of buzzards at Langholm whereby five individuals were fitted with GPS tags and four were fitted with VHF tags. Locations of these nine birds at dawn and dusk revealed that they regularly used individual roost sites at which regurgitated pellets could be collected and analysed for dietary composition data. By conducting vantage point watches over other apparently suitable roost sites I was able to identify a further 14 sites used by roosting buzzards. The pellets collected from these 23 roost sites revealed that buzzards predominately ate small mammals during the winter. Red grouse remains were identified in 2.9% of pellets and constituted 1.1% of all prey items identified in pellets, although these values were corrected to 5.6% of pellets containing grouse and 1.3% of prey items following results from a recent trial using captive buzzards (Stickler *et al.* unpublished data - see Thesis Appendix, section A1).

The likelihood of a buzzard eating grouse was most affected by the amount of grassland surrounding the roost site: more grassland around a roost site was associated with a tendency for less grouse to appear in buzzard pellets. The amount of heather moorland surrounding the roost site, which was not correlated to the amount of grassland, had no significant effect on the occurrence of red grouse in buzzard pellets. I concluded that this suggested that when buzzards roosted in areas with plenty of non-grouse prey (i.e. grassland habitats typically rich in rabbits, moles, pigeons etc.) they were less likely to hunt in moorland habitats and predate grouse. Whilst the results from this part of the study were not able to demonstrate a temporal response of buzzards to prey or habitat as Chapters 3 & 4 did, they do demonstrate a spatial response to higher abundances of preferred and alternative (non-grouse) prey, which seemed to result in reduced incidental predation of red grouse. From this perspective, these results supported some of the findings of the earlier chapters in suggesting that availability of key prey groups in habitats spatially separated from moorland habitats can reduce predation pressure on red grouse.

7.2.5 Aim 5: to estimate the number of red grouse removed by buzzards from Langholm Moor

Bioenergetics calculations combined with dietary composition data can provide estimates of the number of individual prey items eaten by a predator. In Chapter 6, I attempted to consolidate some of my earlier findings from Chapters 2, 3 and 5, in order to estimate the number of grouse that buzzards could potentially remove from Langholm Moor. To do this, I used estimates of population size together with published bioenergetics calculations to estimate the amount of energy required to support the buzzard population at Langholm Moor. Taking this further, I combined energetic requirement estimates with estimates of the dietary composition of buzzards in summer (Chapter 3) and winter (Chapter 5) to calculate how many red grouse buzzards could eat.

The results suggested that whilst the removal of grouse by an individual buzzard was low (between zero and three grouse in any one summer or winter period) estimates for the total number of grouse removed in summer varied between zero and 26% of all grouse on the moor in spring, and over-winter buzzards were estimated to remove 11% of all grouse present in autumn. In winter, this equated to 31% of the total number of grouse estimated to die over-winter. I detailed the limitations of this approach, and highlighted the areas that would benefit from further empirical study to improve the accuracy of the developed models. The results in Chapter 6 showed that in order to consider the total impact of buzzard predation on red grouse, any cumulative impact from the total buzzard population (including non-breeders) needs to be considered. The results highlighted that there is a potential for this impact to be considerable, although more research is needed to establish the extent to which buzzard predation was additive to other mortality causes.

7.3 Synthesis of key results

In this section I will discuss the links between the results of my thesis, and in doing so identify some pervasive themes that have become apparent. The aim here is to achieve a synthesis of my results in order to discuss how my results contribute to our understanding of the predator-prey relationship between buzzards and red grouse. Specifically, I aim to discuss four key questions:

1. What are the pervasive themes of this study?
2. Are buzzards having an impact on red grouse at Langholm Moor?
3. Would we be likely to observe similar results on other moors?
4. What additional research is needed to improve our knowledge of buzzard impact on grouse, and to test the effectiveness of some management options?

7.3.1 Pervasive themes

A number of themes have become apparent throughout this study, the first of which highlights the importance of small mammals, especially field voles *Microtus agrestis* in buzzard diet. Voles were the most frequently recorded prey item by nest cameras in summer and with pellet analysis in summer and winter (field voles were also the most numerous prey item when data were pooled in summer and winter across all methods: Thesis Appendix Table A2). Many previous studies of buzzard diet in the British Isles have emphasised that *Lagomorpha spp.,* especially rabbits, are the main prey of buzzards (Dare 1961; Swann & Etheridge 1995; Graham *et al.* 1995; Rooney & Montgomery 2013). It is notable that all of these studies largely based their findings on analysis of prey remains found at nesting sites. My findings suggest that this method may be underestimating the importance of small mammals to buzzard diet, especially in years when voles are abundant in the environment. There is no doubt that lagomorphs are an important prey to buzzards, and in this study they were the most important prey group in terms of biomass in summer and winter. However, the short persistence period of voles, which renders them difficult to detect during searches for prey remains, means that these earlier studies may have underestimated the importance of voles to buzzards.

We cannot conclude that buzzards are vole *specialists* however. In Chapter 3 I found no evidence that annual variations in vole abundance on Langholm Moor affected the numerical response of buzzards in terms of breeding density and success. It is probable that the opportunistic and generalist feeding habits of buzzards (Tubbs 1974) allowed them to switch to predation of alternative prey, such as rabbits, moles and shrews, leading to no discernible effect on buzzard breeding performance as voles declined. This demonstrates that buzzards are true generalist raptors (Andersson & Erlinge 1977).

This opportunism and flexibility by buzzards to changes in abundance of their main vole prey is the second apparent theme of this study. Vole abundance is cyclical at Langholm Moor, with a typical cycle lasting three to four years (Langholm Moor Demonstration Project 2014), which is similar to other areas in Britain and Europe (Petty 1999; Andreassen *et al.* 2013; Millon *et al.* 2014). This research incorporated a full vole cycle at Langholm Moor, which allowed me to look at the effect of vole abundance on buzzard responses and foraging patterns. In numerous aspects of this study, the plasticity of buzzard behaviour was apparent as vole abundance changed. When vole abundance on the moor declined, buzzards appeared to switch to hunting off the moor where prey groups associated with farmland were abundant. Importantly, this plasticity in buzzard hunting behaviour also seemed to be responsible for varying levels of incidental predation of red grouse on Langholm Moor. Cornell (1976) defines incidental prey as "prey that are not the focus of a directed search by a predator". When vole abundances on the moor were high, I observed more buzzards hunting the heather moorland and more grouse were found in buzzard diet, thus suggesting incidental predation of grouse when the moor was a more profitable habitat to hunt. This was also apparent from diet studies in the winter which showed that buzzards roosting in areas with more grassland and its associated prey were less likely to predate grouse on the moor. These results suggested that predation of red grouse was largely determined by variations in the relative attractiveness of hunting within moorland habitats where red grouse were present.

The third key finding concerns the results from Chapter 6 which showed the potential for buzzards to be having a considerable impact on red grouse at Langholm. Evidence from Chapters 3 & 5 suggested that the impact on grouse by an average individual buzzard is low, owing to a small proportion of total diet consisting of grouse. Indeed this has been the message from numerous previous studies of buzzard impact on gamebirds: that an average buzzard or buzzard pair is unlikely to predate heavily upon gamebirds (Harradine *et al.* 1997; Kenward *et al.* 2001; Park *et al.* 2008). However, Chapter 6 suggested that if buzzard densities are high, diet is similar amongst breeders and non-breeders, and loss of grouse to buzzards is additive to other causes of mortality, then impact could be considerable. Further work is needed to address the caveats and limitations of these estimates including compensation of grouse mortality; the extent to which buzzards predate grouse versus scavenge already dead grouse, and the mitigating effect of buzzards predating other grouse predators. Nevertheless, this study has highlighted a need for greater scrutiny before the assumption is made that overall impact is low because losses to the average individual buzzard are low.

7.3.2 Are buzzards having an impact on red grouse at Langholm Moor?

This question was at the heart of this study, yet it remains a very difficult one to answer definitively. Many predatory species have been recorded killing red grouse, but it is wrong to assume that they must therefore have an impact on grouse populations. In fact, if predators such as buzzards are removing sick, unhealthy or parasitised grouse (Hudson *et al.* 1992) or killing other predators of grouse (Rooney & Montgomery 2013) then they may actually benefit the grouse population (Redpath & Thirgood 1997). Removal experiments are the clearest way to assess the impact of a predator on a prey population (Newton 1998), yet were not suitable to this study involving protected raptors. Whilst I have been unable to definitively quantify buzzard impact on red grouse at Langholm, my study has produced valuable insights into the mechanisms of buzzard predation on red grouse.

In a context of many other predation studies, this study only begins to attribute a level of impact to buzzards. Redpath (1991) compared moors with hen harriers to those without, and showed that 17% fewer red grouse were produced on moors with harriers. While I was unable to compare matched sites in this way, within Langholm Moor, I found no evidence that red grouse mortality was higher in areas where more buzzards congregated to hunt (Chapter 4).

Dietary analysis here has provided evidence of buzzard responses to prey (Chapter 3 & 5), which is vital in predicting variation in predation rates (Redpath & Thirgood 1999). Graham *et al.* (1995) found that red grouse comprised 11% of all prey items found at buzzard nests on Langholm Moor in 1993. Here I found a similar figure for one year (2011), although the proportion declined to 5% the year after and to 2% the year after that. However, without the use of models assessing changes in grouse demographics, providing an assessment of impact is limited (Thirgood *et al.* 2000c; Redpath & Thirgood 2003). Thirgood *et al.* (2000c) produced a model of grouse demographics using data from grouse counts and carcass searches to predict that grouse densities would be 1.9 times greater in spring and 3.9 times greater in autumn in the absence of raptor predation, and concluded that raptor predation was a limiting factor in grouse populations.

Predation of grouse by buzzards in this study also appeared to be of an incidental nature determined by the density of voles on the moor, or the amount of alternative prey away from the moor. During the peak vole years of this study I estimated buzzards could, potentially, remove as much as a quarter of all adult grouse present in spring over the summer, or 11% of those present in autumn over winter. Again it’s important to note that this does not mean that all of these grouse would have survived in the absence of predation by buzzards. Whether this potential removal of grouse represents a severe enough loss of grouse to warrant active management of the buzzard population at Langholm Moor is partly a question of economics as well as stakeholder acceptability (Redpath *et al.* 2004; Elston *et al.* 2014). Nevertheless, this has at least demonstrated the potential for buzzards to remove a large number of grouse from Langholm Moor, given present estimates of buzzard diet and population.

The Joint Raptor Study (JRS) in the 1990’s identified that the most likely reason for the long-term decline in red grouse at Langholm Moor was a 48% decline in heather cover between 1948 and 1988. However, the short-term declines and lack of population cycles of grouse at Langholm Moor during JRS were considered to be primarily due to the larger numbers of raptors present compared to other nearby moors (Redpath & Thirgood 1997). Identifying whether similar factors have been responsible for the lack of red grouse recovery during the last seven years of the Langholm Moor Demonstration Project (LMDP) is currently an on-going process, of which this research will form just one part. Nevertheless, my thesis may be an important first step in stimulating future research into improving our knowledge and testing management options aimed at reducing the impact of buzzards on red grouse. Some of these possible future research directions are discussed below, but first it is useful to discuss how representative these results are of the wider system involving buzzards and grouse in Britain.

7.3.3 Would similar results be observed on other moors?

Whilst I have conducted this study on just one moorland site, a discussion of the relevance of my results to other sites is worthwhile in order to explore the wider buzzard and red grouse issue. In essence, I am interested in exploring how typical Langholm Moor is of other grouse moors.

