Understanding conservation conflicts surrounding predation and game shooting interests

Submitted by George Julius Fraser Swan to the University of Exeter
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

(Signature) ……………………………

Hawk Roosting

“I sit in the top of the wood, my eyes closed.
Inaction, no falsifying dream
Between my hooked head and hooked feet:
Or in sleep rehearse perfect kills and eat.

The convenience of the high trees!
The air's buoyancy and the sun's ray
Are of advantage to me;
And the earth's face upward for my inspection.

My feet are locked upon the rough bark.
It took the whole of Creation
To produce my foot, my each feather:
Now I hold Creation in my foot

Or fly up, and revolve it all slowly -
I kill where I please because it is all mine.
There is no sophistry in my body:
My manners are tearing off heads -

The allotment of death.
For the one path of my flight is direct
Through the bones of the living.
No arguments assert my right:

The sun is behind me.
Nothing has changed since I began.
My eye has permitted no change.
I am going to keep things like this.”

Ted Hughes, 1960

Abstract

Many predatory species cause negative impacts on human interests by threatening game, livestock or human safety. These impacts can create conflicts where stakeholders differ over wildlife management and when one party is perceived to exert their interests at the expense of the other. Finding effective methods to mitigate conservation conflicts requires an interdisciplinary perspective that investigates (i) the reality of the apparent impacts, (ii) the efficacy of any methods intended to remedy them and (iii) the perceptions, motivations and objectives of key stakeholders.

In this thesis, I investigated a conservation conflict in the U.K. surrounding predators and game management. I did so with specific reference to the common buzzard *Buteo buteo,* a species that, due to predation of released pheasants *Phasianus colchicus*, is both subject to illegal persecution and on-going controversy concerning the licenced selective removal of 'problem individuals'.

I first review the literature to assess the ecological evidence that certain 'problem individuals' can be both disproportionately responsible in impacts upon human interests and more likely to reoffend. I show that while there is evidence for these animals across many different taxa, the benefits of their removal can sometimes be short-lived. I highlight possible indirect impacts of selective management and identify it as a potential compromise between different stakeholder groups.

Next, I evaluate the performance of Bayesian stable isotope mixing models (BSIMMs) in quantifying the diets of wild animals. By comparing indirect and direct observations of buzzard foraging, I demonstrate that, with the correct selection of trophic discrimination factors, stable isotope analyses can provide a reliable picture of dietary composition that mirrors direct observations.

I then apply these mixing models to evaluate the ecological basis of selective removal of 'problem buzzards'. The results suggest that the consumption by buzzards of released pheasants is not limited to release pens where gamekeepers perceive buzzard predation to be a problem. However, I then show that stable isotope analysis of blood sampled from two of the four buzzards caught inside pens indicates frequent consumption of released pheasants, relative to the rest of the buzzard population. These results suggest that, while some pheasant consumption may go undetected, selecting only buzzards inside pens for removal is likely to target ‘problem birds’.

I then investigate buzzard foraging and breeding ecology on land managed for pheasant shooting. I find that buzzards nest at higher density in areas with greater abundances of pheasants and rabbits *Oryctolagus cuniculus*. However, records of provisioning from nest cameras showed that only rabbits were caught in proportion to their abundance and only rabbit provisioning rate was associated with buzzard productivity. I suggest that the positive relationship between buzzard and pheasant abundance, although seemingly unconnected to pheasant predation, might influence how gamekeepers perceive buzzard impact.

Next, I conduct semi-structured interviews on the subject of predator control with 20 gamekeepers across the south of England, to explore the underlying beliefs, norms and information sources that motivate their behaviour. From these interviews, I identify a number of separate, but interconnected, motivations that influence predator control including professional norms, potential penalties, and interpretations of what is ‘natural’. The influences of these motivations are discussed in detail and a conceptual model, incorporating the theory of planned behaviour, is developed.

Finally, the key contributions of this thesis are drawn together and discussed in their wider context. Taken together, the results of this thesis illustrate how predator management occurs simultaneously within social and ecological contexts that incorporate the individual attributes of both predators and people. The results of this thesis have direct implications for the management of predators, the representation of stakeholder perspectives and the design of conflict mitigation measures.

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Contents

Tables, Figures and Boxes

Abbreviations

APH	Alternative Prey Hypothesis
BASC	The British Association for Shooting and Conservation
BSIMM	Bayesian Stable Isotope Mixing Model
GWCT	The Game and Wildlife Conservation Trust
NGO	The National Gamekeepers Organisation
SIMM	Stable Isotope Mixing Model
TDF	Trophic Discrimination Factor

Author's declaration for co-authored manuscripts

Chapters 2, 3, 4, 5 and 6 have been published or written for publication as co-authored manuscripts. For Chapter 2 I developed the focus of the paper with my supervisors Robbie McDonald (RM), Stuart Bearhop (SB), and Steve Redpath (SR). I then conducted the literature review and wrote up the findings. For Chapter 3 I designed the study with RM, SB, SR and Richard Inger. I then collected the data, analysed it with assistance from Cecily Goodwin and Matthew Silk (MS) and wrote up the findings. For Chapters 4 and 5 I designed the studies with RM, SB and SR before collecting and analysing the data and writing up the results. For Chapter 5 I designed the study with RM, SR and Sarah Crowley before collecting and analysing the data and writing up the chapter. I conducted all fieldwork, interviews and transcription. I wrote all five chapters, then amended and revised them in response to comments suggestions and advice for RM, SB and SR.

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Chapter 1

INTRODUCTION

Chapter 1: Introduction

People and predators

As human populations continue to grow, so too does the ‘human footprint’. An estimated 75% of the planet’s land surface is now experiencing measurable human pressures (Venter *et al.* 2016). As a consequence, many species have experienced rapid population declines, reductions in their historical ranges and fragmentation of their habitat (Ceballos 2002; Ripple *et al.* 2014; Haddad *et al.* 2015). As the remaining wildlife is forced into closer proximity to people, competition arises for shared resources (Messmer 2000). This competition can have serious consequences for both humans and natural systems (Woodroffe, Thirgood & Rabinowitz 2005a). Wildlife, can negatively impact humans and, in turn, humans can negatively impact wildlife. Although such feedbacks have been referred to as ‘human-wildlife conflicts’ (Conover 2002), this term has been criticised in recent years as positioning wildlife as “*conscious human antagonists*” (Peterson *et al.* 2010: p74) and not distinguishing between the ecological and social aspects of wildlife management (Redpath, Bhatia & Young 2015). Here, following Young *et al.* (2010), I use the term ‘human-wildlife impacts’ to describe situations when wild animals impact on humans and their activities.

Predatory animals are commonly implicated in human-wildlife impacts due to their protein-rich diet that can incorporate prey species of economic, nutritional or social value to people (Treves & Karanth 2003; Graham, Beckerman & Thirgood 2005). Examples include the predation of livestock (Avery & Cummings 2004; Karlsson & Johansson 2010; Suryawanshi *et al.* 2013) and game (Treves & Karanth 2003; Park *et al.* 2008; Arroyo *et al.* 2012; Mazur & Asah 2013). Predators can even threaten the safety of humans themselves (Athreya *et al.* 2011; Neff & Hueter 2013). A common response to predator impacts has been population reduction through the use of lethal methods (Treves & Naughton-Treves 2005). While a few generalist predatory species, such as coyotes *Canis latrans,* have proven resilient to such attempts, population control strategies have been remarkably successful, producing local extirpations and extinctions of their target species (Woodroffe, Thirgood & Rabinowitz 2005a; Ripple *et al.* 2014).

A changing relationship?

Despite these tensions, the relationship between people and predators is a curious one. Even where predators pose a high risk to both humans and their livestock, they can simultaneously provoke "*intense feelings of awe and admiration as well as fear and resentment*" (Goldman *et al.* 2010: p336). Globally, the balance between these two, seemingly opposing, views on predators (and wildlife more generally) appears to be shifting as societies in the developed world move from industrial to post-industrial phases (Inglehart & Welzel 2005; Teel, Manfredo & Stinchfield 2007). As immediate concerns over personal safety, security and economic stability are reduced, some societies are able to place a greater emphasis on self-expression and quality of life, which in turn has a positive relationship with environmentalism (Inglehart 1977; Inglehart & Welzel 2005). This can be most clearly observed in developed countries where there is a shift towards seeing wild animals as individuals, deserving of rights and protection (Jacobs 2007; Teel, Manfredo & Stinchfield 2007). Following this sea-change in public consciousness, predatory species tend to be accorded high 'existence value' by people in the developed world (Dickman, Macdonald & Macdonald 2011). To many, they represent power, beauty and, to an increasingly urbanised population, a disappearing link to the natural world (Montag, Patterson & Freimund 2005; Goldman, Roque De Pinho & Perry 2010). Public interest in predatory species has helped fuel a growing demand for wildlife-based tourism and has enabled many to be used as surrogates for broader conservation causes (Sergio *et al.* 2006; Dickman, Macdonald & Macdonald 2011).

The transition, on the part of some people, away from the framing of predators as 'vermin' and 'pests' might also have been aided to some extent by an increasing recognition of the important roles of predators in regulating ecosystems and sustaining biodiversity (Ritchie & Johnson 2009). For example, apex predators can suppress herbivores and mesopredators through predation, intra-guild aggression or behavioural change (Ritchie & Johnson

2009; Wallach *et al.* 2010; Estes *et al.* 2011) while mesopredators may constrain top predators through competition for resources (Bodey, McDonald & Bearhop 2009). As a result, predator control may disproportionately alter species assemblages with unintended consequences, such as changing disease dynamics or reducing ecosystem services (Ritchie & Johnson 2009; Ripple *et al.* 2014).

Although political pressure from impacted stakeholders was, for a while, the driving force of government wildlife control policies (Bergstrom *et al.* 2014), budding environmental movements have pushed conservation and animal welfare into socio-political agendas (Graham, Beckerman & Thirgood 2005; Bergstrom 2017). Since the early 1970s, there has been a notable transformation in environmental thinking in many countries that has produced more stringent national and international legislative protection of predators (Chapron *et al.* 2014; Sergio *et al.* 2014). Although predator declines continue in many areas (Ripple *et al.* 2014; Wolf & Ripple 2017), there are some success stories beginning to emerge. In mainland Europe, brown bear *Ursus arctos* populations are stable or increasing (Chapron *et al.* 2014), in the United States grey wolves *Canis lupus* are recolonizing parts of their former range (Ripple *et al.* 2014) and in the U.K. red kite *Milvus milvus* and osprey *Pandion haliaetus* have rebounded from reintroduced and remnant populations (Smart *et al.* 2010; Schmidt-Rothmund, Dennis & Saurola 2014).

The return of predatory species to areas from which they had previously been extirpated has produced ecological and economic benefits (Estes *et al.* 2003; Ritchie & Johnson 2009; Dickman, Macdonald & Macdonald 2011). Such benefits are lauded by exponents of ‘rewilding’, a sphere of activity that promotes the restoration of ecosystems through the reintroduction or recovery of key species (Nogués-Bravo *et al.* 2016). Yet the positive effects of predator increases can, on occasion, be overstated (Allen *et al.* 2017) and come to dominate debate over their management (Arts, Fischer & van der Wal 2012). In reality, reintroduced or expanding predator populations can pose sizeable challenges to mitigating human-wildlife impacts, in part because once commonplace practices that reduce wildlife damage have ceased or been forgotten (Thirgood, Woodroffe & Rabinowitz 2005; Chapron *et al.* 2014).

Conflicts over predator management

Conservation conflicts arise over predators when *“two or more parties with strongly held opinions clash over conservation objectives and when one party is perceived to assert its interests at the expense of another”* (Redpath *et al.* 2013: p100). These can either be when conservation objectives are perceived to be under threat or, conversely, when they are perceived to be threatening. Many conflicts incorporate aspects of both. For example, illegal killing threatens the viability of a reintroduced population of white-tailed sea eagles *Haliaeetus albicilla* in Ireland (the threat *to* conservation objectives). Yet the suspected culprits of this killing, disaffected sheep farmers, perceive that the consequences of eagle restoration, i.e. lamb predation and unwanted environmental designations, had been imposed on them without proper consultation (the threat *from* conservation objectives) (O’Rourke 2014).

Recovering predator populations can therefore produce particularly severe conservation conflicts (Chapron *et al.* 2014; Olson *et al.* 2015). When wildlife is perceived to have been imposed on people, the animals themselves become “*symbols of wider political divisions between rural and urban populations and between individuals and groups with fundamentally different value orientations and interests*” (Chapron *et al.* 2014: p1519). Under such circumstances, protective legislation can be seen as unfair, discriminatory and/or lacking in legitimacy and can, therefore, be justifiably flouted (Pohja-Mykrä 2016). Attitudes towards illegal persecution by those who perpetrate or support it can move from deviance into defiance (Von Essen *et al.* 2014). For example, Pohja-Mykrä (2016) observed that illegal wolf hunting in Finland was an act of ‘explicit resistance’ against game management authorities. In situations such as this, positions on both ‘sides’ can quickly become entrenched, making effective mitigation challenging (Redpath *et al.* 2013).

As the number of conflicts over biodiversity and predator management increases globally (Conover 2002; Treves & Karanth 2003; Young *et al.* 2010), one role for conservation scientists is to find effective ways of mitigating impacts on both the human stakeholders and the animal species concerned (Linnell 2011). Nevertheless, "*the field of conservation is rooted in biology*" (Madden & McQuinn 2014: p98) and attempts towards mitigation have typically been undertaken by ecologists, with socio-economic and socio-psychological aspects either downplayed or ignored (St John, Edwards-Jones & Jones 2010; O'Rourke 2014). However, there is a growing appreciation of the 'human dimensions' of these disagreements and of the need of interdisciplinary approaches to tackle them (Redpath *et al.* 2013; Madden & McQuinn 2014).

The role of conservation science

For conservation scientists, taking a holistic view of both the human-wildlife impact and human-human conflicts provides a broad scope for social and ecological investigation. This can best be illustrated along the timeline of a typical, if somewhat idealised, conflict where humans perceive an impact from wildlife:

First, interviews with stakeholders can yield valuable information on the perceived direct costs (Wang & Macdonald 2006) or any hidden indirect impacts (Barua, Bhagwat & Jadhav 2013). For direct costs, independent ecological science might then quantify the reality of these perceptions (Suryawanshi *et al.* 2013). Once impact has been gauged, a stakeholder analysis might then identify *"individuals, groups and organisations who are affected by or can affect*" the conflict or potential management options (Reed et al. 2009: p1933). These stakeholders could be brought together in an attempt to define joint management objectives (Treves *et al.* 2006). Here, skilled facilitators are required to ensure participation emphasises "*empowerment, equity, trust and learning*" (Reed 2008: p2422). Management decisions would then be selected based on social acceptability, practicality and efficacy (each creating further research avenues or drawing from previous studies).

Realistically, however, finding shared ground with opposing parties who hold fundamentally different beliefs and values creates numerous barriers to effective management (Redpath *et al.* 2013). For example, when conflicts involve the illegal killing of predators, conservationists may not be willing to enter negotiations (Thirgood & Redpath 2008). To address these issues requires a broader social and psychological perspective that considers "*all levels and sources of conflict within the social system in which conservation is embedded*" (Madden & McQuinn 2014: p104).

Predators, gamebirds and gamekeepers

Gamebird shooting in the U.K.

In the U.K., the recreational hunting of driven gamebirds on private land is a traditional 'fieldsport' (Loveridge, Reynolds & Milner-Gulland 2006) and can play an important social and economic role in rural communities (Public & Corporate Economic Consultants 2006). It can also provide benefits to biodiversity and its conservation. For instance, landowners who conduct gamebird releases maintain and plant more new woodland and hedgerows than those who do not (Oldfield *et al.* 2003). The crops planted to provide feed to gamebirds can also prove important for passerine species (Sage *et al.* 2005).

Driven gamebird 'shoots' can broadly be split into two categories: 'put and take' and 'wild' game shoots (Sokos, Birtsas & Tsachalidis 2008). Wild gamebird shoots attempt to maximise the 'natural' densities of species such as red grouse *Lagopus lagopus scotica*. In contrast 'put and take' shoots rear and release gamebirds, predominantly ring-necked pheasants *Phasianus colchicus* and red-legged partridges *Alectoris rufa*, (Tapper 1992). In the U.K., these reared birds are initially considered as livestock but then transition into 'wild' animals as their dependency on humans diminishes (Wildlife and Countryside Act 1981). Such releases are substantial both in the quantity of birds and their spatial coverage. An estimated one in twelve woodlands in England contains a release pen (Sage, Ludolf & Robertson 2005), with ~35 million gamebirds being released annually (BASC 2015). This number, thought to be increasing (Martin 2011), already constitutes a significant proportion of the U.K.'s avian biomass (Dolton & Brooke 1999).

In order to rear and release birds and maximise the number available to shoot, many landowners employ gamekeepers (although some gamekeepers lease the shooting rights and run the shoot independently). Gamekeeping is a traditional rural profession, largely conducted on a solitary basis (Munsche 1981; Martin 2011). Skills are learnt during long apprenticeships although an increasing number of gamekeepers have also qualified from taught courses at agricultural colleges (BASC 2011). Despite the sizeable area still under game management and increasing gamebird releases (Park *et al.* 2008), numbers of gamekeepers have declined from a peak of 20,000 in 1911 (Sharp 2010) to around 3,500 in recent years (BASC 2011).

Predator control

Although yearly releases allow shoots to stock gamebirds at high densities, there are drawbacks. Released birds require supplementary feed and, in some cases, medication, to prevent starvation or the outbreak of diseases. Despite this, when compared to their 'wild' counterparts, released gamebirds have high levels of mortality and lower breeding success (reviewed in Sokos *et al.* 2008). Predation constitutes a significant factor in losses of reared (Parish & Sotherton 2007) and wild gamebird species (Thirgood & Redpath 2008). Therefore, gamekeepers invest substantial effort in reducing predator densities through numerous methods of lethal control (Reynolds & Tapper 1996; Martin 2011). For instance, on the shooting estates where these predators are present, 96.5% of gamekeepers actively cull foxes *Vulpes vulpes*, 96.4% cull magpies *Pica pica* and 84.2% cull stoats *Mustela erminea* (GWCT 2011). Aside from the desired aims of increasing game (Reynolds & Tapper 1996; Reynolds *et al.* 2010), a number of non-game species, such as curlew *Numenius arquata* and lapwing *Vanellus vanellus*, appear to benefit from land managed for shooting (Tharme *et al.* 2001; Draycott, Hoodless & Sage 2007; Baines *et al.* 2008; Fletcher *et al.* 2010).

The systematic lethal control of predators to augment game populations for shooting has created a social conflict centring on animal welfare and threats to conservation objectives, particularly for those species for which illegal persecution is apparent. An especially acute set of conflicts concerns the perceived or actual impact of birds of prey on game species and how these predators should be managed (Valkama *et al.* 2005; Park *et al.* 2008; Redpath & Thirgood 2009; Lees, Newton & Balmford 2013; Elston *et al.* 2014). In the U.K., these birds have been protected by the law for many decades, yet shooting estates have been repeatedly linked to illegal persecution of such protected raptor species as golden eagles *Aquila chrysaetos* (Whitfield 2004), red kites (Smart *et al.* 2010), peregrines *Falco peregrinus* (Amar et al. 2012) and common buzzards *Buteo buteo* (Swann & Etheridge 1995). This persecution has, in some cases, had serious negative consequences, reducing raptor abundance, distribution and nesting success (Newton 1979; Elliott & Avery 1991; Amar *et al.* 2012).

Tensions over the management of birds of prey are particularly well exemplified by a long-running conflict over hen harrier *Circus cyaneus* conservation and red grouse management (Thirgood & Redpath 2008; Redpath & Thirgood 2009). Here, despite concerted attempts to find workable solutions and bring stakeholders together (Redpath, Thirgood & Leckie 2001; Redpath *et al.* 2004; Elston *et al.* 2014), a breakthrough remains elusive (Redpath *et al.* 2013). This conflict has ecological and socio-economic foundations. For instance: (i) there is evidence harriers have a detrimental impact upon grouse densities and make intensive grouse moorland management uneconomic (Thirgood *et al.* 2000), (ii) illegal killing of harriers in the U.K. appears to be widespread and to be imperilling international conservation objectives (Etheridge, Summers & Green 1997; Sim *et al.* 2007) and (iii) stakeholders have divergent value systems making trust and constructive dialogue difficult (Redpath *et al.* 2013).

These factors combine to create an impasse that has, so far, proved difficult to move past constructively. There is however, an emerging conflict in lowland Britain concerning common buzzard predation that, although it contains multiple parallels, appears to have more capacity for compromise on both ‘sides’.

The common buzzard

The common buzzard, hereafter buzzard, is an Old World member of the family Accipitridae (Dare 2015). Of the 28 members of the Genus *Buteo* (Ferguson-Lees & Christie 2001), *B. buteo* is the most abundant across Europe and is the only permanent resident in the U.K. (Cramp & Simmons 1980). The buzzard is a medium-sized bird of prey with a robust body and broad wings. Although commonly dark brown in plumage, this can differ markedly from very dark to very pale, acknowledged in its French vernacular name, '*la buse variable*'.

Although previously ubiquitous across the U.K., historical persecution that intensified during the 19th and early 20th centuries caused the local extirpation of the buzzard from most of its original range (Moore 1957). The sudden loss of their main prey, rabbits *Oryctolagus cuniculus*, following the introduction of myxomatosis in the mid-1950s, further reduced the British population to an estimated 6000-8000 pairs by the end of that decade (Dare 2015). During the latter half of the 20th century, as deliberate killing lessened and rabbit numbers recovered, buzzard populations experienced a resurgence (Robinson *et al.* 2016). Combined data from the Breeding Bird Survey and the Common Bird Census estimated the buzzard population had increased 454% between 1970 and 2014 (Hayhow *et al.* 2016). Consequently, the buzzard has now recovered the full extent of its former U.K. range, recolonizing areas from which it had been absent for several decades (Clements 2002). In 2009, the U.K. breeding population was estimated to be between 57,000 and 79,000 pairs, making it the U.K.'s most abundant bird of prey (Musgrove *et al.* 2013).

Buzzards and released pheasants

While conservationists have heralded the resurgence of the buzzard as a "*conservation success story*" (Harper 2012), wider responses have not been universally positive. Across Europe, they are considered of all birds of prey to have one of the greatest negative impacts on game species (Kenward 2002). This is particularly true in the U.K., where their rapid recovery has raised concerns among parts of the shooting community. Buzzards are believed to have both a direct impact on the numbers of gamebirds available to shoot, and to cause indirect mortality and financial loss due to disturbance (Harradine, Reynolds & Laws 1997; Parrott 2015). In a members' poll by both the National Gamekeepers Association and the Scottish Gamekeepers Association, 97% (n = 910) of respondents reported having buzzards on their shoots. Of these, 76% (n = 693) identified buzzards as having a negative effect on gamebirds (GWCT 2011). This appears to be a marked increase from a survey conducted in 1995 by the BASC, in which only 61% of 996 gamekeepers reported problems by any raptors, of which only 20% were attributed to buzzards (Harradine, Reynolds & Laws 1997). The concerns of gamekeepers about the impact of buzzards may continue to intensify as the number and value of gamebirds, particularly pheasants, that are released in the U.K. continues to increase (BASC 2009).

In the face of perceived impact, it is worth reviewing the available data concerning buzzard predation of gamebirds. A number of dietary studies have been conducted (Appendix 1), particularly in recent years (Rooney & Montgomery 2013; Francksen et al. 2016; Francksen, Whittingham & Baines 2016; Prytherch 2016). Mammals, specifically rabbits and voles, are most often the main prey although birds do occasionally dominate. Invertebrate prey and livestock carrion may increase in importance over the autumn and winter (Newton, Davis & Davis 1982; Manosa & Cordero 1992). Gamebirds constitute a relatively low percentage of the diet (0 - 9.6% by number), with the three exceptions of Graham *et al.* (1995), Francksen, Whittingham & Baines (2016) and Tornberg & Reif (2007) (15.1%, 21.6% and 34.8% respectively). It should be considered, however, that these high records are from data based on analysis of prey remains, a technique that is known to significantly over-represent large avian prey species, particularly gamebirds (Redpath *et al.* 2001; Tornberg & Reif 2007; Francksen, Whittingham & Baines 2016). For example, in Francksen, Whittingham and Baines's (2016) recent study, camera footage revealed pheasants to be only 1% of the total prey items, compared to the 15.1% estimated from prey remains.

Despite the apparently low contribution of gamebirds to buzzard diet, it has been hypothesised that shooting estates, through habitat maintenance and legal predator control, create high densities of prey species (Tharme *et al.*

2001; Oldfield *et al.* 2003; Beja *et al.* 2008) enabling generalist predators, like buzzards, to reach densities at which they have a detrimental impact on game species. This has already been observed for hen harrier on moorland managed for red grouse (Redpath 1991; Thirgood *et al.* 2000).

Quantifying the impact of predators on released game presents an interesting challenge to ecologists. Unlike wild birds (for which an assessment of the impact of predation might incorporate breeding success), perceptions of impact focus on a seven-month window (June - February) between the release of poults and the end of the shooting season. Indeed, buzzards are not thought to regularly predate adult gamebirds, and thus the majority of losses are likely to occur within the first two months of release (Parrott 2015).

Studies have attempted to quantify the impact of buzzard predation in terms of gamebird losses. Questionnaires revealed that, on average, gamekeepers estimate 3.2% of pheasants are lost to buzzards (Harradine, Reynolds & Laws 1997). Field studies have also attempted to quantify raptor impact through necropsies of predated gamebirds. However, many have been unable to differentiate between raptor species from carcass examination (Allen 2001; Parish & Sotherton 2007; Watson *et al*. 2007). In perhaps the most extensive study, Turner and Sage (2003) estimated that fewer than 1% of 486 released pheasants were killed by raptors. Of those studies that have succeeded in identifying the predator, attribution of the degree of loss to buzzards vary. For instance, buzzard predation accounted for 23.5% of the total mortality of grey partridges *Perdix perdix* in Switzerland (Buner & Schaub 2008) and 4.3% of the total mortality of released pheasants in England (Kenward *et al.* 2001).

Conflicts over buzzard management

Despite the literature suggesting that buzzard predation is minimal in relation to other sources of mortality (e.g. road collisions) (Lees, Newton & Balmford 2013), perceptions of buzzard impact remain. This is perhaps most clearly reflected in the records of bird crime compiled by the Royal Society for the Protection of Birds. These show that buzzards continue to be the most widely persecuted bird of prey in the U.K. (RSPB 2016). For instance, in Scotland between 1994 and 2014 buzzards comprised the majority (59.2%, n = 461) of all the confirmed bird of prey victims of poisoning, shooting, trapping and nest destruction (RSPB 2015a). Levels of illegal killing also appear to be high in the south of England, where one study attributed 24% of the observed mortality of fledgling buzzards to illegal persecution (Kenward *et al.* 2000). As a result, it has been suggested that illegal killing might be restricting population densities in some (Elliott & Avery 1991; Gibbons *et al.* 1995; Swann & Etheridge 1995), but not all (Arraut, Macdonald & Kenward 2015), localities.

Perceptions of 'problem buzzards'

Attempts to reduce illegal persecution and mitigate conflict are being sought by different means. Conservation groups are requesting tougher enforcement and penalties for those that break the law. In contrast, landowners and gamekeepers have applied repeatedly for licences that would permit the lethal control of a limited number of individual birds. While initially the licencing requests were rejected by the statutory licensing body, Natural England (NGO 2011), a subsequent Judicial Review brought by one of the applicants determined that "*public opinion was unlawfully taken into account*" in these rejections (McMorn v. Natural England 2015, para. 167). In 2016, the first licences for the lethal control of buzzards were granted to four shooting estates, resulting in the deaths of 11 buzzards (Natural England 2016a).

Although the granting of these licences present little threat to conservation objectives, they are nonetheless ecologically interesting as the license conditions direct the holder to selectively target specific birds. For example:

> *"Note that overflying birds must not be shot, and that birds feeding on baits must not be shot. Specific problem birds may be targeted where they are flying into stocked release pens, or where they are predating on pheasant poults in or immediately around stocked release pens."* (Natural England 2016b: p2)

This wording is a consequence of the belief on the part of gamekeepers that specific 'problem birds' are the cause of disproportionately high losses of pheasants by effectively specialising on predating gamebirds (Parrott 2015). The perception that only a few individual animals are responsible for the majority of damage is not new. The ‘problem individual paradigm’ was first articulated by Linnell *et al.* (1999) in a paper on large carnivore predation of livestock. However, despite a growing body of evidence documenting consistent differences in the behaviour of individuals of the same species (Bolnick *et al.* 2003) and much anecdotal evidence, individual level variation ecology is still rarely considered by conservation scientists in relation to wildlife management (Linnell 2011).

Though the evidence available thus far, as summarised above, suggests that gamebirds are only a small proportion of buzzard diet at a population level, little scientific attention has been paid to the notion that specific buzzards contribute disproportionally to economic losses. This is despite such problem animals being common in anecdotal reports (Allen *et al.* 2000; Viñuela & Arroyo 2002) and many studies of raptor diet reporting high intraspecific variation in diet composition and foraging strategies (although see Rooney & Montgomery 2013). In the most comprehensive study to date, Kenward *et al.* (2001) monitored 136 radio-tagged buzzards following fledging and showed that a small subset (8%) had a significantly higher association with pheasant pens than other birds. However, this study was unable to link these birds to the minority of pens that suffered persistent losses.

In order to appropriately mitigate buzzard impact and the associated social conflict, research on the existence of problem buzzards is urgently needed (Parrott 2015). Although such evidence would ideally come from randomised trials (Treves, Krofel & McManus 2016), experimental removal of buzzards is unlikely to be possible, due to the controversy surrounding the policy. Indeed, in 2012 government funding for just such research was withdrawn following public outcry (Gray 2012; Monbiot 2012). In the absence of trials, I suggest that elements of the efficacy of selective removal can be explored indirectly by studying how buzzards respond to variation in the abundance of gamebird prey at both a population and individual level.

This will require investigation of buzzard ecology, including diet, both inside and outside of the breeding season. Studies of raptor diet have traditionally been conducted through the analysis of prey remains and regurgitated pellets (Graham, Redpath & Thirgood 1995; Rooney & Montgomery 2013; Prytherch 2016). However, over the last few decades the application of remote cameras to observe prey items during provisioning have come to the fore (Rogers, DeStefano & Ingraldi 2005; Smithers, Boal & Andersen 2005). Although potentially financially costlier (Tornberg & Reif 2007) this method provides the most accurate description of raptor diet (Lewis, Fuller & Titus 2004; García-Salgado *et al.* 2015). Despite this development, assessing raptor diet outside of the nesting period has proved tricky. Studies have had to rely primarily on collecting pellets at roosting sites (Clarke, Combridge & Combridge 1997; Francksen *et al.* 2016). As well as making it difficult to collect data on individuals, this method is known to contain large biases towards certain prey groups (Simmons, Avery & Avery 1991; Francksen, Whittingham & Baines 2016).

It would seem, therefore, that additional methods are needed in order to quantify intraspecific dietary variation outside of the nesting period. Stable isotope analysis has show real promise in identifying animals involved in human-wildlife impacts (Cerling *et al.* 2006; Hopkins *et al.* 2012; Bentzen, Shideler & O'Hara 2014). This method determines the relative contribution of assimilated food to diet (Peterson & Fry 1987) as the isotopic ratios in the tissues of consumers reflect those of their food sources (DeNiro & Epstein 1978). For example, Bentzen, Shideler & O'Hara (2014) analysed stable isotopes in the hair of grizzly bears *U. a. horribilis* to show which individuals had a history of anthropogenic food use. Another advantage of this approach is that tissues with different metabolic turnover rates reflect dietary information from different time periods (Hobson *et al.* 1996). This allows individual dietary consistency to be assessed where multiple tissues are sampled from the same animal (Inger & Bearhop 2008). Although stable isotope methods have been evaluated against other indirect methods (Weiser & Powell 2011; Resano-Mayor *et al.* 2014), the difficulty of obtaining observational data of wild animals means that an evaluation of stable isotope analysis using direct methods in natural conditions is currently lacking.

Thesis outline and aims

In this thesis, I apply ecological and social research methodologies to explore conflicts over predator management. I aim to produce a body of work that contributes to knowledge on the motivations of key stakeholders, the reality of the perceived impacts and the efficacy of any methods intended to remedy them. Following this general introduction, the thesis is arranged into five chapters, concluding with a general discussion. Each of the five chapters addresses one of the five aims outlined below.

The specific aims of this thesis are to:

1. Assess the evidence of the existence of ‘problem’ animals in human-wildlife impacts and evaluate if ‘selective removal’ is a generally viable policy.
2. Evaluate the use of dietary stable isotope analysis as a potential method for studying the diet of wild predators.
3. Assess the ecological evidence that, within buzzard populations, there is a limited number of ‘problem’ buzzards that disproportionately feed on released gamebirds.
4. Investigate the numerical and functional responses of buzzards to gamebird abundance on shooting estates.
5. Explore the motivations behind predator management from the perspective of those that conduct it, the gamekeepers.

In Chapter 2, I conduct a literature review to explore the efficacy of ‘selective’ wildlife management. Drawing on studies on a diversity of taxa I identify and evaluate five key questions that determine whether selective management is a generally viable management strategy: (i) can most of the problem be ascribed to few individuals? (ii) Is it possible to accurately identify and target problem individuals? (iii) Does targeting problem individuals mitigate impacts? (iv) Can indirect effects be avoided or minimised? And (v), can targeting individuals help achieve social objectives? Using these five questions I discuss the potential costs and benefits of selective management in the round.

In Chapter 3, I evaluate dietary stable isotope analysis as a potential method for investigating the diet of wild predators, using buzzards as my model species, at both population and individual scales. During the breeding season, buzzards offer a rare window into predator feeding ecology, as food items are brought back to the nest, presenting a focal point for dietary observations (Gaglio *et al.* 2017). I use detailed provisioning observations, obtained using remote cameras, to compare dietary stable isotope analysis against conventional methods of assessing buzzard diet based on analysis of prey remains and pellets.

In Chapter 4, I apply stable isotope analysis more broadly, adding an analysis to provide dietary estimates for adult buzzards from their moulted feathers. This allows the exploration of variation in diets over time periods when released pheasant poults are available, something that has proven difficult in previous studies (Kenward *et al.* 2001). Using these data, I explore whether buzzard consumption of released pheasants is higher at pens where gamekeepers perceive predation problems. I add to this analysis by quantifying the diet of a small sample of putative ‘problem buzzards’, consistent with the terms of the Natural England license in that I trapped them in or around pheasant pens. By analysing tissues (feather, red blood cells and blood plasma) assimilated over different time periods, I am able to provide an indication of the extent and consistency of poult consumption.

In Chapter 5, I explore how pheasant populations on lowland shooting estates influence buzzard breeding success and density. I analyse how the numerical (breeding density and nestling number) and functional (dietary composition) responses of buzzards correlate with indices of relative abundance for rabbits, voles and gamebirds. I am able to take this analysis further than previous studies (Graham, Redpath & Thirgood 1995), by linking prey abundance to provisioning rate (obtained from the nest cameras) and then by linking provisioning rate to nestling number.

In Chapter 6, I apply methods developed in the social sciences to explore the human side of predator management. Successful conflict mitigation requires an understanding of both social and ecological contexts (Madden & McQuinn 2014). Despite the central role of gamekeepers in conflicts concerning predator control, little attention has been paid to their perspectives and motivations. Drawing from the theory of planned behaviour (Ajzen 1985), I use qualitative enquiry to explore how the beliefs, norms and information sources of gamekeepers create motivations for predator management. The influence of these motivations is discussed in detail and a framework is developed.

My thesis concludes with a general discussion, during which I synthesise the key findings and the contributions of this work to conservation conflicts. Although much of the thesis focuses on the management of predators in relation to released gamebirds, I detail in this section how this research can contribute more broadly to a general understanding of how predators are perceived and managed.

Chapter 2

ECOLOGY OF PROBLEM INDIVIDUALS AND EFFICACY OF SELECTIVE WILDLIFE MANAGEMENT

Chapter 2: Ecology of problem individuals and the efficacy of selective wildlife management

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Abstract

As a result of ecological and social drivers, management of problems caused by wildlife is becoming more selective, often targeting specific animals. Narrowing the sights of management relies upon the ecology of certain ‘problem individuals’ and their disproportionate contribution to impacts upon human interests. I assess the ecological evidence for problem individuals and confirm that some individuals or classes can be both disproportionately responsible and more likely to reoffend. The benefits of management can sometimes be short-lived and selective management can affect tolerance of wildlife for better or worse, but when effectively targeted, selective management can bring benefits by mitigating impact and conflict, often in a more socially acceptable way.

Current challenges in wildlife management

Predators, large herbivores and ‘pest’ species are often managed to mitigate their negative impacts upon human livelihoods and well-being, and upon conservation objectives (Redpath *et al.* 2013). This management can be controversial, particularly when the targeted species are charismatic or are themselves of conservation concern. Strategies that attempt to mitigate wildlife impacts can therefore be challenging to develop and implement because effective management requires an understanding of both the ecology of the problem (Greggor *et al.* 2016), the animals causing it and its wider social context (Redpath *et al.* 2013). Allowing actual or perceived impacts to go unmanaged could result not just in on-going or escalating threats to human interests (Fernando *et al.* 2012) but might also lead to increased animosity towards conservation objectives (Olson *et al.* 2015) and perhaps to the illegal killing of wildlife (Redpath & Thirgood 2009). Currently the predominant approach to reducing wildlife impact tends to be pro-active or generalised culling (Ripple *et al.* 2014; Bergstrom *et al.* 2014). There can be advantages to this approach, particularly where routine harvesting or hunting effort can be harnessed (Treves & Naughton-Treves 2005; Cromsigt *et al.* 2013; Redpath *et al.* 2017). Benefits can arise in terms of economic and social gains (Redpath *et al.* 2017) and reduction of impacts (Bradley *et al.* 2015), potentially by reducing population size or effecting behavioural change. Such generalised approaches to controlling impacts can, however, incur high financial costs (Bergstrom *et al.* 2014), result in reduced ecosystem function (Ripple *et al.* 2014), have unforeseen ecological outcomes (Bodey, Bearhop & McDonald 2011) and give rise to ethical and welfare concerns (Ramp & Bekoff 2015); all of which can challenge societal and political support (Treves *et al.* 2015).

In integrating these ecological and social considerations, ecologists and managers are, in some instances, moving away from generalised removal of wild species and towards coexistence (Carter & Linnell 2016). This can include narrowing sights from control at a population level towards targeting individual animals (Treves & Naughton-Treves 2005; Massei *et al.* 2010; Doherty & Ritchie 2016). Indeed, there have been recent calls for the cessation of all wildlife control methods that are not highly selective (Ordiz, Bischof & Swenson 2013; Bergstrom *et al.* 2014).

To be effective, this concentration of effort upon specific animals relies upon the ecology of these individuals and their disproportionate contribution to deleterious impacts. In framing this issue for the specific case of large carnivore predation of livestock, Linnell *et al.* (1999) identified and evaluated the ecological evidence for 'problem individuals'. This notion of disproportionate contribution is clearly evident beyond livestock predation and has been applied to 'man-eating' lions (Yeakel *et al.* 2009), food-conditioned bears (Bentzen, Shideler & O'Hara 2014), problem elephants (Fernando *et al.* 2012; Mutinda *et al.* 2014) and 'rogue' sharks (Neff & Hueter 2013), as well as to smaller taxa such as seabirds (Sanz-Aguilar *et al.* 2009), birds of prey (Parrott 2015) and feral cats (Moseby, Peacock & Read 2015). Targeting these problematic animals might be intuitively appealing, as it is often the apparent actions of particular individuals, and not those that behave 'normally', that engender hostility among human stakeholders (Goldman, de Pinho & Perry 2013; Neff & Hueter 2013). It might also be assumed that concentrating management efforts upon fewer, specific animals could incur reduced ecological, social, ethical and logistical costs.