Firstly, it is important to explore whether the buzzard population at Langholm Moor is typical of grouse moors elsewhere. There are a few reasons why Langholm Moor may support a higher buzzard population than many other grouse moors. Buzzards were strictly protected on Langholm Moor throughout this study, and persecution is believed to be a factor limiting the distribution of buzzards in Britain (Gibbons *et al.* 2008). Persecution of raptors including buzzards is believed to occur on many other grouse moors (Etheridge *et al.* 1997; Whitfield & Fielding 2004; Hayhow *et al.* 2013; RSPB 2014), so many may hold fewer buzzards because of this. In addition to the absence of persecution, Langholm Moor may support a greater population of buzzards than other grouse moors due to habitat and landscape differences. Langholm Moor is surrounded by large areas of coniferous and mixed woodland, and many wooded gullies occur across the moor (Redpath & Thirgood 1997, pers. obs.), all of which are favoured nesting habitats for buzzards (Tubbs 1974; Hardey *et al.* 2009). Buzzards will occasionally nest on the ground; although Tubbs (1974) states that this is probably more out of necessity than choice. During this study, all successful buzzard nests were in woodlands on the moorland periphery or in wooded gullies throughout the moor. One buzzard nested on the ground in 2013 during this study, however even this was propped against a tree in a wooded gulley (pers. obs.). Therefore, on other grouse moors with fewer trees and surrounding woodland than is found at Langholm Moor, we might expect there to be a lower density of nesting buzzards.

There may also be reasons why Langholm Moor is more attractive for buzzards to hunt compared to other grouse moors. Throughout this thesis I have demonstrated that buzzards were attracted to hunt on the moor when vole indices were high, and this appeared to increase incidental predation of red grouse. The habitat of Langholm Moor, consisting chiefly of a mosaic of heather and grass, is likely to increase vole densities compared to areas of continuous heather cover (Wheeler 2008). Buzzards may therefore be attracted to hunt on grassier moors and those with a heather-grass mosaic, typical of many moors in southern Scotland and northern England (Thompson *et al.* 1995). Any further fragmentation of heather moorland and promotion of grassland from livestock grazing may exacerbate this effect in the future (Calladine *et al.* 2002; Wheeler 2008).

In Chapter 3, I identified that buzzards appeared to respond to grouse densities in a linear fashion, i.e. a type 1 functional response, during a peak vole year. However, as I noted in that chapter, I was not able to assess how buzzards would respond at higher grouse densities. During the period encompassing this study, post breeding red grouse densities averaged 92.5 individuals per km^2 (derived from distance sampling estimates on ten block counts and 18 transects between 2011 – 2013 (see Table 6.A1)). However, the average post-breeding density on a sample of 24 other managed grouse moors in Scotland during the same time period was 129 grouse per km^2, and on 25 moors in Northern England post-breeding density averaged 323 grouse per km^2 (GWCT 2014). The implication of this is that density dependent processes in buzzard predation on red grouse (i.e. how the rate of grouse predation varies at varying grouse density) could not be well explored in this study, and this remains an important area of future research. As outlined in the introduction (section 1.5.2), the nature in which buzzards respond, either numerically or functionally, to changes in prey (red grouse) density, greatly influences the density dependence of grouse predation. Since the variation in grouse density on Langholm Moor during this study was limited (relative to the densities they can reach on other moors), my assessment of any density dependence is also limited. Ecological studies would predict that incidental predation of grouse would increase as buzzards encountered more grouse while hunting for voles in areas with higher grouse densities (Vickery *et al.* 1992; Mckinnon *et al.* 2013). However, the proportion of grouse predated is likely to plateau or decline at higher grouse densities (Redpath & Thirgood 1999).

In summary, my results suggest that in the absence of buzzard control, predation on grouse is likely to be highest on moors with more trees available as nesting sites, and on grassier moors where vole abundances are greater. It is also possible that incidental predation of grouse would increase with increasing grouse densities, but the proportion of grouse predated by buzzards would probably plateau or decline at higher grouse densities. The extent of this density-dependent relationship is currently unknown.

7.4 Future research directions

Further research would help to improve our understanding of buzzard impacts on red grouse, and could also aid in testing the effectiveness of management techniques aimed at reducing the impact of buzzards on red grouse.

7.4.1 Improving our knowledge

There are a number of aspects of this study that would benefit from additional empirical or experimental study. By identifying some of these, I hope to acknowledge some of the key caveats and limitations of my study.

Firstly, as with any ecological study such as this one, the reliability of the results presented here could be increased by conducting a longer term study. Predator diet and populations are both likely to vary over time as prey density and availability changes (Korpimäki & Norrdahl 1991; Redpath & Thirgood 1999; Salamolard *et al.* 2000; Reif *et al.* 2004; Dupuy *et al.* 2009; Sundell *et al.* 2013). One of the main findings of this thesis was the opportunism and flexibility in buzzard foraging behaviour which can affect predation rates on red grouse. However, these findings are based on just four years of study. To accurately assess the extent and impact of these responses, it would be beneficial to study buzzard responses over a greater variation in prey abundances, whether this is increasing grouse density or throughout more vole cycles (Redpath & Thirgood 1999).

A longer study period would also allow the effect of weather conditions and their interaction with buzzard predation on red grouse to be assessed. Wet and cold weather in May and June can reduce the availability of important invertebrates, which can result in grouse chicks having to spend longer foraging which increases their exposure and vulnerability to predators (Park *et al.* 2001; Calladine *et al.* 2002; Thirgood *et al.* 2002). There is emerging evidence suggesting that the effects of climate change on weather patterns could also be altering the phenology of both buzzards (Jonker *et al.* 2014) and grouse (Fletcher *et al.* 2013), which may complicate the study of predator-prey relationships. Furthermore, recent evidence also showed that an increased occurrence of mild and wet winters caused by climate change and its effects on wintertime North Atlantic Oscillation patterns, may be dampening the amplitude of vole cycles (Millon *et al.* 2014). Considering the importance of voles and their cycling abundances that I highlighted in this study, this phenomenon will be important to understand better in the future.

As well as greater temporal replication, greater spatial replication would also benefit our understanding of this system. Had I been able to study buzzard responses on other grouse moors, I would have been able to conduct more robust analysis, controlling for a greater range of potential confounding factors (Redpath & Thirgood 1997). This thesis has also demonstrated that heterogeneous habitats can produce complex predator-prey relationships. By testing the observations of this thesis on other sites with differing habitat compositions, we could further improve our knowledge of these responses.

There are also a number of limitations and reasons why the results in this thesis should be treated with caution until further research is conducted. Firstly, and crucially, I have been unable to address whether buzzard predation was additive to other causes of grouse mortality. As discussed in Chapter 6, there are a number of reasons in which buzzard predation on red grouse could be compensated for by a reduction in mortality from other causes, or if buzzards are only removing non-territorial grouse that would never breed. If compensation is occurring, removal estimates will be overestimating the total impact of buzzards on grouse. It should be noted that additive and compensatory mortality are not mutually exclusive processes. Instead they lie at opposite ends of a continuum, and predation can be partly additive and partly compensatory (Newton 1998).

A key aspect of any study ecological study of raptors is an understanding of the breeding and non-breeding components of the total population (Kenward *et al.* 2000; Penteriani *et al.* 2011). In this study, I estimated the size of the breeding population at Langholm Moor by systematically searching for nests and territorial adults. Nests and territorial adult buzzards are conspicuous (Hardey *et al.* 2009) and it is likely that all pairs were identified on the moor, although it is possible that some pairs nesting in the large coniferous plantations on the moor periphery were overlooked. When it was necessary to estimate the number of these, I extrapolated from the nesting density on the moor to account for these potentially missed pairs. As such, the estimates of the breeding population in this study are likely to be fairly accurate. Conversely, estimates of the size of the non-breeding buzzard population are far less robust and would benefit from additional data in the future. Experimental removal of breeding individuals has shown that non-breeders may form a large part of the total population (Newton 1979), although estimating their total numbers is difficult (Penteriani *et al.* 2011). In this study I attempted to estimate the size of the non-breeding population by applying a breeding rate of 35.5%, which was an approximate rate from ringing data from Britain as a whole (Kenward *et al.* 2000). However, these data are now over 15 years old, during which time the range and population of buzzards in Britain has continued to expand (Balmer *et al.* 2014), which may have affected the breeding rate. Similarly, these data are not specific to Langholm Moor and will be affected by breeding rates in lowland areas which may be different from upland and moorland areas like Langholm. In southern Britain, surveys in late winter estimated that breeding buzzards formed just 21-25% of the total population (Kenward *et al*. 2000). However, the availability of nesting sites in southern Britain is likely to be greater than on moorland sites (Hardey *et al*. 2009), which may mean that the breeding rate at Langholm is less than southern Britain. Conversely, if the buzzard population is still expanding at Langholm and has not yet reached saturation, then a high proportion of the population may be breeders (Newton 1979). The non-breeding proportion of a population has been estimated with data on survival and recruitment rates (Newton 1985), by conducting radio-tagging and demographic studies (Hunt 1998; Kenward *et al.* 1999); and by comparing nest survey data with mark-re-sighting estimates of total population (Kenward *et al.* 2000). Improving the current estimates of the non-breeding buzzard population at Langholm remains a key area where more data are needed. This will require further study including the use of some of the techniques mentioned here, as well as regular updating of estimates as populations and breeding rates change over time (Newton 1979; Hunt 1998).

Further study of grouse limitation factors, such as parasitism, habitat quality and territory availability are on-going at Langholm Moor (Langholm Moor Demonstration Project 2014). Monitoring at Langholm Moor has shown that parasite burdens amongst red grouse (including *Trichostrongylus tenuis* nematode worms, louping-ill virus, and ticks) are all either absent or below thresholds considered to be seriously detrimental to red grouse health, and nematode worms continue to be controlled with the use of grit treated with anthelmintic drugs at Langholm Moor (Hudson *et al.* 1992, 1997; Langholm Moor Demonstration Project 2014). Red grouse habitat quality and extent have also both improved during the current LMDP period (Langholm Moor Demonstration Project 2014). Further study of these factors and their interaction with red grouse breeding success and mortality will aid in disentangling the impacts of buzzards on red grouse relative to other limiting factors.

The degree to which grouse mortality is density dependent will also be important in this respect. As stated above, I was unable to identify strong evidence of density dependence of grouse losses to buzzards in this study. If density dependent mortality in grouse is strong, then any drop in grouse density, however small, could be compensated for, and grouse densities would be expected to rapidly return to equilibrium, wherever that may lie (Newton 1998; Thirgood *et al.* 2000c). The point here is that without knowledge of the grouse carrying capacity of Langholm Moor, which may be set by other factors such as habitat, territory availability or predation from other predators, then I can only draw tentative conclusions about the impact of buzzards on red grouse. The best approach, scientifically, to investigating this further would be experimental removal of buzzards. However, it could also be addressed by conducting a long-term study, involving multiple sites, with more data on the demographics and condition of predated red grouse (Hudson *et al.* 1992) and the timing of predation events (Redpath & Thirgood 1997).

To measure the total impact of buzzard predation on grouse populations it will also be important for future studies to quantify the extent to which buzzards killed grouse versus scavenged them after the grouse had died from other causes. The presence of grouse remains in buzzard diet only confirms that buzzards *eat* grouse, but does not prove that the buzzard *killed* the grouse. Although an adult red grouse is within the range of prey that a buzzard can kill (Kenward *et al.* 2001), buzzards are also known to scavenge carcasses from other predators or following other causes of mortality (Tubbs 1974). Recent monitoring at Langholm Moor between 2008 and 2013 has shown that 78% of radio-tagged red grouse found dead between April and August (N = 33) and 64% of tagged grouse found between September and March (N = 39) showed signs of raptor predation (Langholm Moor Demonstration Project 2014). However, attributing predation events to individual raptor species is difficult (Thirgood *et al.* 1998; Watson *et al.* 2007; Park *et al.* 2008). A better understanding of the rate at which buzzards scavenge versus predate grouse could help disentangle their impact from that of other raptors further. Furthermore, monitoring at Langholm Moor suggests that red grouse condition is good – all red grouse caught for the purposes of tagging were found to be in good condition which is supported by the observation that clutch sizes were higher than on most other British moors (Langholm Moor Demonstration Project 2014). Nevertheless, a better understanding of the condition of grouse eaten by buzzards could further aid our understanding of buzzard predation mechanisms in the future (Cooper 2002).