Here, I broaden Linnell et al's (1999) underlying assumption of the problem individual paradigm, that "*a small proportion of the individuals…are responsible for most livestock depredation*." I define the problem individual as "*any individual animal that is responsible for a disproportionately large negative impact on human interests",* acknowledging that such interests extend beyond the ecological into matters of health, wellbeing and economics. I use this definition to examine selective wildlife management, drawing on a diversity of research in ecology, animal behaviour and wildlife biology. While I concentrate on lethal control as the most typical form of selective management (Treves & Naughton-Treves 2005), I also consider non-lethal practices such as translocations or those that seek to change individual behaviour *in situ* (see Box 2.1).

I identify and evaluate five key questions (Figure 2.1) that are fundamental to determining whether targeting problem individuals is a generally viable management strategy: (I) Can most of the problem be ascribed to few individuals? (II) Is it possible to accurately identify and target problem individuals? (III) Does targeting problem individuals mitigate impacts? (IV) Can indirect effects be avoided or minimised? (V) Can targeting individuals help achieve social objectives?

Box 2.1: Non-lethal alternatives in problem individual management

Translocation: Despite occasional successes (Weise *et al.* 2015), translocating problem individuals often fails due to high mortality, animals returning to capture sites and a persistence of problem behaviour in the remaining individuals (Massei *et al.* 2010; Fontúrbel & Simonetti 2011). Indeed, in extreme cases, it resulted in an increase in threats to human safety (Athreya *et al.* 2011; Fernando *et al.* 2012). The translocation of problem leopards in India, for example, is thought to have increased attacks on people (Athreya *et al.* 2011).

Diversionary feeding is "*the use of food to divert the activity or behaviour of a target species from an action that causes a negative impact, without the intention of increasing the density of the target population*" (Kubasiewicz *et al.* 2016: p3). Targeting sub-sets of wild animal populations with diversionary feeding has shown promise in reducing impacts (Kubasiewicz *et al.* 2016). In Scotland for example, Amar *et al.* (2004) used habitat data to predict which hen harriers *Circus cyaneus* pairs were likely to have the highest predation rates on red grouse *Lagopus lagopus scotica* chicks and they were able to successfully reduce grouse chick predation by providing diversionary feed to specific harrier nests. The benefits of diversionary feeding have, however, been reduced by unintentional increases in population sizes and anthropogenic dependency (Kubasiewicz *et al.* 2016).

Aversive conditioning: Attempts have been made to change the behaviour of individual animals through associations with a negative stimuli introduced during a human-wildlife impact (Linnell, Odden & Mertens 2012). Despite some encouraging indications (e.g. shock collars on individual wolves, resulted in whole packs developing an aversion to specific baited 'shock zones'; Rossier *et al.* 2012) field trials attempting to use aversive conditioning to prevent carnivore predation of livestock have so far all failed (Linnell, Odden & Mertens 2012). However, 'hazing' (a form of aversive conditioning), has proved successful with many nuisance bears around human settlements, particularly on those bears that are not already ‘food conditioned’ (Hopkins *et al.* 2012). This proactive approach could be targeted either at animals displaying the characterises of future trouble makers (such as ‘bold’ personality types in ungulates; Found & St. Clair 2016) or towards animals responsible for teaching problem behaviour, such as female bears (Morehouse *et al.* 2016).

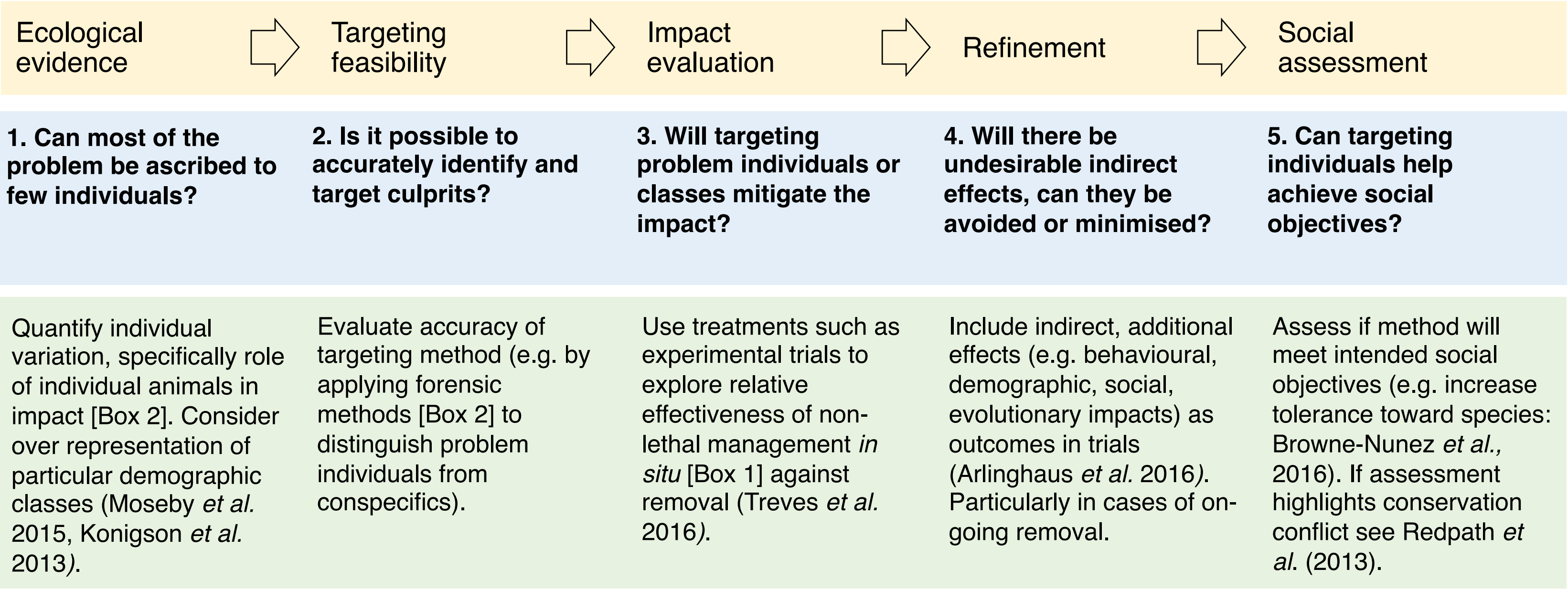
Physically handicapping: This non-lethal method is on the furthest extreme of impact mitigation. In one of the few cases where such an approach was attempted it was remarkably successful: in Kenya the de-tusking of specific ‘destructive’ bull elephants resulted in their fence breaking behaviour being 1.7-14.5 times lower and the mean rate of attack falling six-fold (Mutinda *et al.* 2014).

(I) Can most of the problem be ascribed to few individuals?

Evidence of individuality in wild animals is clearly central to the efficacy of managing problem individuals (Figure 2.1) but is also fundamental to ecology and evolution. To understand the phenomenon in this context, it is necessary to look at the ultimate and proximate mechanisms that give rise to individual variation (Araújo, Bolnick & Layman 2011). Ultimately, theory suggests that intraspecific variation reduces intraspecific competition (Bolnick *et al.* 2011). As a result, it might be expected that individual variability is particularly pronounced in species experiencing low *inter*specific competition, such as ecological generalists (Bolnick *et al.* 2011) or those occupying upper trophic levels (Araújo, Bolnick & Layman 2011). More proximately, intraspecific behavioural variation can stem from a complex combination of genetic variability and phenotypic plasticity. Considering, for example, the ontogeny of a predator’s foraging specialisation (a foraging behaviour consistently expressed by an individual that is uncommon relative to their population), individual behaviour might be influenced by variables common to local conspecifics such as group size, environmental conditions, prey species identity and abundance, and by individual variables, such as its personality type (a particular combination of behavioural tendencies that are consistently expressed; Wolf & Weissing 2012), size, sex, age, and reproductive status (Dickman & Newsome 2015; Pettorelli *et al.* 2015). These individual variables will also determine the extent to which a behaviour is consistently or intermittently expressed (Modlmeier *et al.* 2014). Where a behaviour is consistently expressed by an individual there is evidence that it can be passed on to offspring (Morehouse *et al.* 2016) or to associates through social learning (Schakner *et al.* 2016). As a consequence of individual variation, animals with access to the same resources can exploit them very differently (Araújo, Bolnick & Layman 2011). This can be observed in diverse taxa through individual variation in risk-taking (Ciuti *et al.* 2012), diet (Elbroch & Wittmer 2013), or foraging (Patrick *et al.* 2014).

Growing awareness of intraspecific behavioural variation has prompted a raft of research exploring how the phenomenon could influence ecological and evolutionary processes, natural and sexual selection (Dall *et al.* 2012), ecological invasions (Sih *et al.* 2012) and predator-prey dynamics (Pettorelli *et al.* 2015). These studies identify the major roles of within-population variation in community ecology (Bolnick *et al.* 2011). As yet, however, the influence of individual behaviour on how wild animals interact with humans has received little attention, despite clear pathways by which it might be important (Greggor *et al.* 2016). Intraspecific variation could mean that only a small proportion of animals within a population are responsible for most of the negative impacts. For instance, when local human livelihoods (Graham *et al.* 2011; Königson *et al.* 2013) or conservation objectives (Festa-Bianchet *et al.* 2006; Sanz-Aguilar *et al.* 2009; Dickman & Newsome 2015) are threatened by individual predators with foraging specialisations. Individual variation can also lead to non-selective management strategies inadvertently selecting specific traits or demographic classes (Greggor *et al.* 2016; Leclerc, Zedrosser & Pelletier 2017). This has already been observed for species under selection from recreational hunting where animals with 'bolder' personality types appear to be overrepresented (Ciuti *et al.* 2012; Madden & Whiteside 2014).

There is now considerable support for the notion that, in many situations where wildlife causes problems for people or conservation objectives, problem individuals are involved. This evidence can be direct, for example studies



Ecological evidence	Targeting feasibility	Impact evaluation	Refinement	Social assessment
1. Can most of the problem be ascribed to few individuals?	**2. Is it possible to accurately identify and target culprits?**	**3. Will targeting problem individuals or classes mitigate the impact?**	**4. Will there be undesirable indirect effects, can they be avoided or minimised?**	**5. Can targeting individuals help achieve social objectives?**
Quantify individual variation, specifically role of individual animals in impact [Box 2]. Consider over representation of particular demographic classes (Moseby *et al.* 2015, Konigson *et al.* 2013).	Evaluate accuracy of targeting method (e.g. by applying forensic methods [Box 2] to distinguish problem individuals from conspecifics).	Use treatments such as experimental trials to explore relative effectiveness of non-lethal management *in situ* [Box 1] against removal (Treves *et al.* 2016).	Include indirect, additional effects (e.g. behavioural, demographic, social, evolutionary impacts) as outcomes in trials (Arlinghaus *et al.* 2016). Particularly in cases of on-going removal.	Assess if method will meet intended social objectives (e.g. increase tolerance toward species: Browne-Nunez *et al.*, 2016). If assessment highlights conservation conflict see Redpath *et al.* (2013).

Figure 2.1: A conceptual framework to evaluate selective management.

The framework illustrates the recommended stages of selective management (yellow), the questions that determine its viability (blue) and methods to answer them (green).

showing that specific individuals (Chiyo *et al.* 2011; Elbroch & Wittmer 2013) and demographic classes (Moseby, Peacock & Read 2015) are disproportionately involved in incidents or that problem behaviours are taught to offspring (Morehouse *et al.* 2016) or associates (Schakner *et al.* 2016). Indirect evidence points towards the involvement of problem individuals, where all animals contribute to an impact but to markedly varying degrees (Cavalcanti & Gese 2010), or where sudden increases in impact are observed but are apparently unrelated to animal abundance (Festa-Bianchet *et al.* 2006).

Box 2.2: Methods for exploring and evaluating problem individual management

To develop selective management, research that explores individuality and validates management strategies is needed and the toolbox for these tasks is expanding:

Exploring individuality:

Marking animals with tags can facilitate individual identification, though this usually requires recaptures, resightings or carcass recovery (Bentzen, Shideler & O'Hara 2014; Madden & Whiteside 2014).

Camera trapping and image analysis can help identify the individuals involved in impacts when animals can be individually distinguished. Camera traps have been successfully used to identify problem individuals in terrestrial (Karanth, Kumar & Vasudev 2014) and aquatic environments (Königson *et al.* 2013).

GPS and other tracking technologies provide spatial data on individual movements that can be linked to human-wildlife impacts (Cavalcanti & Gese 2010). For example, by investigating the spatial clumping of puma *Puma concolor* locations, researchers found that only a minority of individuals were involved in livestock depredation (Elbroch & Wittmer 2013).

Molecular methods allow the forensic identification of individuals. For example, DNA fragments sampled from faeces (Archie & Chiyo 2012) or attack wounds (Caniglia *et al.* 2013) have been used to identify individual animals responsible for crop and livestock losses.

Stable isotope analysis allows an inference of the relative contribution of different food items to an individual's diet (Inger & Bearhop 2008). This method has been used to help identify food conditioned bears (Hopkins *et al.* 2012) and crop raiding elephants (Cerling *et al.* 2006).

Evaluating management:

Removal experiments with random assignment to control and treatment groups are considered the 'gold standard' to evaluate wildlife management (Treves, Krofel & McManus 2016). Theoretical experiments that quantify the rate at which specific behaviours reoccur will help inform the required frequency of management actions (Modlmeier *et al.* 2014).

Analysing impact records has allowed studies to evaluate problem individual removal by observing the change in impact levels following treatments. Studies have focused on specific case studies (Mutinda *et al.* 2014) or used data collected over broad areas for a number of years (Bradley *et al.* 2015; Artelle *et al.* 2016).

Analysing involvement records requires data on individual animals. For example, by knowing which individual grizzly bears were involved in impacts, Morehouse *et al.* (2016) were able to link 'conflict behaviours' with social learning and thereby critique guidelines for problem bear management.

Social network theory has the potential to advance our understanding of the social aspects of problem behaviour (Modlmeier *et al.* 2014). For example, Schakner *et al.* (2016) used a network-based diffusion analysis to first demonstrate the social transmission of unwanted behaviours in California sealions *Zalophus californianus* and model the impact of management interventions.

(II) Is it possible to accurately identify and target problem individuals?

Even if we know that subsets of animals are responsible for most of the problem, correctly identifying the problem individual(s) presents a key challenge in selective management (Treves & Naughton-Treves 2005) (Figure 2.1). Three broad approaches emerge whereby animals can be targeted, based on individual identity, location, or demographic class (Table 2.1).

First, identifying those responsible can prove straightforward when individuals are marked (Box 2.2) or easily distinguishable. The Kenyan Wildlife Service's photographic database of African elephants *Loxodonta africana* involved in conflict incidents allows them to recognise repeat offenders (Mutinda *et al.* 2014). This approach is also applicable where management action only requires the individual to be caught in the act of a single impact event. For example, in parts of South Africa any fur seal *Arctocephalus pusillus* observed eating endangered seabirds can be shot (David *et al.* 2003).

Second, individuals can be targeted based on their location (Box 2.3). This approach should have highest accuracy if problems are spatially concentrated (Voyles, Treves & MacFarland 2015), management is conducted within a short time fame of the impact (Bradley *et al.* 2015) or during particular times when the impact is heaviest (Butler *et al.* 2011). Again in Kenya, lions *Panthera leo* that have killed cattle have been targeted by traps set near recent livestock kills (Woodroffe & Frank 2005). Yet zoning specific areas for removal should be considered with care. On-going removal coupled with rapid immigration of new problem animals or non-target animals, might create a sink, or ecological trap, influencing the population dynamics of a much larger area (Woodroffe & Frank 2005; Selier *et al.* 2014; Treves *et al.* 2015). To minimise this threat, it has been suggested that problem individuals can be more effectively targeted if specific attractants (Dickman & Newsome 2015) or trap designs (Königson *et al.* 2013) are used.

Third, several recent studies on managing wildlife have suggested that animals be removed based on their demographic class (Cromsigt *et al.* 2013; Königson *et al.* 2013; Hiller *et al.* 2015; Kauhala *et al.* 2015; Moseby, Peacock & Read 2015). In Australia, removing large male cats *Felis catus* is considered a conservation priority due to their ability to take large native prey (Moseby, Peacock & Read 2015), while in the Baltic Sea, adult male grey seals *Halichoerus grypus* are significantly more likely to be responsible for damage to fishing gear (Kauhala *et al.* 2015). This classification has been described as "*predator profiling*" (Moseby, Peacock & Read 2015: p332) and I suggest the term 'problem animal profiling' (using data on previous human-wildlife impacts to identify those demographic classes most likely to have a negative impact) to allow for its wider use in wildlife management.

With the exception of incidents where individuals can be recognised 'at the scene of the crime', we can otherwise assume that few strategies are perfectly accurate in their targeting (Table 2.1). Measures of targeting accuracy, sensitivity or specificity (e.g. proportion of true problem individuals identified and removed, proportion of true non-target individuals identified and removed) are therefore needed to allow practitioners to evaluate alternative methods. While these evaluations can be supported by ecological data, forensic methods including detailed necropsies, stable isotope and DNA analysis might also prove useful (Box 2.2).

(III) Does targeting problem individuals mitigate impacts?

If problem individuals have been identified and a means of targeting them found, it is important to consider whether their removal will decrease impact and, if so, the timescale of any benefit (Figure 2.1). Wildlife managers can see the removal of individual animals as the only practical, humane and cost-effective option available (Hall & Kress 2008; Sanz-Aguilar *et al.* 2009; Massei *et al.* 2010; Schakner *et al.* 2016), even for species of conservation concern (see Boxes 2.3 & 2.4). Indeed, if an uncommon behaviour, such as a foraging specialisation, is the cause of a problem, generalised measures to reduce impacts will likely fail if certain individuals are missed (Moseby, Peacock & Read 2015; Pettorelli *et al.* 2015). Where removal of the problem individual has been achieved, studies have reported minimal loss to the overall population (Graham, Harris & Middlemas 2011), little stress to the remaining individuals (Burke *et al.* 2008) and both perceived (Königson *et al.* 2013) and actual (David *et al.* 2003; Hall & Kress 2008; Sanz-Aguilar *et al.* 2009) decreases in wildlife impact. On Stratton Island, USA, culling a single black-crowned night-heron *Nycticorax nycticorax* with a specialisation on common tern *Sterna hirundo* chicks resulted in the number of tern chicks per pair increasing from 0.42 to 1.9 (Hall & Kress 2008). In Namibia, after the translocation of ‘problem leopards’ *Panthera pardus*, livestock losses stopped for at least 16 months, despite new leopards moving into the vacated territory after only 6 weeks (Weise *et al.* 2015). There are also circumstances where the timely removal of problem animals might minimise future interventions by preventing the spread of undesirable behaviours (Schakner *et al.* 2016).

Box 2.3: Case Study - Managing foraging specialisations in seals

In northern Scotland grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina* are perceived to impact fisheries through a reduction in Atlantic salmon *Salmo salar* available to recreational anglers (Redpath *et al.* 2013). Traditional management involved non-selective population reduction through culling seals at their haul out sites (Thompson *et al.* 2007) but was replaced with a more selective form of lethal removal following conservation and welfare concerns (Young *et al.* 2012). This new management regime attempted to remove individual seals by issuing licenses to trained marksmen to target individuals frequenting rivers and netting systems (Butler *et al.* 2011). Graham *et al.* (2011) set out retrospectively to test the efficiency of this strategy using photography to identify individual seals that were using rivers to forage. Their study provided evidence that only a small proportion (<1%) of the local seal populations were consistently sighted in rivers. They complimented this analysis with forensic methods that suggested that these *"river-specialist"* seals had a higher proportion of salmonids in their diet than those seals found at haul out sites (Graham *et al.* 2011). Although this research falls short of quantifying the losses seals cause to recreational fisheries, it strongly suggests that river specialist seals will have the greatest per capita impact. Indeed, despite requiring on-going lethal control, the refinement of seal culling to these individuals represents a workable compromise for parties interested in both the protection of salmon stocks and the conservation of seals (Young *et al.* 2012).

Figure 2.2: *A grey seal eating a mature salmon on the River Ness, Scotland. (Photo: © Rob Harris, University of St. Andrews)*

Table 2.1: *Examples of methods for targeting animals and their assumed accuracy for selecting specific individuals. Selectivity is based on: [1] identity, [2] location, [3] demographic class (problem animal profiling) and [4] assumed non-selective.*

Accuracy	Method	Example	Reference
Highest	Targeting animals that can be individually recognised[1]	Using records of individual involvement to inform management.	Mutinda *et al.* (2014)
	Targeting individuals during human-wildlife impact[1]	Enacting management actions during human-wildlife impact.	Schakner *et al.* (2016)
	Targeting individuals based on evidence from impact event[1,2]	Using tracking hounds to locate specific animals (see also Box 2.2)	Peebles *et al.* (2013)
	Targeting individuals post human-wildlife impact[2]	Targeting those individuals found at or near recent impact events.	Woodroffe & Frank (2005)
	Targeting individuals using specific lures, attractants or traps[2]	Using specific lures or attractants aimed at those individuals most likely cause impact.	Königson *et al.* (2013)
	Targeting individuals within specific territories[2]	Removing animals when territory, not individual identity, is known.	Sanz-Aguilar *et al.* (2009)
	Targeting individuals based on pre-established geographic areas[2]	Identifying specific areas where individuals are most likely to cause impact.	Hoare (2001)
	Targeting individuals based on problem animal profiling[3]	Identifying specific demographic classes within a population most likely to cause impact.	Moseby, Peacock & Read (2015)
	Population control or eradication[4]	Generalised control or eradication of a species.	Treves & Naughton-Treves (2005)
Lowest	Excluding access[4]	Attempting to exclude all individuals of a species from an area.	Mutinda *et al.* (2014)

Despite these successes, many studies report that the benefits of removing problem individuals are short-lived (Woodroffe & Frank 2005; Selier *et al.* 2014; Bradley *et al.* 2015). The rapid recurrence of (Selier *et al.* 2014), or increase in (Artelle *et al.* 2016), wildlife impact following the removal of individuals could indicate the presence of a problem component within the population (Hoare 2001), the social transmission of behaviours (Schakner *et al.* 2016), compensatory immigration or population growth (Doherty & Ritchie 2016), a specific site effect (Zarco-González *et al.* 2012), inadequate prevention measures (Treves & Naughton-Treves 2005), or behavioural changes in the residual population (Smith, Wang & Wilmers 2015). Whatever the cause, if benefits are short-lived and frequent interventions are necessary, increased ecological, economic and social costs can be expected.

The utility of problem individual removal has been analysed in two cases using long-term datasets. Bradley *et al.* (2015) compared the consequences for livestock losses of selectively and entirely removing packs of grey wolves *Canis lupus*. Although this study failed to identify those animals specifically responsible for predation, their analysis suggests that removing the breeding female, or a > 1 year old male (the demographic class most likely to lead livestock hunts) did not significantly increase the time to reoccurrence of depredation, when compared to the effect of removing any other member of the pack. Furthermore, this study found that removing whole wolf packs reduced subsequent livestock depredation events by 79% over the next five years, when compared to 29% for partial pack removal (Bradley *et al.* 2015). At least in this situation, the selective removal of individual wolves was ineffective. Second, Artelle *et al.* (2016) analysed attacks on humans and the consequent lethal control of grizzly bears *Ursus arctos horribilis* in Canada. They found evidence that the primary driver of these attacks was not the number of conflict-prone (risk-tolerant, bold) individual bears but shortages in their food supply (Artelle *et al.* 2016). This finding suggests that proactively addressing ecological stressors might be a better long-term strategy than responsive bear removal.

(IV) Can the indirect effects of selective management be avoided or minimised?

Although there are promising non-lethal methods to mitigate wildlife impact (Box 2.1; see also Johnson & Wallach, 2016; Treves, Krofel & McManus, 2016), problem individual management often involves the lethal removal of animals (Box 2.3). This removal is non-random, targeted at behaviours that create impacts, and therefore likely to remove correlated phenotypes and demographic classes. While my focus is on removal of individuals for wildlife management purposes, my findings draw from, and are relevant to, animal populations under non-random selection from harvesting (Leclerc, Zedrosser & Pelletier 2017). Following Greggor *et al.* (2016), I consider the possible additional and unintended effects of selectivity (Figure 2.1).

In selective management there is a general trend for males to be overrepresented in removal records. This bias was first identified in relation to large carnivores (Linnell *et al.* 1999) but is apparent in other taxa (Fernando *et al.* 2012; Selier *et al.* 2014; Fukuda, Manolis & Appel 2014) and can be extremely pronounced. Only 2 of 38 seals caught raiding salmon traps in the Baltic Sea were female (Königson *et al.* 2013). Only male Australian magpies *Cracticus tibicen* were observed attacking people (Warne, Jones & Astheimer 2010). In Kenya, male elephants were responsible for 86% of fence breaking incidents (Mutinda *et al.* 2014). In an attempt to refine lethal management, several recent studies have explicitly directed wildlife managers towards removing male animals (Königson *et al.* 2013; Hiller *et al.* 2015; Kauhala *et al.* 2015). The deliberate or unintentional targeting of males can, however, have broader detrimental effects; male removal and the skewing of natural sex ratios can alter community structure and sexual selection processes, produce an increase in infanticide and female harassment and potentially remove the benefits of biparental care (Milner, Nilsen & Andreassen 2007; Rankin & Kokko 2007).

To reduce impacts in social species, individuals can be targeted to elicit behavioural change in others. This could be by removing individuals responsible for leading group behaviour. For example, the culling of specific alpha coyotes *Canis latrans* has been recommended to reduce livestock depredation by preventing co-operative killing behaviour (Mitchell, Jaeger & Barrett 2004). Individuals might also be removed to induce a behavioural change in those animals that remain. Cromsigt *et al.* (2013: p547) have proposed utilising fear to induce behavioural change, stating "*it might be easier to induce fear for social ungulates where one individual is shot and escaping individuals learn about risk*". Aside from the unintended behavioural consequences of elevating the perception of risk (Smith, Wang & Wilmers 2015), targeting individuals in group-living species carries additional uncertainty due to the uneven roles that individuals play in group dynamics. For instance, the removal of 'keystone individuals' ("*an individual that has a disproportionately large, irreplaceable effect on other group members and/or the overall group dynamics*"; Modlmeier *et al.* 2014: p55) during management might have unforeseen negative consequences on the fitness of other individuals in the group through loss of knowledge or the destabilisation of social structures (Milner, Nilsen & Andreassen 2007; Modlmeier *et al.* 2014). Modlmeier *et al.* (2014) identify social network theory as a promising approach for investigating these concerns (see Box 2.2).

In the longer term, selective management can exert a strong artificial selection against certain behaviours (Woodroffe & Frank 2005; Mysterud 2011), possibly causing rapid changes to correlated phenotypes and genotypes (Darimont *et al.* 2009)**.** Long-standing, historical control of European brown bears *U. a. arctos* might have resulted in the selection of certain traits leading these bears being better suited to coexistence with people than their North American counterparts (Zedrosser *et al.* 2011). Although it would appear that changing the behaviour of a population through the selective removal of individuals would be a win-win situation, the "*semi-domestication*" of a species through trait selection can itself yield undesirable evolutionary effects by removing certain phenotypes (Mysterud 2011; Leclerc, Zedrosser & Pelletier 2017).

(V) Can targeting individuals help achieve social objectives?

Conservation conflicts can arise due to disagreement between parties over the methods or objectives of wildlife management (Redpath *et al.* 2013). Mitigating or working within these conflicts is often a difficult task as social variables, such as politics or stakeholder attitudes can be of equal or greater importance to ecological variables in determining policy, practice and outcomes (Massei *et al.* 2010; Dickman 2010). While selective management itself is not typically seen as socially contentious, methods utilised to remove individuals, such as lethal control, can be (e.g. Box 2.4). An assessment is therefore needed as to whether focussing management on individual animals can help navigate the diverse, and often opposing, attitudes, objectives and ethical positions of a broad range of people (Figure 2.1).

The lethal control of wild animals is unpopular amongst those who value wildlife in an intrinsic and non-consumptive way (Ramp & Bekoff 2015). Yet it has been suggested that, when compared to population control, removing only the problem individuals will create less of an impact upon the sensibilities of such groups (Linnell 2011). This might be due to selective management being seen as 'more ethical' (Schakner *et al.* 2016) or that the label of 'problem' or 'rogue' gives the animal a 'malicious agency' (Neff & Hueter 2013). There certainly appears to be increased support for killing an individual once it has committed an act that could impact upon humans (Martínez-Espiñeira 2006; Browne-Nunez *et al.* 2015). Despite these findings, lethal control is likely to be met with at least some opposition (see Box 2.4).

Stakeholders who are negatively and directly impacted by wildlife rarely share the protectionist values of others (Treves & Naughton-Treves 2005), favouring hunting, population control (Treves, Naughton-Treves & Shelley 2013) and translocation (Fernando *et al.* 2012). The perception that the impact is caused by an individual animal appears to catalyse calls for lethal control (Goldman, de Pinho & Perry 2013; Neff & Hueter 2013; Parrott 2015). In Kenya, Maasai communities refused monetary compensation aimed at preventing retaliatory lion hunts as they perceived that individual lions developed foraging specialisations on livestock that would continue indefinitely until those particular lions were removed (Goldman, de Pinho & Perry 2013). Where appropriate, allowing stakeholders to participate actively in the hunting of problem animals might offer a form of bottom-up collaborative governance that promotes coexistence (Redpath *et al.* 2017), especially if methods with high accuracy are used (Table 2.1).

Wildlife managers that choose to apply lethal control of individuals to ease social tensions tend to follow a utilitarian approach (Dubois & Harshaw 2013), whereby the removal of a few animals is acceptable when compared to the negative consequences that other strategies (including inaction) might produce, such as a breakdown in trust between stakeholders and management agencies or increased illegal persecution (Goldman, de Pinho & Perry 2013; Olson *et al.* 2015). Yet those that see problem individual management as a *"quick-fix method*" with a "*high public relations value*" (Hoare 2001: p45) should be alert to the importance of correctly distinguishing between an improvement in stakeholder attitudes towards a management body and an improvement in attitudes towards the species (Treves *et al.* 2015). Indeed, the assumption that the removal of a few individuals will increase tolerance for those remaining is often made by management bodies without clear evidence to suggest this is the case (Treves *et al.* 2015). Recent longitudinal studies attempting to unravel whether lethal grey wolf management increased stakeholder tolerance of wolves in the US have found limited support for this assertion when surveying attitudes (Treves, Naughton-Treves & Shelley 2013; Browne-Nunez *et al.* 2015). This assumption is fundamental to strategies that aim to promote co-existence and reduce illegal killing through control of problem individuals. Further studies across other systems are urgently needed to help those considering the social implications of selective management.

Box 2.4: Case study - 'Bruno the Bear' and the power of the individual

A single animal can sometimes have broad-reaching impacts, extending beyond ecology to international policy. Perhaps the most famous problem individual in recent decades was Bear JJ1. Named 'Bruno' by the media, in May 2006 this brown bear was the first to be recorded in Germany in 170 years (Maderspacher 2007). While there was initially considerable positive attention at Bruno's arrival, a trail of well-publicised incidents, primarily the killing of livestock, led to Bruno being branded a 'problem bear' (Austrian Bear Emergency Team 2006; Maderspacher 2007). It is likely that Bruno's 'bad habits' were, at least in part, a product of his upbringing (Morehouse *et al.* 2016); his mother had displayed similar behaviour during his infancy and his brother also went on to become a 'problem bear' (Austrian Bear Emergency Team 2006; European Commission Technical Report 2015). While Bruno's individuality was perceived as errant by those who had been directly affected (Austrian Bear Emergency Team 2006), it was seen as charismatic by others (Maderspacher 2007). Although Bruno seemed to become less and less fearful of humans, his extensive roaming meant that attempts to capture him were unsuccessful and he was eventually shot by hunters commissioned by the Bavarian government (Austrian Bear Emergency Team 2006). The decision to shoot Bruno was made following a rigorous risk assessment, centred less on threats to livestock, but more on evidence that he had become habituated to people and so posed an imminent threat to human safety (Austrian Bear Emergency Team 2006). By the time he was shot, the character of 'Bruno the Bear' had achieved international celebrity-like status. His death was reported in newspapers from *Das Spiegel* to *The Washington Post* with headlines such as "*Fed up Germany kills its only wild bear*" (Washington Post, 27 June 2006). This single episode had policy implications at national and international levels. Within Germany, comparisons of public attitudes before and after Bruno suggested a significant decline in support for predator reintroductions, particularly in Bavaria (Munchhausen & Herrmann 2007). At an international level, it prompted a special European Commission report focused on "defining, preventing and reacting to problem bear behaviour" (European Commission Technical Report 2015). The story of Bear JJ1 vividly illustrates the impact of animal individuality.

***Figure 2.3.** A taxidermy mount of Bruno the Bear raiding a beehive.*
This photograph is of a display at the Museum of Man and Nature, Munich (Photo: © Museum Mensch und Natur)

Concluding remarks

I have looked at the ecological basis for, and efficacy of, selective wildlife management. As ethical and environmental concerns over traditional forms of wildlife management increase, it seems likely that the current trend toward selectivity will continue. Evidence is broadly supportive and I am hopeful about what can be achieved and about prospects for future research (Box 2.5: Outstanding questions). Problem individuals can indeed be found in wild animal populations, and the clearest examples are found in generalist species with high behavioural plasticity. Tailoring management to focus on individual animals displaying unwanted traits, although at times logistically challenging, can generally be thought of as a less harmful strategy when compared to population-level intervention. There are instances of where this selective management has produced sudden drops in impact, without threatening conservation objectives and/or has presented a workable compromise for stakeholders with opposing views.

However, targeting problem individuals should not be seen as a general solution. The behaviour these animals display, though often uncommon, rarely appears to be truly exceptional. As a result, benefits can be short-lived as problem animals are replaced, meaning such strategies must rely on on-going management, which is usually lethal. Where this is the case, in addition to increased economic costs, it seems likely that selection on certain traits, behaviours or demographic classes will be strong and disruption to social dynamics is likely. Those responsible need to ensure that they have considered subtle, indirect impacts of these new selective processes.

For practitioners, decisions about selective management should be based on a combination of the economic, ecological and social costs and benefits (Figure 2.1). A decision-making process that is both transparent and flexible, should help account for any uncertainty or change in these variables (Redpath *et al.* 2013; Milner-Gulland & Shea 2017). Ultimately management will benefit greatly from improved understanding of the underlying causes of problem behaviours, e.g. Artelle *et al.* (2016), Morehouse *et al.* (2016) and Schakner *et al.* (2016). Such research, though rare, represents the best long-term prospect for mitigating, minimising and preventing impact and conflict.

Box 2.5: Outstanding questions

I highlight four areas of research that will add to our understanding of the ecology of problem individual management.

(i) What are the ecological drivers of problem behaviours, and can proactive management of such drivers alleviate impact and conflict?
(ii) Can we build end-to-end ecological appraisals of selective management, where the behaviour and biology of individuals are used to understand problems, develop solutions, and evaluate actions in practice?
(iii) In which environmental contexts is management confounded by rapid re-emergence of problem behaviours?

(iv) Can we effectively integrate ecology and social science in developing mitigation options and investigating the longer-term effects of selective management on those affected by, and engaging with, the problem?

Chapter 3

EVALUATING BAYESIAN STABLE ISOTOPE MIXING MODELS OF WILD ANIMAL DIET

Chapter 3: Evaluating Bayesian stable isotope mixing models of wild animal diet

Abstract

Ecologists quantify animal diets using direct and indirect methods, including analysis of faeces, pellets, prey items and gut contents. For stable isotope analyses of diet, Bayesian stable isotope mixing models (BSIMMs) are increasingly used to infer the relative importance of food sources to consumers. Although a powerful approach, it has been hard to test BSIMM performance as the necessary fine-scale data for wild animals are difficult to collect. I evaluated the performance of BSIMMs in quantifying animal diets when using $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios from the feathers and blood of common buzzard *Buteo buteo* nestlings. I analysed model outcomes with various trophic discrimination factors (TDFs) and with and without informative priors, and compared these to direct camera observations of prey provisioned to nestlings at nests. BSIMMs with different TDFs varied markedly in their performance and the best fits to observations were obtained using the statistical package SIDER to derive TDFs. These models produced strong agreement at the population level and, for the main prey item, at the individual nest level. The inclusion of informative priors from conventional analysis of prey remains appears to have transferred biases into model posteriors, markedly reducing model performance. BSIMMs can provide highly accurate assessments of diet in wild animals at population and finer scales. TDF estimates from the SIDER package perform better than those from taxonomically similar species.

Introduction

Stable isotope analysis of consumer tissues is an effective indirect method for determining animal diets that, when used in combination with other methods, can provide an estimate of the proportional contributions of food sources (Inger & Bearhop 2008; Parnell *et al.* 2013). The method works because naturally-occurring variation in the stable isotope ratios of foods is incorporated into consumer tissue (Hobson & Clark 1992). By analysing isotope ratios in the tissue of consumers and their putative food, it is possible to model isotope mixing and infer the relative importance of food groups to the consumer (Inger & Bearhop 2008). Recent advances have moved stable isotope mixing models (SIMMs) into a Bayesian framework (BSIMMs), which incorporates uncertainty in parameter estimates and error and gives probabilistic predictions of diet composition (Moore & Semmens 2008; Parnell *et al.* 2013; Phillips *et al.* 2014). These models also allow prior knowledge of feeding behaviours or food preferences to be taken into account, guiding the model fitting process. The inclusion of 'informative priors' from complementary field and dietary information, is a widely advocated means of improving SIMM performance (Moore & Semmens 2008; Bond & Diamond 2011). Indeed, in reconstructing known diets from captive feeding trials, Derbridge *et al.* (2015) were unable to produce comparable pictures of wolf *Canis lupus* diet without including priors. Ecologists have used priors derived from assessments of diet (Doucette, Wissel & Somers 2011), resource availability (Derbridge, Krausman & Darimont 2012) and other biologically relevant information such as prey abundance and handling times (Yeakel *et al.* 2011). Despite this, the potential influence of informative priors on model outcomes, or 'posteriors' (Derbridge *et al.* 2015), raises concerns that inappropriate priors could confound important information within the basic isotopic data (Franco-Trecu *et al.* 2013).

A further challenge in formulating mixing models is trophic discrimination, which is the change in isotope ratios arising from physiological processes during incorporation of dietary protein into consumer tissue. Trophic discrimination factors (TDFs) account for this change in mixing models and can have a profound influence upon their outcomes (Caut, Angulo &

Courchamp 2008; Bond & Diamond 2011). To derive TDFs, researchers have used values from taxonomically similar species, often from captive feeding trials or means from other studies (Caut, Angulo & Courchamp 2009). However, TDFs can vary with species, nutritional status, tissue type, individual physiology and isotopic composition of diet (Vanderklift & Ponsard 2003; Caut, Angulo & Courchamp 2009). Although BSIMMs allow for uncertainty in TDFs the ‘true’ ranges within which they lie are difficult to determine, particularly for wild animals (Phillips *et al.* 2014).