In the future, it will also be important to gain a better understanding of the degree to which individual buzzards specialise in grouse predation. Variation in foraging behaviour and diet composition amongst individuals has been documented in goshawks whereby some individuals regularly predated adult hares while others apparently never did (Kenward 2006). A high degree of variation between individuals was also documented amongst buzzards predating released pheasants (Kenward *et al.* 2001). In this study, the amount of red grouse in the diet of buzzards varied between individuals by 0 – 26% of all prey items in summer (from cameras, prey remains and pellets collected and analysed from nests, Chapter 3) and by 0 – 7% of all prey items in winter (from pellets collected and analysed from roosts, Chapter 5). However, these variations are likely to be greatly affected by methodological differences during summer (Chapter 2), and by differences in the local availability of red grouse as prey (in turn affected by grouse abundance and habitat composition and structure). Disentangling the effects of any individual-based differences (specialisation) from these effects is a complex issue in itself and was not explored in detail in this study. In the future, gaining a better understanding of any specialisation amongst individual buzzards will be an important component of studies exploring impacts of predation, but also for the design of effective management interventions (see below). Targeting management interventions at only those individual buzzards which can be shown to disproportionately impact on gamebirds (once other deterrent measures had been tried) may increase their effectiveness while simultaneously reducing any deleterious impact on local buzzard populations.

Intensive following of buzzards, for example with remote tracking technology, can give information on kill rates by raptors (Kenward *et al.* 1981a; Rutz 2003). In the future it may be possible to use bird-borne video-cameras to observe hunting behaviours and predation versus scavenging rates of buzzards. Such technology is currently under development and already in use with some studies involving seabirds (Tremblay *et al.* 2014), and may become available to raptor researchers soon, although it should be ensured that the use of such technology does not alter the natural behaviour of the bird carrying it (Thirgood *et al.* 1995a; Kenward 2001; Hays 2014).

It is also important to note that in this thesis I have focussed on exploring the lethal effects of buzzards, i.e. predation. However, predators can affect the behaviour of their prey by increasing stress and vigilance, and reducing time available for foraging, which can reduce prey condition and increase mortality (see review in Lima 1998). Although, as stated above, red grouse condition at Langholm Moor is thought to be good (Langholm Moor Demonstration Project 2014), any effects in the future could be tested for by relating condition scores of grouse to indices of foraging raptors, although this would most likely need to be conducted at multiple sites in multiple years in order to adequately control for confounding variables.

Finally, it will be important to further explore the interactions between habitat and predation. Here I have explored some key habitat composition variables driving buzzard foraging patterns (Chapter 4). However, I have not explored the effects of micro-habitat variables or habitat fragmentation on the vulnerability of grouse to buzzard predation. Edge effects of habitat patches, increased by habitat fragmentation, can influence predation risk (Whittingham & Evans 2004), and a better understanding of these would be beneficial in any future studies.

7.4.2 Testing management options

The results of this research may have value in helping to design new methods for limiting losses of grouse to buzzards. Some of these potential management options and how we can assess their effectiveness at reducing grouse losses to buzzards are now discussed. Here, I am mainly concerned with how these options could be trialled and scientifically monitored, rather than their logistic, economic or social implications.

Various management options have been proposed as a means of potentially reducing the impact of raptors on prey, including gamebirds (FERA 2012; Redpath *et al.* 2013). These management options can be placed on a scale according to their level of intervention into the natural habits of the raptor. Techniques such as removal of nesting pairs, whether lethally or non-lethally, can be considered as options at the more interventionist end of the scale of possible management (Thirgood & Redpath 2008). It is assumed that these would reduce the number of predators taking the prey of interest, and therefore reduce overall impact. However, as many removal experiments have demonstrated, this may not always be the case if there exists a large non-breeding population which readily replace the removed territorial adults (Newton 1979). Any experiment involving removal must therefore quantify if a reduction in the number of individuals has been achieved. Similarly, the removal of chicks, eggs or nests could be conducted in an attempt to eliminate the requirement of adults to hunt to feed their chicks. Breeders could also be disturbed to prevent nesting to achieve the same effect. In theory, this should translate to a lessening of predation on the prey of interest. However, as my analysis in Chapter 6 suggests, the energetic requirements of chicks in the nest constitute a small overall proportion of the requirement of the total buzzard population (approximately 5%), so this may in fact not have a dramatic effect on reducing overall impact. Furthermore, targeting these interventions at any known ‘problem individuals’, or specialists of gamebird predation are likely to be far more successful (Kenward 1999; FERA 2012). To date, no monitored trial aimed at quantifying the effect of these interventions on buzzard predation rates of prey has been conducted. A rigorously conducted trial with sufficient spatial and temporal replication and monitoring of the predator and prey responses is needed to quantify the merits of these interventions prior to their widespread uptake (Kenward 1999).

It is notable that removal of nesting adults, chicks or eggs will not directly address predation during the winter, unless it reduces the overall population throughout the year. A less interventionist approach, which would aim to reduce predation by breeders and non-breeders in both summer and winter, involves attempting to divert buzzards from hunting in grouse habitats (Kenward 1999). We have seen that buzzard predation rates on grouse may depend on the attractiveness of moorlands to foraging buzzards, chiefly when vole abundances are high in moorland habitats. Encouraging more continuous heather cover and reducing grass on moorland sites would probably make habitats less favourable to voles (Wheeler 2008), which may discourage buzzards from hunting on moorlands (Redpath *et al.* 1997; Chapter 3 & 4). Similarly, buzzards could be encouraged to hunt away from grouse habitats. This could take the form of encouraging prey rich grassland habitats away from moorland habitats in which buzzards could focus their hunting (Kenward 1999; Chapter 5).

Buzzards may also be tempted by the provision of food, in the form of carrion, which reduces their need to hunt or draws them away from hunting in grouse habitats. This 'diversionary feeding' is well illustrated using the example of hen harriers. This involves providing nesting hen harriers with carrion, usually rats and cockerel chicks, in an attempt to reduce their predation pressure on red grouse chicks. This technique was shown to reduce predation of grouse chicks by 86% (Redpath *et al.* 2001b). Rooney *et al.* (2014) showed that buzzards would readily accept carrion offered to them at their nest site. However, Rooney *et al.* (2014) also found that provision of carrion can increase buzzard productivity when pairs are nesting in sub-optimal habitats, which to some extent may reduce the effectiveness of this technique in reducing predation on grouse, unless juveniles disperse away from the natal area post-fledging. There is also a concern that artificial food provision could increase predation rates of grouse chicks and nests by corvids and gulls attracted by the carrion (Redpath *et al.* 2001b), and this has limited its uptake as a solution (Redpath *et al.* 2010). Further research into the effectiveness of diversionary techniques, in terms of its effect on buzzard breeding performance, attraction of other predators and ultimately its effect on reducing grouse losses would be a useful avenue of further study.

Finally, intra-guild disturbance by apex predators such as golden eagles may reduce buzzard foraging intensity and breeding density. Niche separation between buzzards and eagles can occur as buzzards attempt to avoid predation (Fielding *et al.* 2003). Therefore, in the presence of golden eagles, buzzard density may be lower than currently observed in many areas where golden eagles are no longer present, although to my knowledge there are no data directly showing this relationship. Intra-guild disturbance could be achieved by flying captive eagles in an attempt to discourage buzzards from settling and nesting on heather moorland areas, although effects on other raptors, as well as the predation of red grouse by golden eagles, would obviously need to be considered. However, a longer term option may be to establish resident, wild golden eagles on areas of moorland where buzzards are perceived to be a problem. This form of 'trophic upgrading' could be achieved by encouraging the natural re-colonisation of upland areas by golden eagles, or by reintroducing them, as already achieved in parts of Ireland (O'Toole *et al.* 2002). Monitoring the effect of re-colonising golden eagles, on both buzzards and red grouse, would be required to assess whether this option was of benefit to managers of grouse moors.

In summary, future research aimed at increasing our knowledge of the buzzard-grouse system should focus on increasing temporal and spatial replication in order to increase the accuracy of my results. Testing my observations on other sites, over longer time periods and with greater variations in prey densities and habitat compositions are all of key importance in assessing the relevance of my results to the wider issue of buzzards and grouse moor management in Britain. Further research is required to assess the extent to which buzzard predation is additive to other forms of mortality. Exploration of habitat-predation interactions and sub-lethal effects of buzzards on grouse would also improve our understanding. Research that tests the efficacy of potential solutions to the buzzard-grouse conflict is required to inform discussions aimed at reconciling grouse moor management with buzzard conservation. The acceptability of these potential solutions will depend on economic and social considerations. Nevertheless, many potentially acceptable techniques are poorly researched and some of these should be trialled now and their impacts assessed.

7.5 Conclusions

My research suggests that buzzard predation on red grouse at Langholm Moor was largely incidental in nature, apparently driven by temporal changes in vole abundance affecting the relative attractiveness of heather moorland to foraging buzzards. Loss of grouse to buzzards could be considerable if populations of buzzards are high. However, further work is needed to establish whether predation by buzzards is additive to other causes of grouse mortality, and the extent to which buzzards scavenge versus kill grouse. The impact of buzzards on red grouse is likely to be highest when and where moorlands support high abundances of alternative prey that coexist with red grouse, for example grassy moors in peak vole years. Further research should be targeted at investigating the effectiveness of diverting buzzards away from grouse habitats, either by making these habitats less attractive or by providing alternative habitats and food resources away from grouse habitats.

7.6 Final remarks

Finding solutions to human conflicts over wildlife can be a challenging endeavour. Whilst socio-political, economic and cultural issues can present hurdles to the pursuit of these solutions, none would be possible without a sound grounding in current and robust ecological understanding of the natural system in which these conflicts operate. This thesis makes a potentially important contribution to our knowledge of the predator-prey relationship between buzzards and their red grouse prey. It is my hope that this knowledge will inspire more research into these systems, which will be necessary to inform solutions to this conflict. Results of future research are more likely to be widely accepted when a broad range of stakeholders have been involved in the data collection process, as exemplified by the current Langholm Moor Demonstration Project. All stakeholders involved in the British Uplands share a common concern for the future of healthy heather moorlands. For this reason, evidence should always be at the heart of how we continue to manage these landscapes for the benefit of people and wildlife alike.

Appendix

A.1 Captive buzzard feeding trial (Adam Stickler - MSc project)

The following is a draft manuscript, resulting from an MSc project conducted by Adam Stickler (Newcastle University) in 2014. Some of the results of this study have been utilised in aspects of Chapters 3, 5 & 6 of this thesis, and this is acknowledged in the text.

Data collection and writing of the draft manuscript were conducted by Adam Stickler, who was supervised throughout by Richard Francksen and Mark Whittingham

What goes in must come out? Feeding trials show red grouse Lagopus lagopus scotica *underestimated in pellets of Common Buzzard* Buteo buteo

ADAM G. STICKLER[1], RICHARD M. FRANCKSEN[1] & MARK J. WHITTINGHAM[1]

[1]School of Biology, Newcastle University, Newcastle upon Tyne, NE1 7RU

Summary: Known quantities of freshly dead red grouse *Lagopus lagopus scotica* and field voles *Microtus agrestis* were fed to individual captive Common Buzzards *Buteo buteo* (n = 4 buzzards, 24 trials for each buzzard). The probability of detecting the presence of a single red grouse in a pellet was only 51.8% compared with 98.7% for voles (a highly significant difference).

Reliable data on diet are important to measure impacts of predators on prey populations. Analysis of pellets (regurgitated parcels of food) is a non-invasive method of collecting diet data for raptors (Bakaloudis, 2012; Rosenberg and Cooper, 1990). It has been used to investigate a range of issues concerning the impact of raptors on grouse moorland (Redpath 2001) and the efficacy of management activities such as supplementary feeding (Rooney *et al*. 2015). However, it is thought to bias towards certain prey types so it is often used alongside other methods such as observational data, analysis of prey and faecal remains (Rosenberg and Cooper, 1990; Simmons *et al*., 1991). The aim of this study was to quantify potential differences in detecting red grouse relative to small mammal prey in buzzard pellets. To explore this, we examined the visibility of grouse in buzzard pellets relative to one of their principle prey groups (voles) (Selàs et al. 2007).

A feeding study using captive buzzards (used for falconry) was conducted from May to August 2014. We manipulated the proportions, by weight, of grouse and field vole in the buzzard's meal prior to the production of a pellet. Each buzzard was housed in a 2m cube, roofed pen with solid walls on three sides and open on the fourth. Birds were tied to perches with 60cm leather tethers. Four buzzards were used; one from Kielder Water Bird of Prey Centre (55°10' 54''N02°31'59''W) and three at Suffolk Owl Sanctuary (52°11' 16''N 01°08'23''W). All buzzards were trialled alone.

During the study a total of 49 voles and 17 grouse were fed during 24 trials (to each buzzard), each trial ended upon the production of one pellet. Grouse were fed to buzzards in 17 trials, 15 of these trials included vole/s in the meal. For two trials only grouse were given to each buzzard and in a further seven trials only voles were supplied.

Buzzards were not fed for 24 hours prior to the start of a trial. The experiment did not start until a pellet was obtained from the buzzard on the morning of each trial to ensure an empty crop. Experiments began in the afternoon, as this was the usual time buzzards were fed. The buzzard was weighed each day before the experiment. Of the grouse obtained, 10 were whole carcasses and 7 had been partially consumed by wild birds of prey so the breast cavity was open. All grouse had died of natural causes on Langholm Moor (Scotland). Voles were also obtained from Langholm Moor as part of a long-term vole cycle monitoring study. Once grouse and voles were removed from the moor they were frozen immediately, to be thawed when needed. A single grouse was always the first prey presented to the buzzard; this was due to the practical constraint of getting the buzzards to consume the grouse after its preferred vole meal. The grouse was laid breast up in front of the buzzard; this was to encourage the buzzard to feed on the grouse. The amount of time the buzzard was allowed to feed on the grouse was varied from 1 to 10 minutes to manipulate the weight of grouse consumed. The buzzard was then weighed again to obtain the weight of grouse consumed. Directly after consumption of the grouse, up to three voles were weighed and hand-fed to the buzzard, in order to manipulate the biomass ratio of grouse to vole prey. Buzzards were observed until the entire vole meal was consumed. The proportion of each prey item in each trial was calculated from the total weight of the meal.

Pens containing buzzards were checked approximately hourly for pellets. Pellets were bagged, dated and frozen immediately. A buzzard produces 0.9-1 pellets per day (Dare, 1961) so it was reasonable to expect that a buzzard would produce one pellet the morning after each meal. On six occasions the buzzard ‘held over’ (Dare, 1961) the pellet for two days and on one occasion for three days (average 1.33 days). When this happened the experiment would proceed as normal, using the same grouse as used the previous day, the proportion of food items being summed from prey weights over multiple days.

Frozen pellets were dried before analysis. Dates, locations and individual birds were concealed prior to analysis under laboratory conditions in order to avoid bias in pellet analysis. Pellet analysis was undertaken following Yalden (2009). A 20x-18mm hand lens was used to aid identification. All identifiable features were recorded and where possible remains were identified down to species level. Identifiable grouse remains from nine pellets included identifiable feathers (nine pellets), large bone fragments (three pellets) and beaks (one pellet). Vole remains from 49 pellets constituted vole fur, teeth, skull and bone remains. Of the 17 occasions grouse were supplied, 16 of the recurrent pellets contained identifiable bird remains (feathers/quill tips/bones). However, only nine of these pellets contained remains that could be specifically identifiable as grouse other (unidentifiable) avian remains were referred to as ‘bird’. All pellet analysis was carried out by AGS.

The first 10 pellets collected from the study were re-analysed blind by a second observer (RF) to provide validation of the pellet analysis undertaken. It was found that there was a 100% concordance with AGS’s analysis for presence of identifiable grouse and vole characteristics in each pellet.

Statistical analyses were undertaken in R version 3.0.2. A Binomial General Linear Model (GLM) using a Logit link function was constructed to explore how the proportions of grouse fed to a buzzard affected prey composition in pellets. Grouse detection in pellet was used as a response variable and tested against predictors of proportion of grouse consumed by the buzzard in the meal compared to vole by weight, individual buzzard, days to produce pellet and whether the grouse carcass had been intact or the breast cavity previously opened for all pellets containing grouse (referred to as ‘state’). Buzzard was treated as a fixed effect, as there were only four individuals, which is insufficient to specify as a random effect (Bolker *et al.*, 2009). Extent of deviance explained was analysed by removing each predictor individually and testing using a likelihood ratio test against the original ‘full’ model (following Whittingham *et al.* (2006)).

Detection rates were created for each prey type from the difference between the known presence of prey in the pellets and the prey presence detected in the pellet analysis. Each buzzard fed was treated as a replicate and the mean detection rates from pellets containing vole and grouse were arcsine square root transformed prior to analysis. These transformed data were used to calculate a mean detection rate and confidence intervals (95%), which were subsequently back transformed to produce adjusted proportional means and confidence intervals (95%). A comparison between the detectability of both grouse and vole in pellets was explored using the mean detection rate.

The presence of grouse identified in the pellet was not significantly affected by individual buzzard, the state of the grouse presented (whether or not the carcass had been previously opened or fed on) or days to produce a pellet (Table 1). The proportion of grouse eaten did not affect the presence of identifiable remains in pellets. However, only two meals consisted of less than 40% grouse to vole by weight, so more results are needed to confirm this result.

Grouse showed an adjusted mean detection rate of 51.8%, calculated from the transformed value of nine pellets containing identifiable grouse remains from 17 pellets known to contain grouse (Figure 1). The mean detection rate for vole presence was 98.7% from 22 pellets containing vole. This is in contrast to the number of voles detected: of 49 voles fed, remains of 25 individuals were identified in the pellets, which is an under representation of 52.6% (mean= 0.526, CL 95%, +0.634, -0.416). Due to the fact that the buzzards were never fed more than one grouse for each pellet produced (one grouse equates to a full meal), the number of recovered individual grouse found in the pellets was identical to the detectable presence of grouse at 51.8%.

Caution must be taken when using these detection rates to calibrate data from pellets collected from the wild. A single grouse carcass may be revisited multiple times and therefore appear in multiple pellets thus over-estimating the impact on grouse populations from wild pellet data if the assumption is that one grouse detection equates to one grouse meal.

During the study ‘bird’ was still discernible from pellets on 16 out of 17 occasions it was clear that some elements of grouse were still visible, but insufficient to determine anything more accurate (e.g. gamebird). A study by Simmons *et al.* (1991) found that large avian prey species comprised 30-40% of the African marsh harrier *Circus ranivorus* diet as indicated by prey remains, but were impossible to recover from pellets. In this study it was impossible to quantify biases in wild pellets for avian prey due to the large amount of unidentified avian prey in pellets. Similar results have been found for other raptors (Bakaloudis *et al*. 2012, Real 1996).

This study, albeit based on a small sample size, found that analysis of buzzard pellets, under-estimates the detectability of red grouse within the diet. A more accurate picture of the diet of wild buzzards could be obtained using molecular techniques such as stable isotope analysis (Resano-Mayor *et al*. 2014), however this would necessitate greater expense and require greater disturbance of raptors. Field voles, as a small prey item, are unbiased in terms of presence in diet but under-represented in terms of number. These results may impact how past and future studies relying on buzzard, or other raptor pellets are interpreted. Our work suggests it is hard to detect grouse (as opposed to ‘bird’) from buzzard pellets and so previous studies, and future work, should bear in mind that red grouse were detected from only 52% of pellets.

Table A1. Results from Binomial GLM using a logit link function exploring the detection of grouse in pellets. Note for brevity parameter estimates for each buzzard (n = 4) are not given. Neither the days it took to produce a pellet by a buzzard, the proportion of grouse fed to the buzzard in the trial nor whether the breast cavity had already been opened or not (state of grouse fed) significantly impacted on the detection of red grouse in the pellets.

Variable	**Parameter Estimate (full model)**	**LR Test χ^2 (d.f.)**	**P-value (χ^2)**	**Deviance**
Individual Buzzard	n/a	3	0.939	-0.405
State of Grouse fed	1.780	1	0.124	-2.362
Proportion of Grouse	2.214	1	0.444	-0.585
Days to produce pellet	-0.572	1	0.632	-0.229

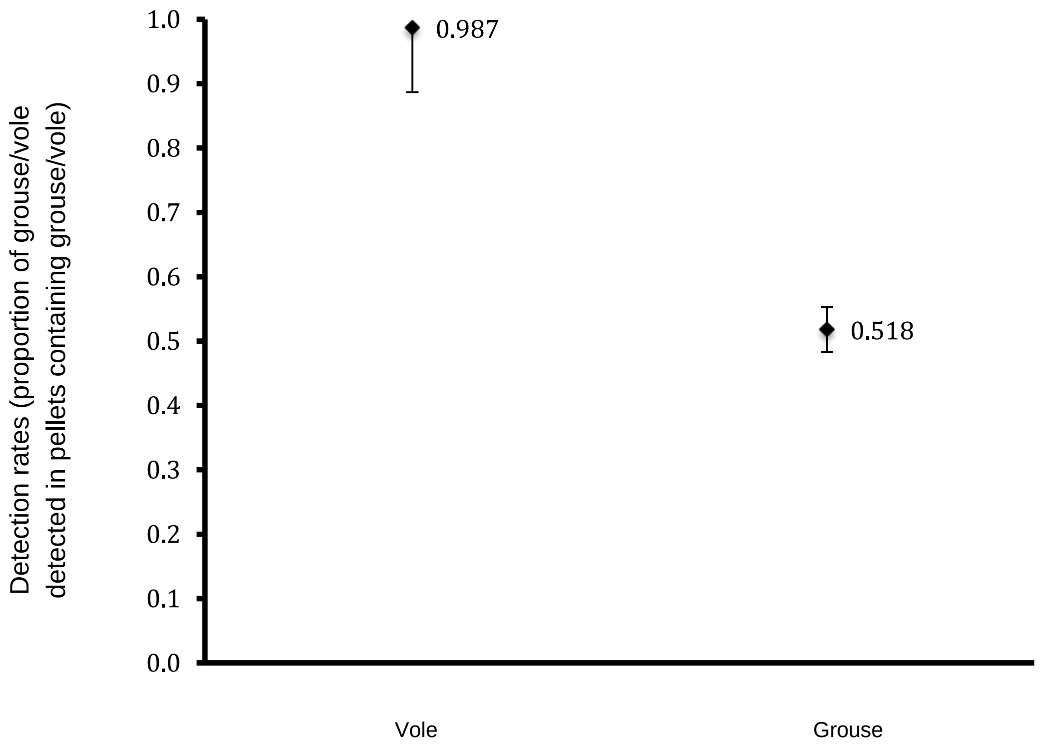

Figure A1. Interval plot for the detection rates of grouse in pellets containing grouse (n=17) and vole in pellets containing vole (n=22). Vole was found to be significantly more detectable than grouse, T-test, (p=0.001, T=5.56). The mean detection success for grouse and vole are 0.518 and 0.987 respectively. 95% confidence limits for vole are +0.988, -0.887 and confidence limits for grouse are +0.553, -0.483. Data were arcsine square root transformed so that data conformed to a Gaussian distribution.

ACKNOWLEDGEMENTS

We are grateful to Kielder water bird of prey centre and Suffolk Owl Sanctuary for their time, patience and allowing access to facilities for the study with specific thanks to Ray Lowden, Matt Lott and Dean Winham for the use of their buzzards. We thank Matt Grainger and David Baines for their input and comments into this manuscript.

REFERENCES

Bakaloudis, D. E., Iezekiel, S., Vlachos, C. G., Bontzorlos, V. A., Papakosta, M. & Birrer, S. 2012. Assessing bias in diet methods for the Long-legged Buzzard (Buteo rufinus). *J. Arid. Environ* **77:** 59-65.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends ecol. evol* ***24*****(3):** 127-135.

Clements, R. 2002. The common buzzard in Britain: a new population estimate. *British Birds* **95:** 377-383.

Dare, P. J. 1961. Ecological observations on a breeding population of the Common Buzzard, Buteo buteo (L): with particular reference to the diet and feeding habits. PhD Thesis. University of Exeter.

Real, J. 1996. Biases in diet study methods in the Bonelli's eagle. *J. Wildlife Manage* **60(3):** 632-638.

Resano-Mayor, J., Hernández-Matías, A., Real, J., Parés, F., Inger, R. and Bearhop, S. 2014. Comparing pellet and stable isotope analyses of nestling Bonelli's Eagle *Aquila fasciata* diet, *Ibis* **156(1):** 176-188.

Rooney, E., Reid, N., & Montgomery, W. I. 2015. Supplementary feeding increases Common Buzzard *Buteo buteo* productivity but only in poor-quality habitat. *Ibis* **157(1):** 181-185.