The creation of open source packages for BSIMMs has led to an increase in usage (Phillips *et al.* 2014). If properly implemented, BSIMMs can produce accurate, probabilistic estimates of animal diets (Moore & Semmens 2008; Parnell *et al.* 2013), yet concerns have been raised over misuse and sensitivity to input parameters (Martínez Del Rio *et al.* 2009; Boecklen *et al.* 2011; Polito *et al.* 2011; Franco-Trecu *et al.* 2013; Derbridge *et al.* 2015). This has led to attempts to evaluate BSIMMs through experimental and observational studies (Weiser & Powell 2011; Derbridge, Krausman & Darimont 2012; Franco-Trecu *et al.* 2013; Flemming & van Heezik 2014; Resano-Mayor *et al.* 2014; Derbridge *et al.* 2015; Newsome, Collins & Sharpe 2015). However, studies of captive animals in controlled conditions (Caut, Angulo & Courchamp 2008; Derbridge *et al.* 2015) lack the variation in diet and physiology found in wild animals (Boecklen *et al.* 2011). This variation will change patterns of nutrient incorporation into different tissues (isotopic routing; see Podlesak & McWilliams, 2006), meaning that models validated in captivity might be less applicable to wild systems. Attempts to evaluate BSIMMs in field conditions have, so far, been constrained to comparing outcomes with those of alternative indirect methods. While some studies demonstrated similarity between indirect methods and BSIMMs (Resano-Mayor *et al.* 2014; Newsome, Collins & Sharpe 2015), others have reported mixed results related to biases associated with prey size and digestibility (Weiser & Powell 2011; Franco-Trecu *et al.* 2013; Flemming & van Heezik 2014).

To measure BSIMM performance, a system is required for which accurate dietary data from a direct method can be collected and aligned with stable isotope analysis of tissue integrated over a comparable period. During the breeding season, predatory birds offer such a system, as food is brought to the nest, allowing direct observation and sampling of nestling diet (Gaglio *et al.* 2017; Resano-Mayor *et al.* 2014). Direct observation of feeding at the nest has been aided by remote cameras (Rogers, DeStefano & Ingraldi 2005; Smithers, Boal & Andersen 2005). Although this method might fail to identify small prey (García-Salgado *et al.* 2015) and can be costly (Tornberg & Reif 2007), dietary estimates from cameras can represent the most complete assessments of raptor diets (Lewis, Fuller & Titus 2004; García-Salgado *et al.* 2015) and have been used to evaluate other analytical methods (Lewis, Fuller & Titus 2004; Selås, Tveiten & Aanonsen 2007; Tornberg & Reif 2007).

I compare dietary inference from BSIMMs against observations of food provisioning at nests of common buzzards *Buteo buteo*. Buzzards are a medium-sized bird of prey found across much of the Palaearctic (Cramp & Simmons 1980). In the U.K., buzzards have a diverse diet (Rooney & Montgomery 2013; Francksen, Whittingham & Baines 2016) and rapid increases in buzzard populations has created growing interest in their diet (Parrott 2015). I assessed how TDF choice influences the accuracy of model posteriors and then used these results to demonstrate how informative priors influence model performance.

Materials and Methods

Fieldwork was conducted from May to August 2015 on three study sites in Cornwall, U.K. (the central point of three study sites is 50.35°N, 4.85°W). Buzzard nests were located during the early nesting phase and accessed three times during the nesting season (Table 3.1). Motion-activated cameras (CMOS 380 TVL, HandyKam, Cornwall) were installed on each nest between early June and mid-July. Cameras recorded up to 5 minutes of video when movement was detected (Appendix 2). Each camera was active over a mean of 15 days (*SD* = 5.1) encompassing a mean of 207 ‘hunting hours’ (*SD* = 82).

Videos of prey deliveries were watched by a single observer (GS). Where possible, prey items were recorded at a species level but were otherwise identified to category (Table 3.2). Each item was classed as small, medium or large in relation to the mean size for that species or category (Appendix 3, 5 & 6). For larger prey items (> 100g), the proportion of the whole carcass brought to the nest was noted, as adults often partially consume large prey before returning to the nest (Resano-Mayor *et al.* 2014). Weights were allocated for each item based on species, size and proportion provisioned. For items that could not be identified, biomass was calculated from the approximate size and the length of time it took to consume. The proportion of biomass was calculated for unidentified items but did not feature in further analysis. For each of the 20 nests, the total biomass was used to calculate the contribution of each prey category to nestling diet.

Table 3.1: *Periods of data and sample collection in relation to nesting stage.*

Nesting stage	**Hatching confirmed**		**Nestlings 18-25 days old**			**After fledging**	
	May 1-15	May 16-31	June 1-15	June 16-30	July 1-15	July 16-31	August 1-15
Prey remains and pellets	■	■	■	■	■	■	■
Nest cameras			■	■	■		
Prey tissue	■	■	■	■	■		
Nestling bloods and feathers			■	■	■		

At each nest, prey remains and egested pellets were located by searching the nest cup, tree and a 10m radius at ground level at each visit. Pellets were dissected and the contents sorted by species (or category, as above) and the minimum number of each prey type was identified. When feather remains in pellets could not be identified, size class was estimated from feather size. Remains without edible parts were removed from the nest to avoid recounting. I did not record invertebrates as, even when frequently recorded, their importance as a dietary item is negligible due to their low biomass (Rooney &

Montgomery 2013). Following Resano-Mayor *et al.* (2014), I used estimates of prey weights to convert frequency of occurrence into percentage biomass (Table 3.2; Appendix 6 & 7). Prior to analysis, data from prey remains and pellet collections were combined. This approach is commonly used to assess raptor diet (Rooney & Montgomery 2013), though the biases from indirect methods can vary between species (Simmons, Avery & Avery 1991; Redpath *et al.* 2001) and years (Francksen, Whittingham & Baines 2016) and I acknowledge that combining methods may not always be appropriate.

Approximately 0.2ml of blood and four growing or freshly grown body feathers were sampled under licence (Appendix 4) from nestlings that were 18-25 days old. Bloods were centrifuged and red blood cells (RBCs) separated. Feathers were cleaned with de-ionised water to remove surface contaminants. All tissues were stored at -80°C. The turnover rate of RBCs and the age-class at which natal down is replaced by body feathers means both RBCs and body feathers can represent nestling diets during the rearing period (Hobson & Clark 1993; Bearhop *et al.* 2000). As a result, some of the sampled tissue might have been formed prior to the deployment of the cameras, creating some temporal disparity in my datasets.

Access to food sources between delivery by the parent and ingestion by the nestling is a particular benefit of this system, assuring that tissue samples are more directly representative of those eaten (Doucette, Wissel & Somers 2011). Therefore, all fresh prey items found within the nest cup were sampled by taking up to 0.5 g of muscle before the remaining prey was returned to the nest. Additional amphibian tissue was collected opportunistically from carcasses found in or near the study area. Tissue samples were immediately put on ice before being stored at -80°C.

Table 3.2: *Frequency of prey items identified from video footage from cameras on 20 buzzard nests. The six most important prey groups are shown in bold. N denotes frequency of occurrence. BIO denotes biomass.*

Taxonomic group	**Prey group**	**Species**	***N***	***N* %**	**Total BIO (g)**	**Total BIO (%)**
Lagomorpha	**Rabbits**	Rabbit *Oryctolagus cuniculus*	178	12.6	33161	37.4
Rodentia	**Small rodents**	Vole *Myodes/Microtus* spp.	359	25.5	6427	7.2
	Small rodents	Wood mouse *Apodemus sylvaticus*	49	3.5	1044	1.2
	n/a	Rat *Rattus norvegicus*	22	1.6	3196	3.6
	n/a	Squirrel *Sciurus carolinensis*	9	0.6	3306	3.7
Soricomorpha	**Shrews & moles**	Mole *Talpa europaea*	59	4.2	5109	5.8
	Shrews & moles	Shrew Soricidae spp.	66	4.7	470	0.5
Carnivora	n/a	*Mustela* spp.	6	0.4	352	0.4
Galliformes	**Gamebirds**	Pheasant *Phasianus colchicus*	30	2.1	5760	6.5
	*	Released poults	39	2.8	7836	8.8
Passeriformes	n/a	Thrush Turdidae spp.	26	1.9	1984	2.2
	n/a	Unidentified Passeriformes	39	2.8	594	0.7
	Corvids	Corvid Corvidae spp.	30	2.1	4719	5.3
Columbiformes	n/a	Woodpigeon *Columba palumbus*	7	0.5	1627	1.8
Accipitriformes	n/a	Buzzard *Buteo buteo*	1	0.1	50	0.1
Gruiformes	n/a	Moorhen *Gallinula chloropus*	1	0.1	230	0.3
Anura	**Frogs & toads**	Frog *Rana temporaria*	104	7.4	2704	3.0
	Frogs & toads	Toad *Bufo bufo*	108	7.7	3196	3.6
Squamata	n/a	Slow worm *Anguis fragilis*	2	0.1	26	0.0
	n/a	Grass snake *Natrix natrix*	5	0.4	353	0.4
	n/a	Adder *Vipera berus*	1	0.1	83	0.1
Anguilliformes	n/a	European eel *Anguilla anguilla*	2	0.1	600	0.7
Megadrilacea	n/a	Earthworm	9	0.6	37	0.0
Unidentified		Shrew or small rodent	104	7.4	1524	1.7
		Small (est. < 50g)	138	9.8	2236	2.5
		Medium (est. 50-150g)	10	0.7	1040	1.2
		Large (est. > 150g)	5	0.4	1050	1.2
Total			1409	100	88715	100
Total identified			1152	82	82865	93
Total in 6 prey groups			983	70	62590	71

Stable isotope analysis

Prior to analysis, samples were freeze dried for >48 hours. Samples were homogenised and ~0.7mg aliquots were weighed into tin cups. All stable isotope analyses were carried out using a Sercon (Crewe, U.K.) INTEGRA2 elemental analyser-isotope ratio mass spectrometer at the University of Exeter. Stable carbon and nitrogen isotope ratios are expressed as δ values and expressed in ‰ where

$$\delta X = [(R_{sample} \,/\, R_{standard}) - 1] \, * \, 1000$$

and X = ^{15}N or ^{13}C, R_{sample} = heavy to light isotope ratio derived from the sample, and $R_{standard}$ = heavy to light isotope ratio derived from the Vienna Pee Dee Belemnite (VPBD) for δ^{13}C and atmospheric nitrogen for δ^{15}N. Based on within-run standards, analytical precision was ± 0.1‰.

Trophic discrimination factors

I searched the literature for feather and blood TDFs of ecological relevance to my species. I found none for *B. buteo* or other *Buteo* species (although Li *et al.* (2001) provide TDFs for *B. hemilasius* but for a different tissue type, i.e. muscle), but identified four sources of blood and feather values from taxonomically similar species and results of meta-analyses (Table 3.3). Specifically, the two TDFs sources from taxonomically similar species were from laboratory feeding trials of peregrine falcons *Falco peregrinus* (Hobson & Clark 1992) and California condors *Gymnogyps californianus* (Kurle *et al.* 2013). For the third source, with the exception of blood Δ^{13}C, I used the mean values from a meta-analysis of 61 avian TDFs for Δ^{13}C and 52 for Δ^{15}N (Caut *et al*. 2009). Blood Δ^{13}C was calculated from the blood δ^{13}C of nestlings using a regression reported by Caut *et al*. (2009). The fourth source was a recently developed R package (SIDER; Healy *et al.* 2016) that uses a Bayesian imputational approach to estimate TDFs based on a species' ecology, physiology and phylogeny. TDFs estimated from the SIDER package may also have the added benefit of a measure of precision within its estimates producing a more realistic parameter of uncertainty (Healy *et al*. 2016).

Table 3.3: *Trophic discrimination factors (TDFs) for common buzzards used in Bayesian stable isotope mixing models. TDFs were from taxonomically similar species: (a) peregrine falcon* Falco peregrinus *fed on Japanese quail* Coturnix japonica *(Hobson & Clark 1992); (b) California condor* Gymnogyps californianus *fed on laboratory rats* Rattus norvegicus *(Kurle et al. 2013), (c) from a meta-analysis of 61 avian TDFs for* $\Delta^{13}C$ *and 52 for* $\Delta^{15}N$ *reported by Caut et al. (2009) and (d) from Bayesian inference in the R package SIDER (Healy et al. 2016).*

Source	**Blood**		**Feather**	
	$\Delta^{13}C$	$\Delta^{15}N$	$\Delta^{13}C$	$\Delta^{15}N$
a. Peregrine falcon	+ 0.20 ± 0.01	+ 3.30 ± 0.40	+ 2.10 ± 0.08	+ 2.70 ± 0.50
b. California condor	- 0.70 ± 0.10	+ 1.70 ± 0.10	+ 0.40 ± 0.40	+ 3.10 ± 0.20
c. Meta analysis	+ 1.27 ± 0.17*	+ 2.25 ± 0.20	+ 2.16 ± 0.35	+ 3.84 ± 0.26
d. SIDER	+ 1.51 ± 1.46	+ 2.35 ± 0.99	+ 2.37 ± 1.49	+ 2.79 ± 1.03

**Blood* $\Delta^{13}C$ *was calculated from the blood* $\delta^{13}C$ *of nestlings using a regression provided by Caut et al. (2009).*

Only prey items identified to taxonomic Order or lower, were included in the direct observations data. For comparison of methods, all three datasets, i.e. BSIMMs, direct observations and conventional methods, were grouped into the same prey categories (Phillips *et al.* 2014). Only prey categories that comprised >5% biomass from the direct observations were selected for comparison, as the exclusion of uncommon dietary items tends to improve mixing model accuracy (Phillips & Gregg 2003). For all methodological comparisons, I used biomass rather than frequency of occurrence, as the former provides the most appropriate measure of relative importance in diet. Biomass estimates from provisioning observations and conventional methods were calculated for every prey category at each nest. I used a bootstrapping procedure (sampling the proportions of each prey category 1000 times) to create distributions that could be compared to BSIMM posteriors.

Statistical analysis

R version 3.2.2 (R Core Team 2016) was used for all analyses. To validate my assumption that red blood cells and feathers contained isotopic information assimilated over comparable time periods, I fitted linear regressions between feather and blood $\delta^{15}N$ and $\delta^{13}C$. To assess the significance of variation in $\delta^{15}N$ and $\delta^{13}C$ among prey groups, I fitted one-way ANOVAs and Tukey's post-hoc tests. I used SIMMR in R (Parnell *et al.* 2010; Parnell & Inger 2016), to infer the relative contribution of the six prey groups to the diet of buzzard nestlings. Models included the mean and standard deviation of $\delta^{15}N$ and $\delta^{13}C$ for the prey groups (Table 3.4). To account for the non-independence of buzzard nestlings from the same nest I used mean $\delta^{15}N$ and $\delta^{13}C$ values per nest.

To test the effects of different TDFs, the similarity of model outputs using the four TDF sources were compared to direct observations, using Bhattacharyya's Coefficient (BC). BC varies from 0 (no similarity) to 1 (identical). Catry et al. (2009), Bond and Diamond (2011) and Jardine et al. (2015) have previously considered a BC of > 0.6 to represent a significant overlap in the distributions of a dietary source. Here, we use BC to evaluate variation in dietary estimates but do not infer statistical significance from this value. As I was interested in *within* prey category agreement, as well as overall agreement, I conducted pairwise model comparisons for each prey category and used mean BC (± SD) as an overall measure. The TDF inputs that led to the BSIMM with the highest BC were then used to explore model performance at a finer scale by reconstructing nestling diet in individual nests, using SIMMRsolo (Parnell *et al.* 2010; Parnell & Inger 2016). Separate models were run for blood and feather samples. The relationship between diet estimates from direct observations and BSIMMs were then tested using Spearman's rank correlation for each prey category. To demonstrate the effect of informative priors on model posteriors, the BSIMMs with the highest similarity index for each tissue were run again with informative priors. For each prey category, I used mean and SD of proportional biomass, estimated by conventional methods (pellets and prey remains) across all nests.

Table 3.4: *The stable isotope signatures of six main prey groups of common buzzards.*

Prey category	***n***	**Mean δ^{15}N (SD)**	**Mean δ^{13}C (SD)**
Rabbits	24	6.11 (1.69)	-28.76 (0.52)
Small rodents	17	4.18 (2.59)	-28.33 (1.49)
Shrews & moles	7	9.01 (1.73)	-25.77 (1.01)
Gamebirds	9	6.34 (0.73)	-24.71 (2.13)
Corvids	5	8.60 (1.53)	-24.97 (0.58)
Frogs & toads	7	6.25 (1.47)	-26.54 (0.44)

Prey categories comprised: rabbits (*Oryctolagus cuniculus*), small rodents (3 *Apodemus sylvaticus*, 14 *Myodes glareolus / Microtus agrestis*), shrews & moles (2 *Sorex araneus*, 5 *Talpa europaea*), Gamebirds (1 *Alectoris rufa*, 8 *Phasianus colchicus*), Corvids (2 *Corvus corone*, 3 Corvidae spp.), Frogs & toads (4 *Rana temporaria*, 3 *Bufo bufo*).

Results

334 prey items were identified at 20 nests; 235 prey remains (mean per nest 11.8 ± 5.1 SD) and 99 from pellets (5.0 ± 3.2). For these conventional methods, rabbit was the most frequently identified prey item (frequency of occurrence for prey remains = 32% and pellets = 37%) and the most important (biomass for prey remains = 36% and pellets = 62%) (Appendix 5).

Nest cameras recorded footage for 4144 hours over 300 'nest days' (mean hours per nest per day = 13.8 ± 4.2). 1409 prey items were recorded (mean items per nest = 70.5 ± 30.6), of which 1152 (82%) were identified. Of the 257 that could not be identified, 242 (94.2%) were categorised as 'unknown small prey' due to their rapid (< 1 minute) consumption. This category included 104 (41%) deliveries identified as 'small mammals', but where shrews and small rodents could not be distinguished (Appendix 6 & 7). On seven nests, released pheasant poults, identified by clipped primary feathers, were recorded as prey items towards the end of the monitoring period. Because the release date for poults was after the isotope samples had been taken from the buzzard nestlings, and to allow for the comparison of methods, released pheasants were excluded from further analysis (camera observations: n = 39;

conventional methods: n = 18). Biomass estimates were obtained for all 1409 items. These were based on species, size, proportion remaining and time taken to consume (Appendix 6, 7 & 8). Prey items were grouped by taxonomy and dietary ecology (e.g. corvids were separated from other Passeriformes). This left six prey groups comprising >5% biomass that were used for further analyses (Table 3.2).

I obtained isotope ratio data from red blood cells and feathers sampled from 29 buzzard nestlings from 20 nests. There was a strong positive relationship between the blood and feather signatures for both $\delta^{13}C$ (slope = 0.87, S.E. = 0.11; intercept = -2.56, S.E. = 3.00) and $\delta^{15}N$ (slope = 1.28, S.E. = 0.12; intercept = -1.04 , S.E. = 0.95). 69 prey tissue samples were collected from the six prey categories (Table 3.4). There was significant variation among the prey categories in $\delta^{13}C$ ($F_{5,63} = 25.73$, $P < 0.001$) and $\delta^{15}N$ ($F_{5,63} = 8.87$, $P < 0.001$). Buzzard nestling signatures mainly fell within the range of sampled prey items when TDFs were applied (Figure 3.1), a necessary condition for SIMMs to produce accurate dietary estimates (Phillips *et al.* 2014).