Rosenberg, K. V. & Cooper, R. J. 1990. Approaches to avian diet analysis. *Stud Avian Biol* **13:** 80-90.

Selàs, V., Tveiten, R. & Aanonsen, O. M. 2007. Diet of Common Buzzards (*Buteo buteo*) in southern Norway determined from prey remains and video recordings. *Ornis Fennica* **84:** 97-104.

Simmons, R. E., Avery, D. M. & Avery, G. 1991. Biases in diets determined from pellets and remains: correction factors for a Mammal and bird eating predator. *J. Raptor Res* **25(3):** 63-67.

Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. 2006. Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol* ***75*****(5):** pp. 1182-1189.

Yalden, D. W. 2009. *The analysis of owl pellets 4th edition.* The Mammal Society.

[End of draft MSc manuscript]

Table A2. Total number of records of prey items identified at buzzard nests and winter roost sites at Langholm Moor, 2011 – 2014. Records are pooled across 58 nests (2011-2013), which included failed attempts and those found late in the nestling season, and 23 winter roost sites (2013/14). Summer data are derived from camera images, prey remains and pellet analysis, winter data are derived from pellet analysis only. "Lagomorph" includes European rabbit and brown hare which could often not be reliably separated. "Passerine" includes *Passeriformes spp.* unidentified to species level. "Amphibian" includes common frog and common toad.

Prey species/group	Total records	Prey species/group	Total records
Field vole *Microtus aegrestis*	1358	Jay *Garrulus glandarius*	9
Beetles *Coleoptera spp.*	425	Adder *Vipera berus*	9
"Lagomorph" *Lagomorpha spp.*	409	Wood mouse *Apodemus sylvaticus*	7
Common shrew *Sorex araneus*	287	Stoat *Mustela erminea*	5
Mole *Talpa europaea*	136	Wheatear Oenanthe oenanthe	5
Pheasant poult/chick *Phasianus colchicus*	95	Siskin *Carduelis spinus*	5
"Amphibian" *Amphibia spp.*	79	Bank vole *Myodes glareolus*	5
Pheasant (adult) Phasianus colchicus	75	Blue tit *Cyanistes caeruleus*	5
Meadow pipit *Antus pratensis*	62	Snipe *Gallinago gallinago*	5
Red grouse (adult) *Lagopus l. scotica*	56	Grey squirrel *Sciurus carolinensis*	5
"Passerine" *Passeriformes spp.*	54	Blackbird *Turdus merula*	4
Unidentified small mammal	45	Great tit *Parus major*	4
Carrion crow *Corvus corone*	39	Great spotted woodpecker *Dendrocopus major*	4
Skylark *Alauda arvensis*	38	Curlew *Numenius arquata*	4
Wood pigeon Columba palumbus	32	Stock dove *Columba oenas*	3
Earthworms *Megadrilacea spp.*	22	Whinchat *Saxicola rubetra*	3
Weasel *Mustela nivalis*	19	Greenfinch *Chloris chloris*	3
Red grouse chick *Lagopus l. scotica*	15	Red-legged partridge *Alectoris rufa*	3
Slow worm *Anguis fragilis*	15	Willow warbler *Phylloscopus trochilus*	1
Rook *Corvus frugilegus*	15	Cuckoo *Cuculus canorus*	1
Brown rat *Rattus norvegicus*	14	Pied wagtail *Motacilla alba*	1
Pygmy shrew *Sorex minutus*	12	House martin *Delichon urbicum*	1
Woodcock *Scolopax rusticola*	12	Lapwing *Vanellus vanellus*	1
Chaffinch *Fringilla coelebs*	12	Lesser black-backed gull *Larus fuscus*	1
Song thrush *Turdus philomelos*	11	Barn owl *Tyto alba*	1
Sheep/lamb carrion *Ovis aries*	11	Sparrowhawk *Accipiter nisus*	1
Jackdaw *Coloeus monedula*	10	Domestic chicken *Gallus domesticus*	1
Common lizard *Zootoca vivipara*	9	TOTAL	3,464

References

Aebischer, N.J., Marcström, V., Kenward, R.E. & Karlbom, M. 1993a. Survival and Habitat Utilisation: A Case for Compositional Analysis. *Marked individuals in the study of bird populations* (eds J.D. Lebreton), & P.M. North), pp. 343–353. Birkhauser Verlag, Basel, Switzerland.

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993b. Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. *Ecology*, **74**, 1313–1325.

Allen, D.S. & Feare, C.J. 2003. Birds of prey and lowland gamebird management. *Birds of Prey in a Changing Environment* (eds D.B.A. Thompson),, S.M. Redpath),, A.H. Fielding),, M. Marquiss), & C.A. Galbraith), pp. 427 – 442. The Stationary Office, Edinburgh.

Amar, A., Redpath, S.M. & Thirgood, S.J. 2003. Evidence for food limitation in the declining hen harrier population on the Orkney Islands, Scotland. *Biological Conservation*, **111**, 377–384.

Amar, A., Arroyo, B.E., Redpath, S.M. & Thirgood, S.J. 2004. Habitat predicts losses of red grouse to individual hen harriers. *Journal of Applied Ecology*, **41**, 305–314.

Amar, A., Thirgood, S.J., Pearce-Higgins, J. & Redpath, S.M. 2008. The impact of raptors on the abundance of upland passerines and waders. *Oikos*, **117**, 1143–1152.

Amar, A., Redpath, S.M., Sim, I. & Buchanan, G. 2010. Spatial and temporal associations between recovering populations of common raven Corvus corax and British upland wader populations. *Journal of Applied Ecology*, **47**, 253–262.

Anderson, D. 1982. The home range: a new nonparametric estimation technique. *Ecology*, 103 – 112.

Andersson, M. & Erlinge, S. 1977. Influence of predation on rodent populations. *Oikos*, **29**, 591–597.

Andreassen, H.P., Glorvigen, P., Rémy, A. & Ims, R. 2013. New views on how population-intrinsic and community-extrinsic processes interact during the vole population cycles. *Oikos*, **122**, 507–515.

Angelstam, P., Lindström, E. & Widén, P. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, **62**, 199–208.

Arroyo, B.E., Amar, A., Leckie, F., Buchanan, G., Wilson, J. & Redpath, S.M. 2009. Hunting habitat selection by hen harriers on moorland: Implications for conservation management. *Biological Conservation*, **142**, 586–596.

Aulagnier, S., Haffner, P., Mitchell-Jones, A.J., Mouton, F. & Zima, J. 2009. *Mammals of Europe, North Africa and the Middle East*. Bloomsbury Publishing Plc., London.

Austin, G.E. & Houston, D.C. 1997. The breeding performance of the Buzzard Buteo buteo in Argyll, Scotland and a comparison with other areas in Britain. *Bird Study*, **44**, 146–154.

Baillie, S.R., Marchant, J.H., Leech, D.I., Massimino, D., Sullivan, M.J.P., Eglington, S.M., Barimore, C., Dadam, D., Downie, I.S., Harris, S.J., Kew, A.J., Newson, S.E., Noble, D.G., Risely, K. & Robinson, R.A. 2014. *BirdTrends 2014: Trends in Numbers, Breeding Success and Survival for UK Breeding Birds. BTO Research Report 662*. British Trust for Ornithology, Thetford.

Bainbridge, I.P., Evans, R.J., Broad, R.A., Crooke, C.H., Duffy, K., Green, R.E., Lowe, J.A. & Mudge, G.P. 2003. Re-introduction of white-tailed eagles (Haliaeetus albicilla) to Scotland. *Birds of Prey in a Changing Environment* (eds D.B.A. Thompson),, S.M. Redpath),, A.H. Fielding),, M. Marquiss), & C.A. Galbraith), pp. 393 – 406. Stationery Office, Edinburgh.

Baines, D., Moss, R. & Dugan, D. 2004. Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology*, **41**, 59–71.

Baines, D., Redpath, S.M., Richardson, M. & Thirgood, S.J. 2008. The direct and indirect effects of predation by Hen Harriers Circus cyaneus on trends in breeding birds on a Scottish grouse moor. *Ibis*, **150**, 27–36.

Baines, D. & Richardson, M. 2013. Hen harriers on a Scottish grouse moor: multiple factors predict breeding density and productivity. *Journal of Applied Ecology*, **50**, 1397–1405.

Bairlein, F. 1999. Energy and nutrient utilization efficiencies in birds – a review.

Proceedings of the 22nd International Ornithological Congress (eds N. Adams), & R. Slowtow), Durban Birdlife, South Africa.

Baker, H., Stroud, D., Aebischer, N.J., Cranswick, P.A., Gregory, R.D., McSorley, C.A., Noble, D.G. & Rehfisch, M.M. 2006. Population estimates of birds in Great Britain and the United Kingdom. *British Birds*, **99**, 25–44.

Baker, J.A. & Brooks, R.J. 1981. Distribution patterns of raptors in relation to density of meadow voles. *Condor*, **83**, 42–47.

Balmer, D., Gillings, S., Caffrey, B. & Swann, B. 2014. *Bird Atlas 2007-11: The Breeding and Wintering Birds of Britain and Ireland*. British Trust for Ornithology, Thetford.

Barton, K. 2013. MuMIn: multi-model inference. R package version 1.9.5. Available from: http://CRAN.R-project.org/package=MuMIn.

Barton, N.W.H. & Houston, D.C. 1993. A comparison of digestive efficiency in birds of prey. *Ibis*, **135**, 363–371.

Bates, D., Maechler, M. & Bolker, B. 2012. lme4: Linear mixed- effects models using S4 classes. Available from http://lme4.r-forge.r-project.org/).

Bicknell, J., Smart, J., Hoccom, D., Amar, A., Evans, A., Walton, P. & Knott, J. 2010. *Impacts of Non-Native Gamebird Release in the UK: A Review.* RSPB research report no. 40. Sandy, UK.

Bolton, M., Butcher, N., Sharpe, F., Stevens, D. & Fisher, G. 2007. Remote monitoring of nests using digital camera technology. *Journal of Field Ornithology*, **78**, 213–220.

Bowker, G., Bowker, C. & Baines, D. 2007. Survival Rates and Causes of Mortality in Black Grouse Tetrao terix at Lake Vyrnwy, North Wales, UK. *Wildlife Biology*, **13**, 231–237.

Boyd, I.L. 2002. Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *Journal of Applied Ecology*, **39**, 103–119.

Brown, D., Ferguson, R., Lawrence, J. & Lees, M. 2003. *Tracks and Signs of the Birds of Britain and Europe: An Identification Guide.* Christopher Helm, London.

Bunnefeld, N., Baines, D., Newborn, D. & Milner-Gulland, E.J. 2009. Factors affecting unintentional harvesting selectivity in a monomorphic species. *The Journal of*

Animal Ecology, **78**, 485–92.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach.*, 2nd ed. Springer, New York.

Calladine, J., Baines, D. & Warren, P. 2002. Effects of reduced grazing on population density and breeding success of black grouse in northern England. *Journal of Applied Ecology*, **39**, 772–780.

Carter, I. 2001. *The Red Kite*. Arlequin Press, Chelmsford, UK.

Chamberlain, D.E., Glue, D.E. & Toms, M.P. 2008. Sparrowhawk Accipiter nisus presence and winter bird abundance. *Journal of Ornithology*, **150**, 247–254.

Clarke, R., Combridge, M. & Combridge, P. 2008. A comparison of the feeding ecology of wintering Hen Harriers Circus cyaneus centred on two heathland areas in England. *Ibis*, **139**, 4–18.

Clements, R. 2002. The Common Buzzard in Britain: a new population estimate. *British Birds*, **95**, 377–383.

Collopy, M.W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of Golden Eagles. *The Journal of Wildlife Management*, **47**, 360 – 368.

Conover, M.R. 2002. *Resolving Human-Wildlife Conflicts: The Science of Wildlife Damage Management.* C R C Press, Boca Raton, U.S.A.

Cooper, J.E. 2002. *Birds of Prey: Health and Disease* (ed JE Cooper). Blackwell Science Ltd, Oxford, UK.

Cornell, H. 1976. Search strategies and the adaptive significance of switching in some general predators. *American Naturalist*, **110**, 317.