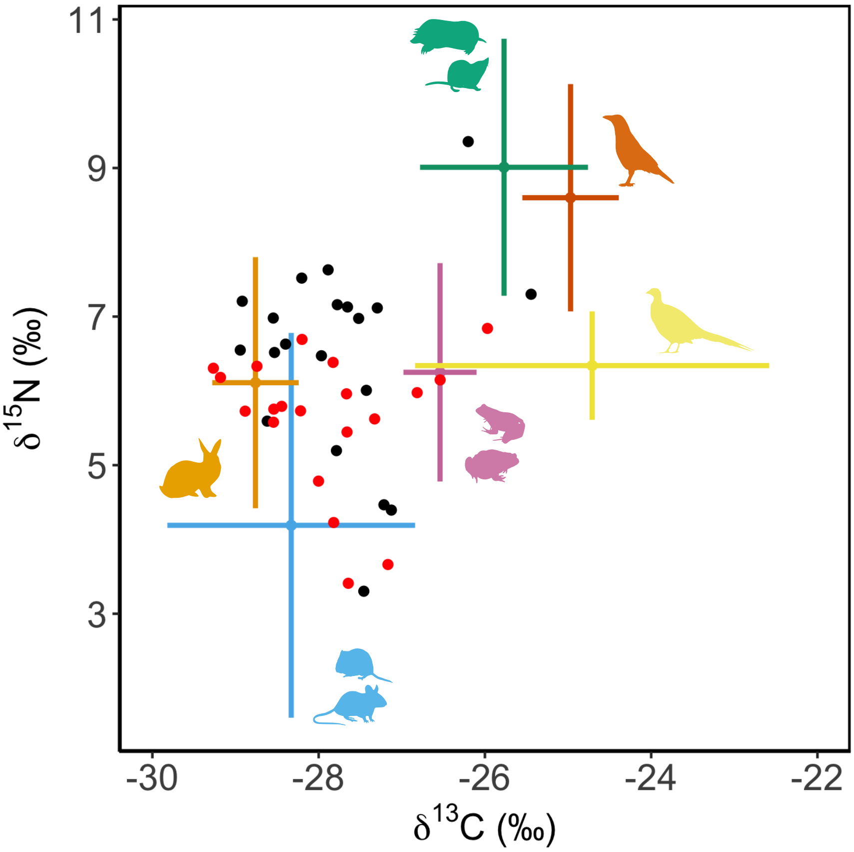


Figure 3.1: *Mean stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) from 20 nests with 29 buzzard nestlings and their main prey categories. Buzzard samples are in black (feathers) and red (red blood cells). Buzzard signatures are corrected by TDF estimates calculated using the SIDER package (feather: 2.37 ‰ for $\delta^{13}C$ and 2.79 ‰ for $\delta^{15}N$, blood: 1.51 ‰ for $\delta^{13}C$ and 2.35 ‰ for $\delta^{15}N$). Bars indicate standard deviation. Prey groups are rabbits (light orange), small rodents (blue), shrews & moles (green), gamebirds (yellow), corvids (dark orange) and frogs & toads (pink).*

The outcomes (posteriors) of BSIMMs varied markedly in their similarity to direct observations of nestling provisioning (Table 3.5). Of the four TDF sources, models run using TDFs from the SIDER package produced the estimates most similar to direct observations, for both feathers and red blood cells (Figures 3.2 and 3.3). The inclusion of informative priors from conventional analysis of prey remains reduced the similarity of mixing model outcomes to the direct observations, to the extent that inclusion of priors rendered the stable isotope approach worse than the analysis of prey remains alone (Table 3.5).

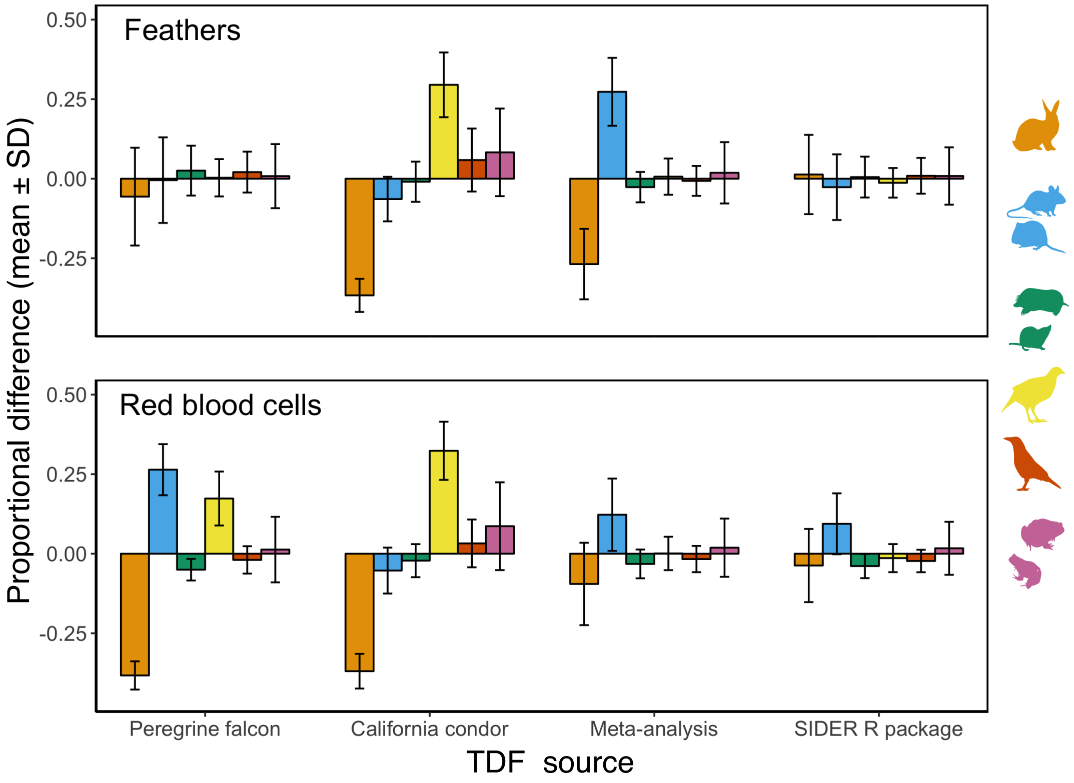


Figure 3.2: *Differences in the proportions of each prey group in the diets of buzzard nestlings when estimated by Bayesian stable isotope mixing models using multiple TDFs and compared to direct observations from cameras. High values indicate large discrepancies.*

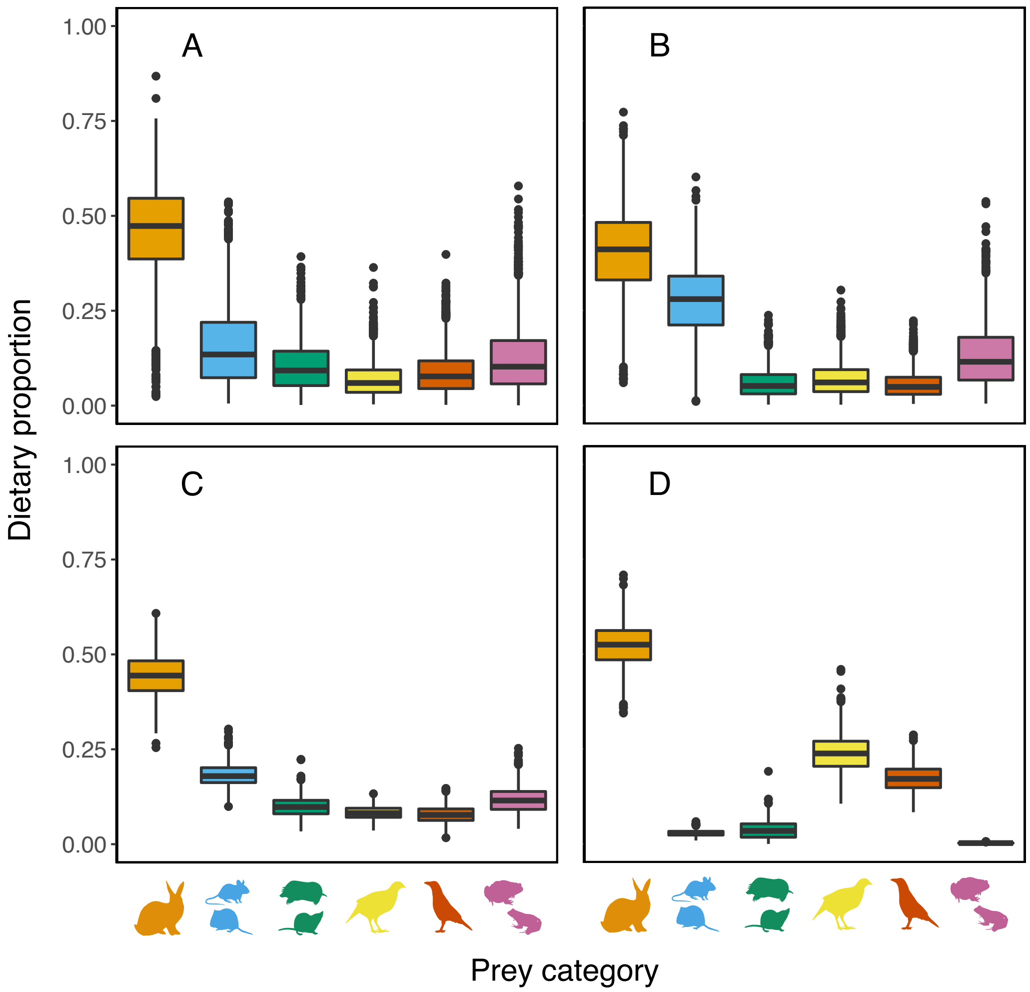


Figure 3.3: *Estimates of the composition of buzzard nestling diet. Estimates are sourced from Bayesian stable isotope mixing models run using (A) feathers and (B) red blood cells, (C) direct observations of adults provisioning nestlings at the nest and (D) conventional analysis of prey remains and pellets. BSIMMs used no priors and trophic discrimination factors from the Bayesian package SIDER.*

When the mixing models for feathers and blood cells using TDFs from SIDER and no priors were run for each nest, a strong positive relationship was observed between mixing model estimates of nestling diet in each nest to those from direct observations, but only for the most important prey item, i.e. rabbits (Feather $r_s = 0.81$, n = 20, $P < 0.001$; Blood: $r_s = 0.77$, n = 20, $P < 0.001$; Figure 3.4). No significant relationships were observed with other prey groups.

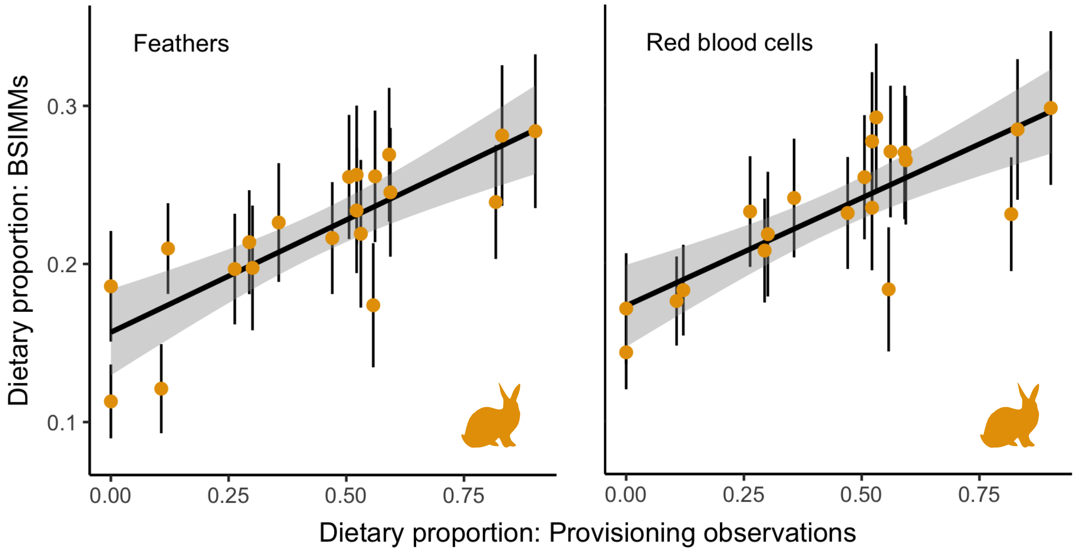


Figure 3.4: *Relationship between estimates of the contribution of rabbit to buzzard nestling diets from direct observations of provisioning at the nest and Bayesian stable isotope mixing models (BSIMMs) run using feathers and red blood cells. TDF estimates were from SIDER. BSIMM estimates are mean proportions (± confidence intervals) for each nest using SIMMRsolo.*

Table 3.5: *Estimates of diet composition of buzzard nestlings using stable isotope analysis and conventional prey/pellet analysis. Bayesian Stable Isotope Mixing Models (BSIMMs) were run with and without informative priors and with four sources for trophic discrimination factors (TDFs). Methods are ranked by their similarity to direct observations from remote cameras. Similarity was assessed by the mean Bhattacharyya's coefficient (BC), ranging between 0 (no similarity) and 1 (identical).*

Rank	**Indirect method**	**Priors**	**Tissue**	**TDF source**	**Similarity to direct observations (Bhattacharyya's coefficient)**						
					Mean ± SD	**Rabbit**	**Small rodent**	**Shrew & mole**	**Game bird**	**Corvid**	**Frog & toad**
1	BSIMM	No	Feather	SIDER	0.772 ± 0.078	0.839	0.639	0.808	0.723	0.835	0.787
2	BSIMM	No	Blood	SIDER	0.759 ± 0.089	0.855	0.614	0.719	0.733	0.811	0.825
3	BSIMM	No	Blood	Meta-analysis	0.729 ± 0.111	0.734	0.516	0.750	0.740	0.824	0.807
4	BSIMM	No	Feather	Peregrine	0.728 ± 0.080	0.781	0.578	0.762	0.697	0.785	0.764
5	BSIMM	No	Feather	Meta-analysis	0.600 ± 0.273	0.323	0.189	0.760	0.699	0.837	0.790
6	BSIMM	No	Blood	Vulture	0.513 ± 0.362	0.009	0.726	0.786	0.090	0.773	0.695
7	BSIMM	No	Feather	Vulture	0.499 ± 0.333	0.019	0.661	0.773	0.130	0.703	0.710
8	BSIMM	No	Blood	Peregrine	0.421 ± 0.336	0.016	0.121	0.600	0.244	0.774	0.772
9	Prey/pellet	n/a	n/a	n/a	0.241 ± 0.310	0.774	0.000	0.434	0.038	0.203	0.000
10	BSIMM	Prey/pellet	Feather	SIDER	0.196 ± 0.247	0.166	0.000	0.334	0.049	0.629	0.000
11	BSIMM	Prey/pellet	Blood	SIDER	0.177 ± 0.265	0.083	0.000	0.148	0.129	0.703	0.000

Discussion

I have used direct observations of wild animal feeding behaviour as a reference against which indirect estimates of diet from stable isotope mixing models and more conventional methods could be compared. Although camera observations are not free from bias (García-Salgado *et al.* 2015), my approach represents a significant advance from testing mixing model performance by comparison among models (Bond & Diamond 2011) or with other indirect methods (Ramos *et al.* 2009; Weiser & Powell 2011; Franco-Trecu *et al.* 2013; Resano-Mayor *et al.* 2014). My results show that, with the right choice of TDFs, and, in this case, by not using priors, BSIMMs produced estimates of diet that closely matched direct observations.

Of the four sources I used to obtain TDFs, the SIDER package (Healy *et al.* 2016) produced outputs with the greatest similarity to direct observations. The accuracy of models for feathers and red blood cells when using SIDER TDFs provides evidence of the value of accounting for the numerous sources of variation (e.g. phylogeny, tissue type, consumer signature) in TDF calculation (Caut, Angulo & Courchamp 2009; Healy *et al.* 2016). Such variation may be missed when TDFs are gleaned from captive animals fed on controlled diets. I recommend future studies either calculate TDFs by incorporating multiple sources of variance or use larger uncertainties in BSIMM parameterisation (Granadeiro *et al*., 2014). I also echo Phillips *et al.*'s (2014) recommendation of a sensitivity analysis to test the influence of TDFs on model outputs.

When the top BSIMMs were applied for individual nests, there was strong agreement with direct observations for rabbits but not other prey groups. The ability of BSIMMs to infer variation in the relative importance of rabbits among nests relates to the dietary importance and distinctiveness of this prey. Although there is a strong relationship between the proportion of rabbit in diet for direct observations and BSIMMs, less than perfect agreement could be attributed to constraints on posteriors when models are run using low numbers of consumer samples (Parnell *et al.* 2010). I did not observe a significant relationship in nest-level estimates between BSIMMs and direct observations for other prey categories and there are several plausible explanations for this. First, there might be dietary items that were underrepresented in the camera observations (e.g. 138 small unidentifiable prey items) or temporal mismatches in data collection (e.g. provisioning of reared pheasants after blood sampling). Second, the contribution that any one food source makes to diet is low, relative to rabbit prey, impeding the discriminatory power of the mixing models. Third, model performance is reduced when signatures of prey sources are less distinctive, either because they overlap and/or lie in between other sources (Phillips *et al.* 2014).

Estimates of diet from conventional analysis of prey remains and pellets differed markedly from direct observations and reflected known biases in favour of large birds and against small, digestible prey (Tornberg & Reif 2007; Francksen, Whittingham & Baines 2016). The contribution of amphibians to buzzard diet is a clear example. Estimates from BSIMMs (feather: 12.5%, SD = 9.0, blood: 13.1%, SD = 8.3) closely matched those from direct observations (11.7 % biomass, SD = 3.4), yet we, like others (Tornberg & Reif 2007; Francksen, Whittingham & Baines 2016), recorded very few frogs or toads among prey remains or pellets (0.2% biomass, SD = 0.1)

When priors from analysis of prey remains and pellets were included in the BSIMMs that were otherwise most similar to direct observations, I observed a substantial reduction in their performance. Here, it appears that the biases within the conventional methods have constrained the models and reduced their similarity with direct observations. I present this result not to show that priors influence posteriors; clearly, this is their purpose (Moore & Semmens 2008). Rather I highlight how the inclusion of information intended to strengthen models can make them considerably worse, if they hide the effects of ‘real’ isotopic variation by introducing bias. One approach for incorporating priors with known biases into BSIMMs could be by expanding their variance or including a bias parameter within the models (*A. Parnell, pers. comm.*). Although this holds promise, such corrections may themselves be difficult to support, as biases can vary among species, time and place. It is trivial to recommend that those considering informative priors should be confident that their data reflects the current diet of their study species, but in reality such information is often unobtainable or requires extensive additional data (Orr *et al.* 2011). Indeed, could such confirmation be sourced, the benefit of deriving a BSIMM estimate would be moot. For future studies I therefore recommend that, rather than combining conventional methods within mixing models as priors, dietary information from isotope analysis and conventional sources be presented in conjunction. This would allow the limitations and biases of these approaches to be considered independently.

The use of direct camera observations provided us with clear insight and a standard against which to evaluate isotopic and other methods of diet determination. The collection of such detailed observational data is rare as it is costly, hazardous and requires sustained effort. For dietary studies where such data are not obtainable, the application of stable isotope analysis, with careful deployment of information from conventional methods, can provide a route to identify and account for the biases and shortcomings of both methods. I have demonstrated that, when variation within and among dietary sources is adequately represented and the correct trophic discrimination factors applied, Bayesian stable isotope mixing models are able accurately to infer diet and the relative importance of food sources at a population and, to a lesser extent, individual level.