Cotgreave, P. 1995. Relative importance of avian groups in the diets of British and Irish predators. *Bird Study*, **45**, 246–252.

Crawley, M.J. 1992. Population dynamics of natural enemies and their prey. *Natural enemies: the population biology of predators, parasites and diseases* (ed M.J. Crawley), pp. 40–89. Blackwell, Oxford.

Crawley, M.J. 2007. *The R Book*. John Wiley & Sons Ltd, Chichester, England.

Crocker, R.E., Hart, A., Gurney, J. & McCoy, C. 2002. *Project PN0908: Methods for Estimating Daily Food Intake of Wild Birds and Mammals.*

Cumberland, R.E., Dempsey, J.A. & Forbes, G.J. 2001. Should diet be based on biomass? Importance of larger prey to the American marten. *Wildlife Society Bulletin*, **29**, 1125–1130.

Dale, B.W., Adams, L.G. & Bowyer, R.T. 1994. Functional Response of Wolves Preying on Barren-Ground Caribou in a Multiple-Prey Ecosystem. *The Journal of Animal Ecology*, **63**, 644.

Dare, P. 1961. *Ecological Observations on a Breeding Population of the Common Buzzard Buteo Buteo, with Particular Reference to the Diet and Feeding Habits*. Ph.D Thesis. Exeter University.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27–46.

Douglas, D.J.T., Buchanan, G.M., Thompson, P., Amar, A., Fielding, D.A., Redpath, S.M. & Wilson, J.D. 2015. Vegetation burning for game management in the UK uplands is increasing and overlaps spatially with soil carbon and protected areas. *Biological Conservation*, **191**, 243–250.

Dupuy, G., Giraudoux, P. & Delattre, P. 2009. Numerical and dietary responses of a predator community in a temperate zone of Europe. *Ecography*, **32**, 277–290.

Eaton, M., Brown, A. & Noble, D.G. 2009. Birds of Conservation Concern 3. *British Birds*, **102**, 296–341.

Elston, D.A., Spezia, L., Baines, D. & Redpath, S.M. 2014. Working with stakeholders to reduce conflict - modelling the impact of varying hen harrier Circus cyaneus densities on red grouse Lagopus lagopus populations. *Journal of Applied Ecology*, **51**, 1236–1245.

Eng, R. & Gullion, G. 1962. The predation of goshawks upon ruffed grouse on the Cloquet Forest Research Center, Minnesota. *The Wilson Bulletin*, **74**, 227 – 242.

Etheridge, B., Summers, R. & Green, R.E. 1997. The effects of illegal killing and destruction of nests by humans on the population dynamics of the hen harrier Circus cyaneus in Scotland. *Journal of Applied Ecology*, **34**, 1081–1105.

FERA. 2012. *Reviews of Selected Wildlife Conflicts and Their Management.* Report to Defra by the Food and Environment Research Agency.

Fielding, A.H., Haworth, P.F., Morgan, D.H., Thompson, D.B.A. & Whitfield, P.D. 2003. The impact of golden eagles (Aquila chrysaetos) on a diverse bird of prey assemblage. *Birds of Prey in a Changing Environment* (eds D.B.A. Thompson),, S.M. Redpath),, A.H. Fielding),, M. Marquiss), & C.A. Galbraith), pp. 221 – 243. The Stationary Office, Edinburgh.

Fletcher, K., Howarth, D., Kirby, A., Dunn, R. & Smith, A. 2013. Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis*, **155**, 456–463.

Francksen, R.M., Whittingham, M.J. & Baines, D. 2016. Assessing prey provisioned to common buzzard Buteo buteo chicks: a comparison of methods. *Bird Study*, http://dx.doi.org/10.1080/00063657.2016.1183111.

Garratt, C., Hughes, M., Eagle, G. & Fowler, T. 2011. Foraging habitat selection by breeding Common Kestrels Falco tinnunculus on lowland farmland in England. *Bird Study*, **58**, 90–98.

Gibbons, D., Gates, S., Green, R.E., Fuller, R.J. & Fuller, R.M. 2008. Buzzards Buteo buteo and Ravens Corvus corax in the uplands of Britain: limits to distribution and abundance. *Ibis*, **137**, 75–84.

Glue, D.E. 1967. Prey taken by the Barn Owl in England and Wales. *Bird Study*, **14**, 169–183.

Graham, I.M., Redpath, S.M. & Thirgood, S.J. 1995. The diet and breeding density of Common Buzzards Buteo buteo in relation to indices of prey abundance. *Bird Study*, **42**, 165–173.

Greenwood, J.J.D., Crick, H.Q.P. & Bainbridge, I.P. 2003. Numbers and international importance of raptors and owls in Britain and Ireland. *Birds of Prey in a Changing Environment* (eds D.B.A. Thompson),, S.M. Redpath),, A.H. Fielding),, M. Marquiss),

& C.A. Galbraith), pp. 22 – 50. The Stationary Office, Edinburgh.

Gremillet, D., Wright, G., Lauder, A., Carss, D.N. & Wanless, S. 2003. Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. *Journal of Applied Ecology*, **40**, 266 – 277.

GWCT. 2014. *Review of 2013. A Full Report of the Activities of the Game & Wildlife Conservation Trust.* Game & Wildlife Conservation Trust, Fordingbridge.

Hardey, J., Crick, H., Wernham, C., Riley, H., Etheridge, B. & Thompson, D.B.A. 2009. *Raptors: A Field Guide for Surveys and Monitoring.*, 2nd ed. Scottish National Heritage, Inverness.

Harradine, J., Reynolds, N. & Laws, T. 1997. *Raptors and Gamebirds: A Survey of Game Managers Affected by Raptors*. Bristish Association for Shooting and Conservation, Wrexham.

Harrison, X.A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2:e616**, DOI 10.7717/peerj.616.

Haworth, P.F., Mcgrady, M.J., Whitfield, P.D., Fielding, A.H. & McLeod, D.R.A. 2006. Ranging distance of resident Golden Eagles Aquila chrysaetos in western Scotland according to season and breeding status. *Bird Study*, **53**, 265–273.

Hayhow, D.B., Eaton, M.A., Bladwell, S., Etheridge, B., Ewing, S.R., Ruddock, M., Saunders, R., Sharpe, C., Sim, I. & Stevenson, A. 2013. The status of the Hen Harrier, Circus cyaneus, in the UK and Isle of Man in 2010. *Bird Study*, **60**, 446–458.

Hays, G.C. 2014. Tracking animals to their death. *The Journal of animal ecology*, **83**, 5–6.

Holling, C.S. 1959. The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. *The Canadian Entomologist*, **91**, 293–320.

Horne, J.S. & Garton, E.O. 2006. Selecting the best home range model: an information-theoretic approach. *Ecology*, **87**, 1146 – 1152.

Hudson, P.J. 1992. *Grouse in Space and Time: The Population Biology of a Managed Gamebird*. The Game Conservancy, Fordingbridge.

Hudson, P.J., Dobson, A. & Newborn, D. 1992. Do parasites make prey vulnerable to predation? Red grouse and parasites. *Journal of animal ecology*, **61**, 681–692.

Hudson, P.J., Newborn, D. & Robertson, P.A. 1997. Geographical and seasonal patterns of mortality in red grouse Lagopus lagopus scoticus populations. *Wildlife Biology*, **3**, 79–87.

Hudson, P.J. & Newborn, D. 1995. *A Manual of Red Grouse and Moorland Management.* The Game Conservancy, Fordingbridge.

Hudson, P.J. & Rands, M.R.W. 1988. *Ecology and Management of Gamebirds.* Blackwell Scientific Publications, Oxford.

Hunt, W.G. 1998. Raptor floaters at Moffat's equilibrium. *Oikos*, **82**, 191–197.

Jenkins, D., Watson, A. & Miller, G. 1963. Population studies on red grouse, Lagopus lagopus scoticus (Lath.) in north-east Scotland. *The Journal of Animal Ecology*, **32**, 317–376.

Jonker, R.M., Chakarov, N. & Krüger, O. 2014. Climate change and habitat heterogeneity drive a population increase in Common Buzzards Buteo buteo through effects on survival (ed F Sergio). *Ibis*, **156**, 97–106.

Kenward, R.E., Marcström, V. & Karlbom, M. 1981a. Goshawk winter ecology in Swedish pheasant habitats. *The Journal of Wildlife Management*, **45**, 397–408.

Kenward, R.E., Marcström, V. & Karlbom, M. 1981b. Goshawk Winter Ecology in Swedish Pheasant Habitats. *The journal of Wildlife Management*, **45**, 397–408.

Kenward, R.E. 1999. Raptor predation problems and solutions. *Journal of Raptor Research*, **33**, 73 – 75.

Kenward, R.E., Marcström, V. & Karlbom, M. 1999. Demographic estimates from radio-tagging: models of age- specific survival and breeding in the goshawk. *Journal of Animal Ecology*, **68**, 1020–1033.

Kenward, R.E., Walls, S.S., Hodder, K.H., Pahkala, M., Freeman, S.N. & Simpson, V.R. 2000. The prevalence of non-breeders in raptor populations: evidence from rings, radio-tags and transect surveys. *Oikos*, **91**, 271 – 279.

Kenward, R.E. 2001. *A Manual for Wildlife Radio-Tagging.* Academic Press, London.

Kenward, R.E., Hall, D.G., Walls, S.S. & Hodder, K.H. 2001. Factors affecting predation by buzzards Buteo buteo on released pheasants Phasianus colchicus. *Journal of Applied Ecology*, **38**, 813–822.

Kenward, R.E. 2006. *The Goshawk*. Poyser, London.

Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K., Bairlein, F. & Alerstam, T. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, **83**, 176–84.

Korpimäki, E. & Norrdahl, K. 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology*, **72**, 814–826.

Krebs, J.R. & Davies, N.B. 1993. *An Introduction to Behavioural Ecology*. Blackwell, Oxford.

Kruger, O. 2005. Age at first breeding and fitness in goshawk Accipiter gentilis. *Journal of Animal Ecology*, **74**, 266–273.

Langholm Moor Demonstration Project. 2007. *The Langholm Moor Demonstration Project Plan*. The Langholm Moor Demonstration Project Ltd., Langholm.

Langholm Moor Demonstration Project. 2014. *The Langholm Moor Demonstration Project: Seven Year Review*. The Langholm Moor Demonstration Project Ltd., Langholm.

Lees, A.C., Newton, I. & Balmford, A. 2013. Pheasants, buzzards, and trophic cascades. *Conservation Letters*, **6**, 141–144.

Lesnoff, M. & Lancelot, R. 2014. Package “aods3.” URL http://th.archive.ubuntu.com/cran/web/packages/aods3/

Levins, R. 1968. *Evolution in Changing Environments; Some Theoretical Explorations.* Princeton University Press, Princeton, N.J.

Lewis, S.B., Fuller, M.R. & Titus, K. 2004. A comparison of three methods for assessing raptor diet during the breeding season. *Wildlife Society Bulletin*, **32**, 373–385.

Lifson, N. & McClintock, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology*, **12**, 46–74.

Lima, S. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*,

48, 25–34.

Limiñana, R., Arroyo, B.E., Terraube, J., McGrady, M. & Mougeot, F. 2014. Using satellite telemetry and environmental niche modelling to inform conservation targets for a long-distance migratory raptor in its wintering grounds. *Oryx*, 1–9.

Linden, H. & Wikman, M. 1983. Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. *The Journal of Animal Ecology*, **52**, 953–968.

Lõhmus, A. 2003. Are certain habitats better every year? A review and a case study on birds of prey. *Ecography*, **26**, 545–552.

MacArthur, R. & Pianka, E. 1966. On optimal use of a patchy environment. *American Naturalist*, **100**, 603–609.

Madden, F. 2004. Creating Coexistence between Humans and Wildlife: Global Perspectives on Local Efforts to Address Human–Wildlife Conflict. *Human Dimensions of Wildlife*, **9**, 247–257.

Mañosa, S. & Cordero, P. 1992. Seasonal and sexual variation in the diet of the common buzzard in northeastern Spain. *Journal of Raptor Research*, **26**, 235 – 238.

Marquiss, M. & Booth, C.J. 1986. The diet of Ravens Corvus corax in Orkney. *Bird Study*, **33**, 190–195.

Martin, J. 2011. The Transformation of Lowland Game Shooting in England and Wales since the Second World War: The Supply Side Revolution. *Rural History*, **22**, 207–226.

Masman, D., Daan, S. & Beldhuis, H.J.A. 1988. Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. *Ardea*, **76**, 64 – 81.

McGilvray, J. 1995. *An Economic Study of Grouse Moors.* The Game Conservancy., Fordingbridge.

Mckinnon, L., Berteaux, D., Gauthier, G. & Bêty, J. 2013. Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos*, **122**, 1042–1048.

Millon, A., Petty, S.J., Little, B., Gimenez, O., Cornulier, T. & Lambin, X. 2014. Dampening prey cycle overrides the impact of climate change on predator population dynamics: a long-term demographic study on tawny owls. *Global change biology*, **20**, 1770–81.

Minta, S. & Mangel, M. 1989. A Simple Population Estimate Based on Simulation for Capture-Recapture and Capture-Resight Data. *Ecology*, **70**, 1738.

Morrison, M.L., Marcot, B. & Mannan, W. 2012. *Wildlife-Habitat Relationships: Concepts and Applications*. Island Press, Washington D.C.

Morton, D., Rowland, C.S., Wood, C.M., Meek, L., Marston, C., Smith, G., Wadsworth, R.A. & Simpson, I.C. 2011. *Final Report for LCM2007 - the New UK Land Cover Map. Countryside Survey Technical Report No 11/07*. NERC/Centre for Ecology & Hydrology.

Moss, R., Picozzi, N., Summers, R. & Baines, D. 2000. Capercaillie Tetrao urogallus in Scotland-demography of a declining population. *Ibis*, **142**, 259–267.

Musgrove, A., Aebischer, N.J., Eaton, M., Hearn, R., Newson, S.E., Noble, D.G., Parsons, M., Risely, K. & Stroud, D. 2013. Population estimates of birds in Great Britain and the United Kingdom. *British Birds*, **106**, 64–100.

Nagy, K.A. 1987. Field Metabolic Rate and Food Requirement Scaling in Mammals and Birds. *Ecological Monographs*, **57**, 111–128.

Nagy, K.A., Girard, I.A. & Brown, T.K. 1999. Energetics of free-ranging mammals, reptiles and birds. *Annual Review of Nutrition*, **19**, 247 – 277.

Natural England. 2013a. License reference WLM/2011/1801. URL http://www.rspb.org.uk/community/cfs-file.ashx/__key/communityserver-blogs-components-weblogfiles/00-00-03-96-75/2043.Licence-B-_2D00_-wlm-11-1801--Buzzard-licence-_2800_trap_2900_-ver-13Mar-signed_5F00_RD.pdf [accessed 15 December 2015]

Natural England. 2013b. Myth buster: Full details of buzzard nest control licence. URL http://www.naturalengland.org.uk/ourwork/regulation/wildlife/species/buzzardlicence.aspx [accessed 15 December 2015]

Newton, I. 1978. Feeding and development of Sparrowhawk Accipiter nisus nestlings. *Journal of Zoology*, **184**, 465–487.

Newton, I. 1979. *Population Ecology of Raptors*. T. & A.D. Poyser, Berkhamstead.

Newton, I., Marquiss, M. & Moss, D. 1981. Age and breeding in sparrowhawks. *Journal of Animal Ecology*, **50**, 839 – 853.

Newton, I. 1985. Lifetime reproductive output of female sparrowhawks. *Journal of Animal Ecology*, **45**, 241–253.

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behaviour. *Biological Reviews*, **67**, 129–173.

Newton, I., Dale, L. & Rothery, P. 1997. Apparent lack of impact of Sparrowhawks on the breeding densities of some woodland songbirds. *Bird Study*, **44**, 129–135.

Newton, I. 1998. *Population Limitation in Birds*. Academic Press, London.

Norrdahl, K. & Korpimäki, E. 2000. Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predators. *Oikos*, **91**, 528–540.

O'Toole, L., Fielding, A.H. & Haworth, P.F. 2002. Re-introduction of the golden eagle into the Republic of Ireland. *Biological Conservation*, **103**, 303–312.

Ormerod, S.J. 2002. Applied issues with predators and predation: Editor's introduction. *Journal of Applied Ecology*, **39**, 181–188.

PACEC. 2006. *The Economic and Environmental Impact of Sporting Shooting*. Public and Corporate Economic Consultants (PACEC), Cambridge.

Parish, D. & Sotherton, N. 2007. The fate of released captive-reared grey partridges Perdix perdix: implications for reintroduction programmes. *Wildlife Biology*, **13**, 140–149.

Park, K.J., Robertson, P.A., Campbell, S.T., Foster, R., Russell, Z.M., Newborn, D. & Hudson, P.J. 2001. The role of invertebrates in the diet, growth and survival of red grouse (Lagopus lagopus scoticus) chicks. *Journal of Zoology*, **254**, 137 – 145.

Park, K.J., Calladine, J., Graham, K.E., Stephenson, C.M. & Wernham, C. 2005. *The Impacts of Predatory Birds on Waders, Songbirds, Gamebirds and Fisheries Interests*. A report to Scotland's Moorland Forum.

Park, K.J., Graham, K.E., Calladine, J. & Wernham, C. 2008. Impacts of birds of prey on gamebirds in the UK: a review. *Ibis*, **150**, 9–26.

Parkin, D.T. & Knox, A.G. 2010. *The Status of Birds in Britain and Ireland*. Christopher Helm, London.

Parrott, D. 2015. Impacts and management of common buzzards Buteo buteo at pheasant Phasianus colchicus release pens in the UK: a review. *European Journal of Wildlife Research*, **61**, 181 – 197.

Penteriani, V., Ferrer, M. & Delgado, M. 2011. Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations. *Animal Conservation*, **14**, 233 – 241.

Penteriani, V., Rutz, C. & Kenward, R.E. 2013. Hunting behaviour and breeding performance of northern goshawks Accipiter gentilis, in relation to resource availability, sex, age and morphology. *Die Naturwissenschaften*, **100**, 935–42.

Peterson, M.N., Birckhead, J.L., Leong, K., Peterson, M.J. & Peterson, T.R. 2010. Rearticulating the myth of human-wildlife conflict. *Conservation Letters*, **3**, 74–82.

Petty, S.J. 1999. Diet of tawny owls (Strix aluco) in relation to field vole (Microtus agrestis) abundance in a conifer forest in northern England. *Journal of Zoology*, **248**, 451–465.

Phillips, R.A., Thompson, D.R. & Hamer, K.C. 1999. The impact of great skua predation on seabird populations at St Kilda: a bioenergetics model. *Journal of Applied Ecology*, **36**, 218 – 232.

Picozzi, N. 1978. Dispersion, breeding and prey of the Hen Harrier Circus cyaneus in Glen Dye, Kincardineshire. *Ibis*, **120**, 489 – 509.

Picozzi, N. & Weir, D.N. 1974. Breeding biology of the Buzzard in Speyside. *British Birds*, **67**, 199 – 210.

Pietersen, D. & Symes, C. 2010. Assessing the diet of Amur Falcon Falco amurensis and Lesser Kestrel Falco naumanni using stomach content analysis. *Ostrich: Journal of African Ornithology*, **81**, 39–44.

Potts, G.R. 1986. *The Partridge, Pesticides, Predation and Conservation.* Collins, London.

Preston, C. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor*, **92**, 107 – 112.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52**, 137–154.

Redpath, S.M. 1991. The impact of Hen harriers on Red grouse breeding success. *Journal of Applied Ecology*, **28**, 659–671.

Redpath, C.J., Thirgood, S.J. & Redpath, S.M. 1995. Evaluation of methods to estimate field vole Microtus agrestis abundance in upland habitats. *Journal of Zoology*, **237**, 49–55.

Redpath, S.M., Clarke, R., Madders, M. & Thirgood, S.J. 2001a. Assessing Raptor Diet: Comparing Pellets, Prey Remains, and Observational Data at Hen Harrier Nests. *The Condor*, **103**, 184–188.

Redpath, S.M., Thirgood, S.J. & Leckie, F.M. 2001b. Does supplementary feeding reduce predation of red grouse by hen harriers? *Journal of Applied Ecology*, **38**, 1157–1168.

Redpath, S.M., Arroyo, B.E., Leckie, F.M., Bacon, P., Bayfield, N., Gutierrez, R.J. & Thirgood, S.J. 2004. Using Decision Modeling with Stakeholders to Reduce Human – Wildlife Conflict : a Raptor – Grouse Case Study. *Conservation Biology*, **18**, 350–359.

Redpath, S.M., Amar, A., Smith, A., Thompson, D.B.A. & Thirgood, S.J. 2010. People and nature in conflict: can we reconcile hen harrier conservation. *Species management: Challenges and Solutions for the 21st century* (eds J. Baxter), & C.A. Galbraith), pp. 335–350. The Stationary Office.

Redpath, S.M., Young, J. & Evely, A. 2013. Understanding and managing conservation conflicts. *Trends in Ecology & Evolution*, **28**, 100–109.

Redpath, S.M., Bhatia, S. & Young, J. 2014. Tilting at wildlife: reconsidering human–wildlife conflict. *Oryx*, 1–4.

Redpath, S.M. & Thirgood, S.J. 1997. *Birds of Prey and Red Grouse*. The Stationery Office, London.

Redpath, S.M. & Thirgood, S.J. 1999. Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal*

Ecology, **68**, 879–892.

Redpath, S.M. & Thirgood, S.J. 2003. The impact of the hen harrier (Circus cyaneus) predation on red grouse (Lagopus lagopus scoticus) populations: linking models with field data. *Birds of Prey in a Changing Environment* (eds D.B.A. Thompson),, S.M. Redpath),, A. Fielding),, M. Marquiss), & C.A. Galbraith), pp. 499 – 510. The Stationary Office, Edinburgh.

Redpath, S.M. & Thirgood, S.J. 2009. Hen harriers and red grouse: moving towards consensus? *Journal of Applied Ecology*, **46**, 961–963.

Reif, V., Tornberg, R., Jungell, S. & Korpimäki, E. 2001. Diet variation of common buzzards in Finland supports the alternative prey hypothesis. *Ecography*, **24**, 267–274.

Reif, V., Jungell, S., Korpimäki, E., Tornberg, R. & Mykrä, S. 2004. Numerical response of common buzzards and predation rate of main and alternative prey under fluctuating food conditions. *Annales Zoologici Fennici*, **41**, 599–607.

Reif, V. & Tornberg, R. 2006. Using time-lapse digital video recording for a nesting study of birds of prey. *European Journal of Wildlife Research*, **52**, 251–258.

Resano-Mayor, J., Hernández-Matías, A., Real, J., Parés, F., Inger, R. & Bearhop, S. 2014. Comparing pellet and stable isotope analyses of nestling Bonelli's Eagle Aquila fasciata diet. *Ibis*, **156**, 176–188.

Rexer-Huber, K. & Bildstein, K.L. 2012. Winter diet of striated caracara Phalcoboenus australis (Aves, Polyborinae) at a farm settlement on the Falkland Islands. *Polar Biology*, **36**, 437–443.

Reynolds, J.C. & Tapper, S. 1996. Control of mammalian predators in game management and conservation. *Mammal Review*, **26**, 127 – 156.

Richards, S.A., Whittingham, M.J. & Stephens, P.A. 2010. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, **65**, 77–89.

Riedstra, B., Dijkstra, C. & Daan, S. 1998. Daily energy expenditure of male and female marsh harrier nestlings. *The Auk*, **115**, 635 – 641.

Robertson, P.A., Park, K.J. & Barton, A. 2001. Loss of heather Calluna vulgaris moorland in the Scottish uplands: the role of red grouse Lagopus lagopus scoticus management. *Wildlife Biology*, **7**, 11–16.

Robinson, R.A. 2005. *BirdFacts: Profiles of Birds Occurring in Britain and Ireland: (BTO Research Report 407)*. BTO, Thetford.

Roby, D. & Lyons, D. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. *Canadian Journal of Zoology*, **81**, 250 – 265.

Rooney, E., Reid, N. & Montgomery, W.I. 2014. Supplementary feeding increases Common Buzzard Buteo buteo productivity but only in poor-quality habitat. *Ibis*, **157**, 181–185.