Chapter 4

DO 'PROBLEM BUZZARDS' EXIST? APPLYING STABLE ISOTOPE ANALYSIS TO UNDERSTAND BUZZARD DIET AND PREDATION OF PHEASANTS

Chapter 4: Do ‘problem buzzards’ exist? Applying stable isotope analysis to understand buzzard diet and predation of pheasants

Abstract

Wildlife management is becoming increasingly selective, often targeting particular individuals for removal. The efficacy of such management actions depends primarily on certain animals having a disproportionate impact upon human interests but also on the accuracy of the removal method. Collecting empirical information on such individuals is challenging, potentially compromising the evidence base for making management decisions. In the U.K., a recent and controversial change in policy has seen the granting of licences to kill ‘problem’ common buzzards *Buteo buteo,* that are perceived to specialise on killing and eating released pheasants *Phasianus colchicus*. I analysed stable isotope ($\delta^{13}C$ and $\delta^{15}N$) signatures of adult buzzards and their putative food sources to estimate the relative contribution that released pheasant poults make to buzzard diets. I use the results to assess selective removal of buzzards as a mitigation method by exploring how buzzard consumption of pheasant poults varies in territories with (i) no pheasant release pen, (ii) a release pen but no perceived predation problem and (iii) a release pen where a predation problem was perceived. The consumption of released pheasant by a small subsample of buzzards caught within release pens was compared to the wider population. Young, released pheasants were isotopically distinct from other buzzard prey, including adult, wild pheasants. I observed significantly higher consumption of released pheasants by buzzards living in territories with a release pen that had a perceived predation problem than those living in territories with no release pen. However, variation in consumption of released pheasants by buzzards living in territories with a release pen but no perceived predation problem suggests that in some pens, pheasant consumption is going undetected or is not a matter of concern. Analysis of the tissue of a small sample of alleged ‘problem buzzards’, that were caught and released under license within pheasant release pens, suggested that buzzards caught within pens consumed significantly higher quantities of released pheasants than their local conspecifics. However, this distinction was

particularly apparent in recently metabolised tissues (red blood cells and blood plasma) suggesting that ‘problem’ behaviour might not be manifested over longer time periods.

Introduction

Disputes among people often arise over the management of predators, due to the perceived threats they pose to human safety, livelihoods or recreation (Treves & Karanth 2003; Woodroffe, Thirgood & Rabinowitz 2005b). Such disagreements can develop into acute incidents or chronic conflict when the species involved have economic or social value and/or are protected by law (Graham *et al.* 2011; O'Rourke 2014), making management or mitigation challenging. Ecology can be applied to uncover the scale of the problem (Redpath *et al.* 2013), the proximate and ultimate drivers underlying the impact (Artelle *et al.* 2016) and the efficacy of potential mitigation measures (Redpath, Thirgood & Leckie 2001; Treves, Krofel & McManus 2016).

In recent decades there has been a shift in predator management from general reductions in predator populations to targeting problem individuals (Treves & Naughton-Treves 2005; Doherty & Ritchie 2016). This trend can be seen as a compromise, made by wildlife practitioners, to balance the benefits of healthy predator populations with their potential impacts. The underlying assumption of such 'selective management' is that, within wildlife populations, individual animals are responsible for a disproportionately large negative impact on human interests (Linnell *et al.* 1999; Swan *et al.* 2017). Impacted stakeholders often perceive a subset of 'problem' individuals to be the perpetrators of wildlife damage (Kenward 2002; Viñuela & Arroyo 2002), but this is rarely addressed scientifically (Linnell 2011), in part due to the difficulties of collecting individual-specific data on the behaviour or diet of wild predators (Linnell *et al.* 1999; Bentzen, Shideler & O'Hara 2014).

Conflicts over buzzard predation

The predation of game species by birds of prey has created a number of conservation conflicts (Valkama *et al.* 2005). Hunters have identified the common buzzard *Buteo buteo* (hereafter buzzard) as second only to the goshawk *Accipiter gentilis* in their negative impact upon quarry species (Kenward 2002). This is especially true in the U.K., where a rapid increase in buzzard abundance and range (Musgrove *et al.* 2013), coupled with declining returns of released game (Bicknell *et al.* 2010), has caused a dispute between game shooting interests and conservation organisations over how buzzards should be managed (Lees, Newton & Balmford 2013; Parrott 2015). This manifests itself most clearly in illegal behaviour and buzzards routinely rank highly in confirmed instances of illegal shooting and trapping of birds of prey (RSPB 2012 - 2015). Indeed, research on radio-tagged buzzards by Kenward *et al.* (2000) estimated that shooting and poisoning accounted for 24% of the 50 deaths in their study population..

Solutions to both the conflict and illegal behaviour are currently being sought by different means. Conservation groups have requested tougher enforcement and penalties for those that break the law while, in stark contrast, landowners and gamekeepers have made repeated calls to be granted licences for lethal control (Parrott 2015). These requests focus on a subset of pheasant *Phasianus colchicus* release pens where gamekeepers perceive high losses due to a small number of 'problem buzzards' that are thought to be disproportionately responsible for depredation (Kenward 2002; Parrott 2015). In 2016, the first licences were issued in England to permit buzzards to be shot to protect released pheasants "*where individual behaviour indicates a risk of serious damage*" (Natural England 2016c). This development has occurred with little ecological evidence that 'problem buzzards' exist (Parrott 2015). In order to mitigate this conflict, and advise future policy, evidence is needed on the ecology of such birds and the potential efficacy of their removal.

Analysis of variation in the abundance of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in animal tissues represents a particularly powerful tool for researching 'problem individuals' in animal populations (Swan *et al.* 2017). The development of Bayesian stable isotope mixing models (BSIMMs) has increased the accuracy of this approach (Phillips *et al.* 2014) by providing quantitative estimates of diet composition, while incorporating multiple sources of uncertainty in the system (Phillips *et al.* 2014). By applying stable isotope analysis to investigate the impact of wildlife upon human interests, ecologists have also been able to generate data on the involvement of specific animals in impacts that are usually difficult to observe, such as crop raiding or livestock depredation (Cerling *et al.* 2006; Bentzen, Shideler & O'Hara 2014; Loudon *et al.* 2014; Voigt *et al.* 2014; Ditmer *et al.* 2016). Recent research using buzzards as a model species has shown that dietary estimates derived from BSIMMs can produce similar estimates to those from direct observations (Chapter 3). Therefore, in this chapter, I analyse the stable isotope ratios of buzzard feathers and blood as well as their putative dietary sources and use this information to address two questions:

(i) Do certain pheasant release pens suffer consistently higher levels of predation by buzzards?

(ii) Is there evidence consistent with the existence of 'problem buzzards' and the possible efficacy of managing the problems they cause?

Methods

Study area

The study was conducted between May and September 2015 across three study sites in Cornwall, in the southwest of the U.K. (50.35°N, 4.85°W). Habitat across all sites was predominantly arable and pastoral farmland, interspersed with areas of broadleaf woodland. Buzzard territories were mapped by locating active nests during April and May. An approximate core territory was established around each nest using half the mean nearest neighbour distance as a radius. A single nest was excluded from this calculation, as I could not be certain that the neighbouring nests had been located. Thiessen polygons were created where core territories overlapped, as territorial buzzards do not share hunting areas (Prytherch 2013).

All three study sites were centred on shooting estates releasing > 10,000 pheasants for shooting each year. The locations of 18 pheasant release pens were recorded. Pens were on average 16,000 m^2 and surrounded by wire-mesh ~2m high to prevent access by terrestrial predators. Pheasant 'poults' aged 5-7 weeks were released into pens during late June – July. Poults' wings were clipped to prevent initial escape. Dispersal from pens began in late August – September, once flight feathers had developed.

Sampling adult buzzards

Adult buzzard tissue was sampled from moulted feathers collected opportunistically from June to August within the core territories. Prior to being stored at -80ºC, all feathers were cleaned with deionised water to remove all surface contaminants. The use of moulted feathers is a common non-invasive way of sampling the tissue of birds (Inger & Bearhop 2008). As feathers are metabolically inert, isotopic information regarding diet (at the time of assimilation) is stored in the keratin (Inger & Bearhop 2008). Adult buzzards undergo an unpredictable partial moult every year, typically starting when nestlings are three weeks old and lasting until November (Zuberogoitia *et al.* 2005; Hardey *et al.* 2013). Consequently, moulted feathers from adults can be seen as representing diet during the previous two summers. In the southwest of England the period of heaviest moult in flight feathers (primaries, secondaries and tail feathers) occurs from the end of June through July (Dare 2015); coinciding with the period of highest pheasant losses (Allen *et al.* 2000; Kenward *et al.* 2001). Alongside these large flight feathers, I collected and analysed smaller body feathers for which the moulting (and assimilation) period is rarely reported, and therefore more uncertain. Although moulted feathers were from unknown individuals, I assume that they reflect dietary information from the pair of adults holding the core territories in which they were collected. This is because adult buzzards are strongly territorial and have low (< 12%) annual mortality (Kenward *et al.* 2000; Walls & Kenward 2001; Prytherch 2013).

Sampling buzzard nestlings

I sampled the blood and feather tissue of buzzard nestlings in the two weeks immediately preceding the pheasant releases. Thus, the tissue of buzzard nestlings effectively allows us to run a null model to check how much of the dietary variation in buzzard chicks the models would erroneously attribute to consumption of released pheasants. Approximately 0.2 ml of blood and the tips of four back feathers were sampled. The turnover rate of blood cells, plasma and the age-class at which natal down is replaced by body feathers means blood and feathers represent nestling diets during the rearing period (Hobson & Clark 1993; Bearhop *et al.* 2000). Blood samples were immediately put on ice before being separated into plasma and red blood cells and frozen at -80ºC.

Identifying predation problems and sampling 'problem buzzards'

To classify territories encompassing a release pen with a perceived predation problem I asked gamekeepers to identify release pens where they perceived persistent buzzard predation of released pheasants. To characterise the signature of 'problem buzzards', I trapped buzzards, in or around (< 10m) the problem pens using spring-net traps placed on fresh poult kills, without pre-baiting. Blood and feather tissue from adult buzzards was sampled following the same procedure used for nestlings.

Sampling buzzard food

To characterise the main dietary sources of buzzards, muscle tissue was collected from all fresh dietary items found within the nest cup during the nesting period (May - July). Dietary sources encompassed all prey groups recorded as > 5% of diet in Chapter 3. Additional tissue was sampled from the carcasses of released pheasant predated by buzzards within pens (July – August). Only dietary sources utilised during the moulting period (Spring – Autumn) were included. For example, although earthworms are an important food source in the winter (Stubing, 1995; Dietrich *et al.* 1995; Tubbs 1975), their contribution during the breeding period is thought to be negligible (Rooney *et al.* 2013; Chapter 3). For each sample, approximately 0.1cm^3 of muscle was removed using a scalpel and tweezers. Tissue samples were immediately put on ice, before being stored at -80^{o}C.

Quantifying the contribution of a single food source using stable isotope analysis requires that source to be isotopically distinct from others. In this context, an investigation of buzzard predation of released pheasants may be aided by the widespread provision to poults of processed gamebird feed, that increases the likelihood of released pheasants being isotopically distinct from other 'natural' food sources for buzzards.

All animal procedures used in this study were conducted under the U.K. Home Office project licence #30/3274 and conformed with the U.K. Animals (Scientific Procedures) Act, 1986. All research received prior ethical approval from the University of Exeter Animal Welfare and Ethics Committee. Animals were handled by trained and experienced personnel under further licences from both the British Trust for Ornithology (CO/6164) and Natural England (2015-7805-SCI-SCI).

Stable isotope analysis

Prior to analysis, feather, plasma, red blood cells from buzzards and muscle tissue from food items were placed in a freeze drier for > 48 hours. Samples were then homogenised using a mortar and pestle (blood and muscle) or scissors (feathers) and ~0.7mg was weighed into a 6 x 4mm tin cup. Stable isotope analysis was conducted using a Sercon Integra Elemental Analysis Isotope Ratio Mass Spectrometer (EA-IRMS) at the University of Exeter and a Sercon 2020 EA-IRMS at Elemtex Ltd, Callington (Cornwall). Tissues were analysed for carbon, ^{13}C, and nitrogen, ^{15}N, isotopes. Carbon and nitrogen isotope ratios are expressed in δ notation in per mil units following the equation:

$$\delta X = [(R_{sample} \ / \ R_{standard}) - 1] \times 1{,}000$$

where X = ^{15}N or ^{13}C, R_{sample} is the heavy to light isotope ratio derived from the sample, and $R_{standard}$ is the heavy to light isotope ratio derived from the Vienna Pee Dee Belemnite (VPBD) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$ using an in-house laboratory standard of alanine (DeNiro & Epstein 1978).

Statistical analysis

Characterising isotopic ratios of buzzard dietary items

To assign prey species into isotopically similar dietary categories, I first grouped all samples by species (or lowest taxonomic equivalent) then used an *a posteriori* approach where the $\delta^{15}N$ and $\delta^{13}C$ values of these groups were tested for equality of means and combined when they were similar (Phillips et al., 2014). This was achieved by fitting one-way ANOVAs and Tukey's post hoc multiple comparisons (where α = 0.05). Released and 'wild' pheasants were kept as separate dietary items as they had distinct isotopic signatures. Once dietary items had been grouped, linear models were fitted with $\delta^{15}N$ or $\delta^{13}C$ as the response and the prey sources as the predictor. In these models 'released pheasant' was set as the intercept to assess the statistical significance of this dietary item relative to the other groupings.

To test my assumption that moulted adult feathers were all assimilated over the same time period, feathers were checked for significant differences in isotopic ratios between feather types by fitting one-way ANOVA and Tukey's post hoc tests for both $\delta^{15}N$ and $\delta^{13}C$. To examine the relationship between adult and nestling feathers, I investigated variation in mean $\delta^{15}N$ and $\delta^{13}C$ signatures of feathers from nestlings and adults from the same nest using linear regression. Adult feathers were collected during the same field season as the nestling feathers, though adult feathers had been assimilated during the previous moult (2013 - 2014).

Buzzard dietary composition

In order to quantify the relative contributions of the various food sources to buzzard diet, I applied Bayesian isotope mixing models using the SIMMR package in R (formerly SIAR; Parnell & Inger 2016; Parnell et al. 2010). All models included the mean and standard deviation of $\delta^{15}N$ and $\delta^{13}C$ for each prey category. Trophic discrimination factors (TDFs) (feather: 2.37 ± 1.49 ‰ for $\delta^{13}C$ and 2.79 ± 1.03 ‰ for $\delta^{15}N$, blood: 1.51 ± 1.46 ‰ for $\delta^{13}C$ and 2.35 ± 0.99 ‰ for $\delta^{15}N$) were derived using the SIDER package in R (Healy *et al.* 2016). To provide a broad overview of buzzard diet, population-level models were run separately for all adult feathers and for the feathers and blood of 'problem buzzards' caught in pheasant release pens. I then ran models using the same inputs for nestling blood and feather tissue. Within nestling models, released pheasant (unavailable to nestlings during tissue assimilation) was kept as a dietary source to examine the proportion of diet the mixing model would erroneously attribute to this source. This 'null' measure allows an estimate of confidence when compared to values obtained from adult tissue. The population-level models for blood tissue included both red blood cells and blood plasma as repeat samples for each buzzard to increase model power. For all models, three parallel MCMC chains were run for 100,000 iterations with a thinning rate of 10 (the first 50,000 iterations excluded as a burn-in). I extracted posterior samples of 10,000 iterations when the Gelman and Rubin convergence diagnostic for all sources was 1 (Gelman & Rubin 1992). Mean values are presented as mean ± SD unless otherwise stated.

Comparing estimates of released pheasant consumption

Variation in released pheasant consumption was analysed by extracting the model posterior estimates and their distributions were compared across ages and tissues using the Bhattacharyya Coefficient (BC) as a measure of distribution overlap (Bhattacharyya 1946; Kailath 1967).

$$\mathrm{BC} = \int \sqrt{p_1\,(x)\,p_2\,(x)\,dx}$$

where p_1 and p_2 are the two distributions to be compared. BC = 0 indicates no overlap and 1 indicates complete similarity (Kailath 1967). Catry *et al.* (2009), Bond and Diamond (2011), Lavoie *et al.* (2012) and Jardine *et al.* (2015) have previously considered a BC of > 0.6 to represent a significant overlap in the distributions of dietary sources. Here, we use BC to evaluate variation between dietary estimates but do not infer statistical significance from this value. I also calculated the probability that the estimate from one BSIMM is less than the estimate from its comparison by subtracting all the values in one posterior from their comparison and giving the percentage of these values under 0.

I then ran separate BSIMMs for each tissue sample using the SIMMRsolo function. Constraining the models to single samples increases the uncertainty of estimates (Parnell *et al.* 2010), but this approach allows us to explore within-population variation in released pheasant consumption. For each model, the mean estimate of ‘released pheasant’ consumption was extracted from the posterior distribution for further analysis.

Do certain release pens suffer consistently higher levels of pheasant predation?

To investigate whether buzzards living in territories where significant predation had been perceived by gamekeepers, ate more released pheasants than in other territories, I applied generalised linear mixed models (GLMMs) using the lme4 package in R (Bates *et al.* 2015). In these models, the response variable was the estimated proportion of released pheasant in the individual’s diet and the explanatory variable, ‘territory category’ was a three-level factor where territories were identified as having (i) no release pen (ii) a release pen with no perceived problems or (iii) a release pen with perceived problems. As the response variable was a non-normally distributed proportion it was logit-transformed (Warton & Hui 2011). A binary variable ‘age’ (nestling or adult) was included as an interaction with ‘territory category’ to account for the difference in pheasant poult availability when buzzard nestling samples were taken. A further binary variable, ‘feather type’ was included to identify those feathers for which the moulting period, and therefore assimilation time, was uncertain (Zuberogoitia *et al.* 2005; Hardey *et al.* 2013; Dare 2015). In this model, study site was included as a fixed effect to account for any variation between study sites, and buzzard territory was included as a random effect to account for repeated sampling of birds from a single territory. Model selection was conducted on fitted models using maximum likelihood. For the most parsimonious model, post hoc comparisons between the ‘territory category’ factor levels were made by calculating least-squares means, with Satterthwaite’s approximation for degrees of freedom, using the lsmeans and lmerTest R packages (Bates *et al.* 2015; Lenth 2016). For GLMMs I present the proportion of variance explained by the fixed effects as the marginal R^2 (Nakagawa & Schielzeth 2013).

Is there evidence to support the existence of ‘problem buzzards’?

Finally, I conducted an analysis to explore the diet of a small sample of ‘problem buzzards’, i.e. those that had been caught in release pens, where gamekeepers identified significant buzzard predation, against the wider population. I applied a GLMM, in which the response variable was the proportion of released pheasant poult in diet (logit-transformed) and the explanatory variable was ‘problem buzzard’. Age, site and buzzard territory were included as above. To examine where the dietary estimates of poult consumption from the tissue samples of the ‘problem buzzards’ sit in the distribution of the broader population, I applied one-sample t-tests with a pooled variance estimate. I present *P* values corrected for the False Discovery Rate to control for multiple comparisons (Benjamini & Hochberg 1995). All analyses were conducted using R (v3.2.2) (R Core Team 2016).

Results

A total of 37 active buzzard nests were located during the breeding season and territories were determined for 36. The mean nearest neighbour distance between nests was 689 m (± 201 m). Core territories were therefore approximated as a 345 m radius around the nest site. Moulted feather samples were collected in 33 of 37 territories (Table 4.1). Sixteen of these 33 buzzard territories contained at least one active pheasant release pen within their core territory. The sites included eighteen pheasant release pens, of which five (28%), were identified by gamekeepers as having a persistent problem with buzzard predation. Six buzzard territories encompassed part or all of these five pens and so were categorised as territories with 'release pen with problems'. The mean distance from the nest to the pen in these territories was 94 m (± 118 m). The 10 territories that encompassed part or all of the 13 pens where buzzard predation was not perceived to be a problem were categorised as territories with 'release pen with no problems'. The mean distance from nest to pen in these territories was 161 m (± 141 m). There were a further 17 territories with 'no release pen', where the mean distance to the nearest pen, which was outside the territory, was 1152 m (± 653 m).