Rooney, E. & Montgomery, W.I. 2013. Diet diversity of the Common Buzzard (Buteo buteo) in a vole-less environment. *Bird Study*, **60**, 147–155.

RSPB. 2014. *Birdcrime 2013: Offences against Wild Bird Legislation in 2013*. RSPB, Sandy.

Rutz, C. 2003. Assessing the breeding season diet of goshawks Accipiter gentilis: biases of plucking analysis quantified by means of continuous radio-monitoring. *Journal of Zoology*, **259**, 209–217.

Rutz, C., Whittingham, M.J. & Newton, I. 2006. Age-dependent diet choice in an avian top predator. *Proceedings of The Royal Society*, **273**, 579–86.

Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V. 2000. Responses of an Avian Predator to Variations in Prey Density at a Temperate Latitude. *Ecology*, **81**, 2428 – 2441.

Schei, E., Holmstad, P. & Skorping, A. 2005. Seasonal infection patterns in Willow Grouse (Lagopus lagopus L.) do not support the presence of parasite-induced winter losses. *Ornis Fennica*, **82**, 137 – 146.

Schoener, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 369–404.

Schuette, P., Creel, S. & Christianson, D. 2013. Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements.

Biological Conservation, **157**, 148–154.

Selås, V. 2001. Predation on reptiles and birds by the common buzzard, *Buteo buteo*, in relation to changes in its main prey, voles. *Canadian Journal of Zoology*, **79**, 2086–2093.

Selås, V., Tveiten, R. & Aanonsen, O.M. 2007. Diet of Common Buzzards (Buteo buteo) in southern Norway determined from prey remains and video recordings. *Ornis Fennica*, **84**, 97–104.

Simmons, R.E., Avery, D.M. & Avery, G. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *Journal of Raptor Research*, **25**, 63–67.

Slagsvold, T., Sonerud, G.A., Grønlien, H.E. & Stige, L.C. 2010. Prey handling in raptors in relation to their morphology and feeding niches. *Journal of Avian Biology*, **41**, 488–497.

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S.M., Thirgood, S.J. & Harwood, J. 2010. The functional response of a generalist predator. *PloS one*, **5(5):e1076**, DOI: 10.1371/journal.pone.0010761.

Snow, D. & Perrins, C. 1998. *The Birds of the Western Palearctic Concise Edition.* Oxford University Press, Oxford.

Soanes, L.M., Arnould, J.P.Y., Dodd, S.G., Sumner, M.D. & Green, J.A. 2013. How many seabirds do we need to track to define home-range area? *Journal of Applied Ecology*, **50**, 671–679.

Solomon, M. 1949. The natural control of animal populations. *Journal of Animal Ecology*, **18**, 1–35.

Sotherton, N., Tapper, S. & Smith, A. 2009. Hen harriers and red grouse: economic aspects of red grouse shooting and the implications for moorland conservation. *Journal of Applied Ecology*, **46**, 955–960.

Steen, R. 2009. A Portable Digital Video Surveillance System to Monitor Prey Deliveries at Raptor Nests. *Journal of Raptor Research*, **43**, 69–74.

Stephens, D.W. & Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, N.J.

Sundell, J., O'Hara, R.B., Helle, P., Hellstedt, P., Henttonen, H. & Pietiäinen, H. 2013. Numerical response of small mustelids to vole abundance: delayed or not? *Oikos*, **122**, 1112–1120.

Svensson, L., Grant, P.J., Mullarney, K. & Zetterstrom, D. 2009. *Collins Bird Guide*, 2nd ed. Harper Collins, London.

Swann, R.L. & Etheridge, B. 1995. A comparison of breeding success and prey of the Common Buzzard Buteo buteo in two areas of northern Scotland. *Bird Study*, **42**, 37–43.

Swarna Nantha, H. & Tisdell, C. 2009. The orangutan–oil palm conflict: economic constraints and opportunities for conservation. *Biodiversity and Conservation*, **18**, 487–502.

Teerink, B.J. 1991. *Atlas and Identification Key. Hair of West-European Mammals.* Cambridge University Press, Cambridge.

Teerink, B.J. 2004. *Hair of West European Mammals*. Cambridge University Press, Cambridge.

Thirgood, S.J., Redpath, S.M., Hudson, P.J., Hurley, M.M. & Aebischer, N.J. 1995a. Effects of necklace radio transmitters on survival and breeding success of red grouse Lagopus lagopus scoticus. *Wildlife Biology*, **1**, 121–126.

Thirgood, S.J., Leckie, F.M. & Redpath, S.M. 1995b. Diurnal and seasonal variation in line transect counts of moorland passerines. *Bird Study*, **42**, 257–259.

Thirgood, S.J., Redpath, S.M., Hudson, P.J. & Donnelly, E. 1998. Estimating the cause and rate of mortality in red grouse Lagopus lagopus. *Wildlife Biology*, **4**, 65–71.

Thirgood, S.J., Redpath, S.M., Newton, I. & Hudson, P.J. 2000a. Raptors and Red Grouse: Conservation Conflicts and Management Solutions. *Conservation Biology*, **14**, 95–104.

Thirgood, S.J., Redpath, S.M., Haydon, D.T., Rothery, P., Newton, I. & Hudson, P.J. 2000b. Habitat loss and raptor predation: disentangling long- and short-term causes of red grouse declines. *Proceedings of The Royal Society*, **267**, 651–6.

Thirgood, S.J., Redpath, S.M., Rothery, P. & Aebischer, N.J. 2000c. Raptor predation and population limitation in red grouse. *Journal of Animal Ecology*, **69**, 504–516.

Thirgood, S.J., Redpath, S.M., Campbell, S. & Smith, A. 2002. Do habitat characteristics influence predation on red grouse? *Journal of Applied Ecology*, **39**, 217–225.

Thirgood, S.J., Redpath, S.M. & Graham, I.M. 2003. What determines the foraging distribution of raptors on heather moorland ? *Oikos*, **1**, 15–24.

Thirgood, S.J. & Redpath, S.M. 1997. Red grouse and their predators. *Nature*, **390**, 2543.

Thirgood, S.J. & Redpath, S.M. 1999. Raptors and red grouse: a conflict in the uplands?

Thirgood, S.J. & Redpath, S.M. 2008. Hen harriers and red grouse: science, politics and human-wildlife conflict. *Journal of Applied Ecology*, **45**, 1550–1554.

Thomas, L. & Buckland, S. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, **47**, 5 – 14.

Thompson, D.B.A., MacDonald, A.J., Marsden, J.H. & Galbraith, C.A. 1995. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*, **71**, 163–178.

Thompson, P.S., Amar, A., Hoccom, D.G., Knott, J. & Wilson, J. 2009. Resolving the conflict between driven-grouse shooting and conservation of hen harriers. *Journal of Applied Ecology*, **46**, 950–954.

Thomson, D.L., Green, R.E., Gregory, R.D. & Baillie, S.R. 1998. The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 2057–2062.

Tornberg, R., Reif, V. & Korpimäki, E. 2012. What Explains Forest Grouse Mortality: Predation Impacts of Raptors, Vole Abundance, or Weather Conditions? *International Journal of Ecology*, **2012**, 1–10.

Tornberg, R. & Colpaert, A. 2001. Survival, ranging, habitat choice and diet of the Northern Goshawk Accipiter gentilis during winter in Northern Finland. *Ibis*, **143**, 41–50.

Tornberg, R. & Reif, V. 2007. Assessing the diet of birds of prey: a comparison of prey items found in nests and images. *Ornis Fennica*, **84**, 21–31.

Tremblay, Y., Thiebault, A., Mullers, R. & Pistorius, P. 2014. Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS ONE*, **9(2):e8842**, DOI:10.1371/journal.pone.0088424.

Tubbs, C.R. 1974. *The Buzzard*. David & Charles, Newton Abbot, London.

Turner, C. & Sage, R. 2003. Fate of released pheasants. *The Game Conservancy Trust Review*, **35**, 74–75.

Valkama, J., Korpimäki, E., Arroyo, B.E., Beja, P., Bretagnolle, V., Bro, E., Kenward, R.E., Mañosa, S., Redpath, S.M., Thirgood, S.J. & Viñuela, J. 2005. Birds of prey as limiting factors of gamebird populations in Europe: a review. *Biological reviews of the Cambridge Philosophical Society*, **80**, 171–203.

Vickery, P., Hunter, M. & Wells, J. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos*, **63**, 281–288.

Votier, S.C., Bearhop, S., Ratcliffe, N., Phillips, R.A. & Furness, R.W. 2004a. Predation by great skuas at a large Shetland seabird colony. *Journal of Applied Ecology*, **41**, 1117 – 1128.

Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E., Caldow, R.W.G., Catry, P., Ensor, K., Hamer, K.C., Hudson, A. V, Kalmbach, E., Klomp, N.I., Pfeiffer, S., Phillips, R.A., Prieto, I. & Thompson, D.R. 2004b. Changes in fisheries discard rates and seabird communities. *Nature*, **427**, 727–30.

Walls, S.S., Kenward, R.E. & Holloway, G.J. 2005. Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal. *Journal of Animal Ecology*, **74**, 190–197.

Walls, S.S. & Kenward, R.E. 1998. Movements of radio-tagged Buzzards Buteo buteo in early life. *Ibis*, **140**, 561–568.

Warkentin, I.G. & West, N.H. 1990. Ecological energetics of wintering Merlins Falco columbarius. *Physiological Zoology*, **63**, 308 – 333.

Warren, P. & Baines, D. 2002. Dispersal, survival and causes of mortality in black grouse

Tetrao tetrix in northern England. *Wildlife biology*, **8**, 91–97.

Watson, A., Moss, R. & Rae, S. 1998. Population dynamics of Scottish rock ptarmigan cycles. *Ecology*, **79**, 1174–1192.

Watson, M., Aebischer, N.J., Potts, G.R. & Ewald, J.A. 2007. The relative effects of raptor predation and shooting on overwinter mortality of grey partridges in the United Kingdom. *Journal of Applied Ecology*, **44**, 972–982.

Weir, D.N. 1978. Wild peregrines and grouse. *The Falconer*, **7**, 98 – 102.

Wheeler, P. 2008. Effects of sheep grazing on abundance and predators of field vole (Microtus agrestis) in upland Britain. *Agriculture, Ecosystems and Environment*, **123**, 49–55.

Whitfield, D. & Fielding, A.H. 2004. The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. *Biological Conservation*, **118**, 249 – 259.

Whittingham, M.J., Swetnam, R.D., Wilson, J., Chamberlain, D.E. & Freckleton, R.P. 2005. Habitat selection by yellowhammers Emberiza citrinella on lowland farmland at two spatial scales: implications for conservation management. *Journal of Applied Ecology*, **42**, 270–280.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. 2006. Why do we still use stepwise modelling in ecology and behaviour? *The Journal of animal ecology*, **75**, 1182–1189.

Whittingham, M.J. & Evans, K. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis*, **146**, 210–220.

Widén, P. 1987. Goshawk predation during winter, spring and summer in a boreal forest area of central Sweden. *Ecography*, **10**, 104–109.

Wilson, S., Davies, T.E., Hazarika, N. & Zimmermann, A. 2015. Understanding spatial and temporal patterns of human–elephant conflict in Assam, India. *Oryx*, **49**, 140–149.

Wolfe, A. & Long, A. 1997. Distinguishing between hair fibres of the rabbit and the mountain hare in scats of the Red Fox. *Journal of Zoology*, **242**, 370–375.

Woodroffe, R., Thirgood, S.J. & Rabinowitz, A. 2005. *People and Wildlife: Conflict or Coexistence?* Cambridge University Press.

Worton, B.J. 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, **70**, 164.

Wuczyński, A. 2005. Habitat use and hunting behaviour of Common Buzzards Buteo buteo wintering in south-western Poland. *Acta Ornithologica*, **40**, 147 – 154.

Yalden, D.W. & Morris, P.A. 2009. *The Analysis of Owl Pellets*, 4th ed. The Mammal Society, London.

Zárybnická, M., Riegert, J. & Kouba, M. 2015. Indirect food web interactions affect predation of Tengmalm's Owls Aegolius funereus nests by Pine Martens Martes martes according to the alternative prey hypothesis. *Ibis*, **157**, 459–467.