Characterising isotopic ratios of buzzard dietary items

A total of 79 muscle samples from buzzard prey were collected and analysed (Appendix 9). Dietary items were grouped into broader, functionally equivalent, categories if their isotopic ratios were similar. This resulted in the grouping of rabbits with small rodents, corvids with shrews and moles, and frogs and toads. As the hypotheses were concerned with losses of released pheasants in and around release pens, I subdivided pheasants into 'wild' (not released that year) and 'released' (released that year). This process resulted in five major dietary categories represented in the models (Table 4.1). Overall, there were significant differences between these dietary sources in δ^{13}C (one-way ANOVA: $F_{4,74}$ = 12.3, $P < 0.001$) and δ^{15}N (one-way ANOVA: $F_{4,74}$ = 48.7, $P < 0.001$). Post-hoc testing revealed that the isotopic ratios of released pheasant tissue differed significantly from those of all other dietary sources, including wild gamebirds, for at least one of δ^{13}C or δ^{15}N (Appendix 10).

Table 4.1: *Isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$ ‰) of common buzzards and five buzzard food groups. Isotope ratios are mean ± SD. The isotopic ratios of dietary categories are from muscle tissue collected from buzzard nests. Additional tissue was sampled opportunistically for frogs, toads and released pheasants.*

Food source	**$\delta^{15}N$**	**$\delta^{13}C$**	**Territories *n***	**Buzzards *n***	**Tissue samples *n***
Adult buzzards					
Feather	9.47 ± 1.11	-24.09 ± 1.03	33	-	86
Red blood cells	7.81 ± 0.89	-24.87 ± 0.71	4	4	4
Blood plasma	7.90 ± 0.76	-25.54 ± 0.82	4	4	4
Nestling buzzards					
Feather	8.94 ± 1.21	-25.57 ± 0.93	27	42	42
Red blood cells	7.71 ± 1.03	-26.64 ± 0.87	26	41	41
Blood plasma	8.50 ± 1.01	-27.35 ± 0.88	26	41	41
Dietary categories					
Rabbits & small rodents	5.31 ± 2.29	-28.58 ± 1.04	-	-	41
Shrews, moles & corvids	8.84 ± 1.59	-25.44 ± 0.92	-	-	12
Amphibians	6.25 ± 1.47	-26.54 ± 0.44	-	-	7
Wild pheasants	6.45 ± 0.69	-24.34 ± 1.94	-	-	8
Released pheasants	3.78 ± 0.42	-25.57 ± 0.11	-	-	11

Notes: Further information on the composition of the dietary sources can be found in Appendix 9.

Characterising isotopic ratios of buzzards

The majority of $\delta^{13}C$ and $\delta^{15}N$ values observed within the sampled buzzards (Table 4.1) fell within the range of the sampled dietary sources (Phillips *et al.* 2014) (Figure 4.1). For moulted adult feathers, no statistically significant variation was observed between feather types in either $\delta^{15}N$ or $\delta^{13}C$. When the isotopic ratios of adult feathers (assimilated 2013 or 2014) were compared to those from nestlings (assimilated 2015) in the same territory (n = 26) a significant relationship was observed in $\delta^{15}N$ ($F_{1,24}$ = 4.5, R^2 = 0.16, P = 0.043) suggesting that between years the adult buzzards were feeding on, and provisioning, prey at the same trophic level. No relationship was observed when the same analysis was conducted for $\delta^{13}C$ suggesting that, within territory, habitat use might vary between years ($F_{1,24}$ = 1.2, R^2 = 0.01, P = 0.284).

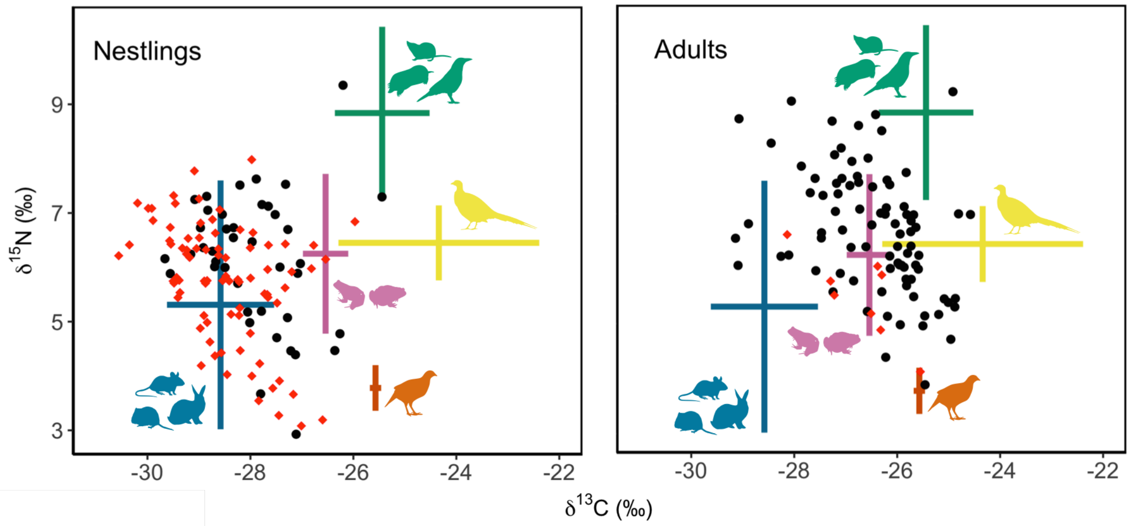


Figure 4.1: *Isotopic values ($\delta^{15}N$ and $\delta^{13}C$) from the feathers (black points) and red blood cells and blood plasma (red points) of common buzzards and their putative food sources (mean ± SD) in Cornwall, southwest England.*

Colours represent food sources: rabbits and small rodents (blue), shrews, moles and corvids (green), amphibians (pink), wild pheasants (yellow) and released pheasants (orange). Stable isotope ratios of buzzards are corrected by trophic discrimination factors derived from the SIDER package: (feather: 2.37 ‰ for $\delta^{13}C$ and 2.79 ‰ for $\delta^{15}N$, blood: 1.51 ‰ for $\delta^{13}C$ and 2.35 ‰ for $\delta^{15}N$).

Relative composition of prey in buzzard diet

Rabbits and small rodents were the most commonly consumed food source for buzzard nestlings (dietary proportion from feathers: 0.58 ± 0.06, blood: 0.68 ± 0.04) (Appendix 11). The model of nestling diet erroneously attributed only 0.05 (± 0.03) and 0.04 (± 0.03) of the diet to the consumption of released pheasants (which were unavailable when tissue was assimilated and sampled) for feather and blood respectively. For adult buzzards, dietary estimates based on the analysis of 79 adult buzzard feathers from territories with non-problem release pens, suggest a more generalised diet than nestlings where rabbits and small rodents (0.25 ± 0.07), shrews, moles and corvids (0.33 ± 0.07) and amphibians (0.24 ± 0.15) are all of importance. Although the consumption of released pheasants by adult buzzards was feasible, models suggested there was only a 3% increase in the estimated contribution of released pheasant (total = 0.08 ± 0.04) when compared to nestling diet.

When models were run using tissue from the four ‘problem buzzards’ that had been caught within release pens where gamekeepers had perceived a problem with predation, a generalist diet was still observed. However, there was an increase in the importance of released pheasant (feathers: 0.18 ± 0.11, blood: 0.26 ± 0.12) in diet, when compared to other adult buzzards and to nestlings (Appendix 11).

Further investigation of the posterior distributions for ‘released pheasant’ in diet, through pair-wise comparisons between different models, produced probability estimates for observed differences as well as similarity indexes for their distributions (Table 4.2). The blood and feathers of ‘problem buzzards’ produced posteriors for released pheasant that had the least overlap and highest estimated contribution when compared to posteriors from analysing other buzzard tissue (Table 4.2; Figure 4.2). In other words, the feathers and blood of ‘problem buzzards’ produced distinct posteriors that suggested a high consumption of released pheasants.

Table 4.2. *Comparison of estimates of released pheasant consumption by buzzard nestlings from Bayesian Stable Isotope Mixing Models (BSIMMs) using different tissues. The probability (%) that the mean from one BSIMM is less than the mean from its comparison is presented as well a similarity index of the two posteriors. Similarity was assessed by Bhattacharyya's coefficient (BC) of paired distribution comparisons for released pheasant. BC values fall between 0 (no similarity) and 1 (complete similarity).*

BSIMM 1	**BSIMM 2**	**Probability BSIMM1 < BSIMM2**	**Bhattacharyya's coefficient**
Problem buzzard blood	Nestling blood	2.1%	0.313
Problem buzzard blood	Nestling feathers	3.8%	0.408
Problem buzzard feathers	Nestling blood	6.3%	0.522
Problem buzzard blood	Non-problem buzzard feathers	7.7%	0.528
Problem buzzard feathers	Nestling feathers	11.8%	0.642
Problem buzzard feathers	Non-problem buzzard feathers	20.1%	0.769
Problem buzzard blood	Problem buzzard feathers	30.7%	0.939
Nestling blood	Nestling feathers	64.1%	0.963
Non-problem buzzard feathers	Nestling feathers	32.4%	0.946
Non-problem buzzard feathers	Nestling blood	20.5%	0.835

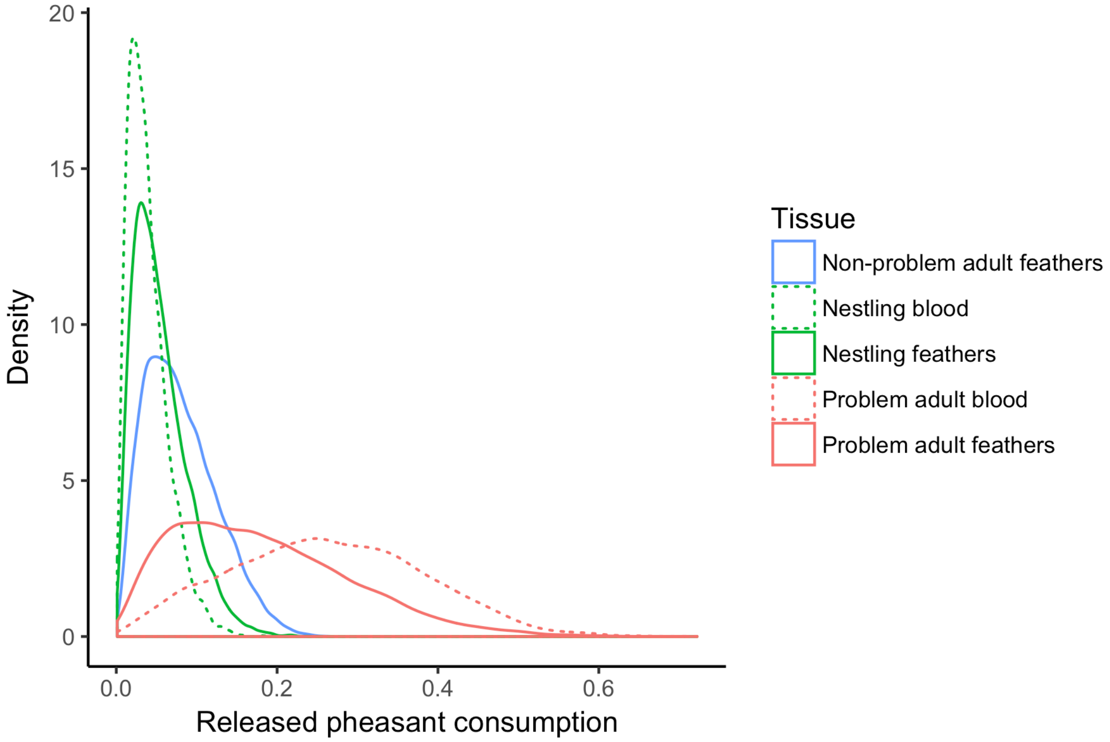


Figure 4.2*: Estimated proportional consumption of released pheasants by nestling, non-problem and problem buzzards from BSIMMs. Proportion of diet was inferred from stable isotope analysis of blood and feathers (10000 model iterations).*

There was no significant effect of 'feather type' on released pheasant consumption ($\mathcal{X}^2_{1,117}$ = 0.25, *P* = 0.62; Appendix 12) and so feather type was removed from further analysis. A significant reduction in the goodness of model fit was observed when the interaction between territory category and age was removed ($\mathcal{X}^2_{1,118}$ = 8.80, *P* = 0.012; Appendix 12). For adult buzzards, estimates of the importance of released pheasant in diet were significantly greater in territories with release pens with perceived problems than in territories with no release pens (Post-hoc comparison test: Estimate = -0.047, SE = 0.017, *t ratio* $_{23.1}$= -2.77, *P* = 0.028). Territories with a release pen but no perceived problem did not have statistically different levels of poult consumption when compared to other types of territories (Figure 4.3; Appendix 13).

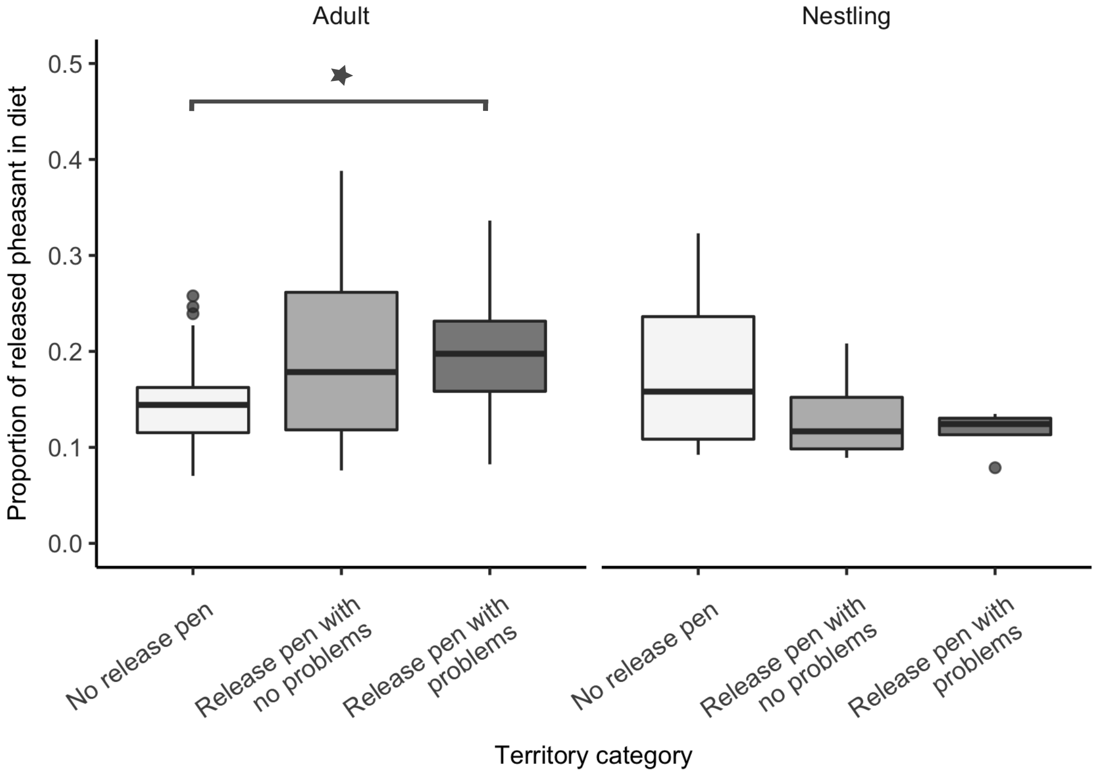


Figure 4.3: *Variation in the estimated proportion of released pheasant poults in buzzard diet between buzzard territories categorised by perceived problems of poult predation. Buzzard territories are those with no pheasant release pen (adults: n = 17; nestlings: n = 17), those with a release pen with no buzzard predation problems (adults: n = 10; nestlings: n = 5) and those with a release pen where buzzard predation problems were perceived by gamekeepers to be significant (adults: n = 6; nestlings: n = 5). Proportions of released pheasants in buzzard diets are estimated from stable isotope analysis of tissues of buzzards and their putative prey and by Bayesian stable isotope mixing models. Adult buzzards in a territory with a problem release pen exhibited a higher proportion of released pheasants in their diets than buzzards in territories with no release pen. The comparison marked with a star indicates a significant difference (P = 0.028).*

There was a significant interaction between ‘problem buzzard’ and tissue type ($\mathcal{X}^2_{1,207}$ = 6.45, R^2 = 0.45, P = 0.040). This interaction was largely a function of ‘problem buzzard’ blood plasma exhibiting signatures indicative of significantly higher levels of poult consumption (Estimate = 0.478, SE = 0.188, $t_{183.9}$ = 2.53, P = 0.012) (Figure 4.4; Appendix 14), in line with predictions given the time periods over which the different tissue types integrate dietary information.

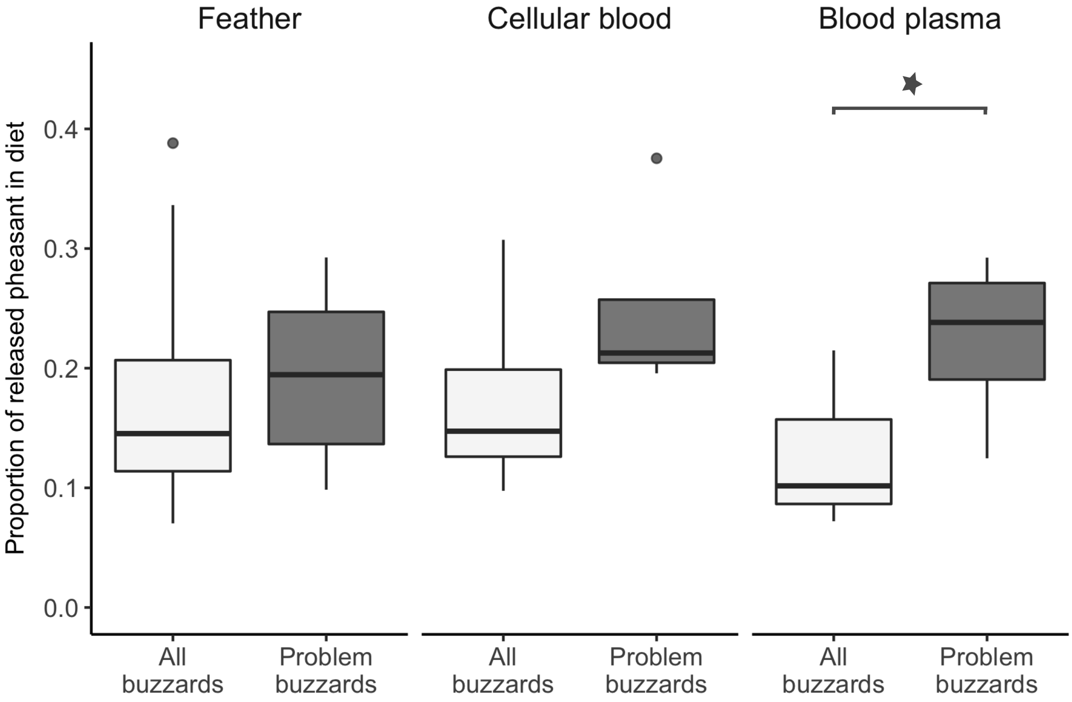


Figure 4.4: *Variation in the estimated proportions of released pheasant poults in the diets of 'problem buzzards' trapped in pheasant release pens and other buzzards. Proportions of released pheasants in buzzard diets are estimated from Bayesian stable isotope mixing models based on stable isotope analysis of three tissue types from buzzards (feather n = 35, cellular blood n = 28 and blood plasma, n = 28) and of their putative prey. The comparison marked with a star indicates a significant difference (P = 0.012), based on post-hoc comparisons, based on differences between least-squares means, after fitting a linear mixed effects model.*

When the different tissues of the 'problem buzzards' were analysed individually, the consumption of pheasant poults estimated from buzzard feathers did not differ significant from the wider population (Table 4.3; Figure 4.5). One bird (B) produced a significantly higher estimate of pheasant consumption for both red blood cells (t = -2.927, df = 40, P_{FDR} = 0.020) and blood plasma (t = -2.891, df = 40, P_{FDR} = 0.024) and another bird (D) produced a significantly higher estimate for blood plasma (t = -2.537, df = 40, P_{FDR} = 0.030).

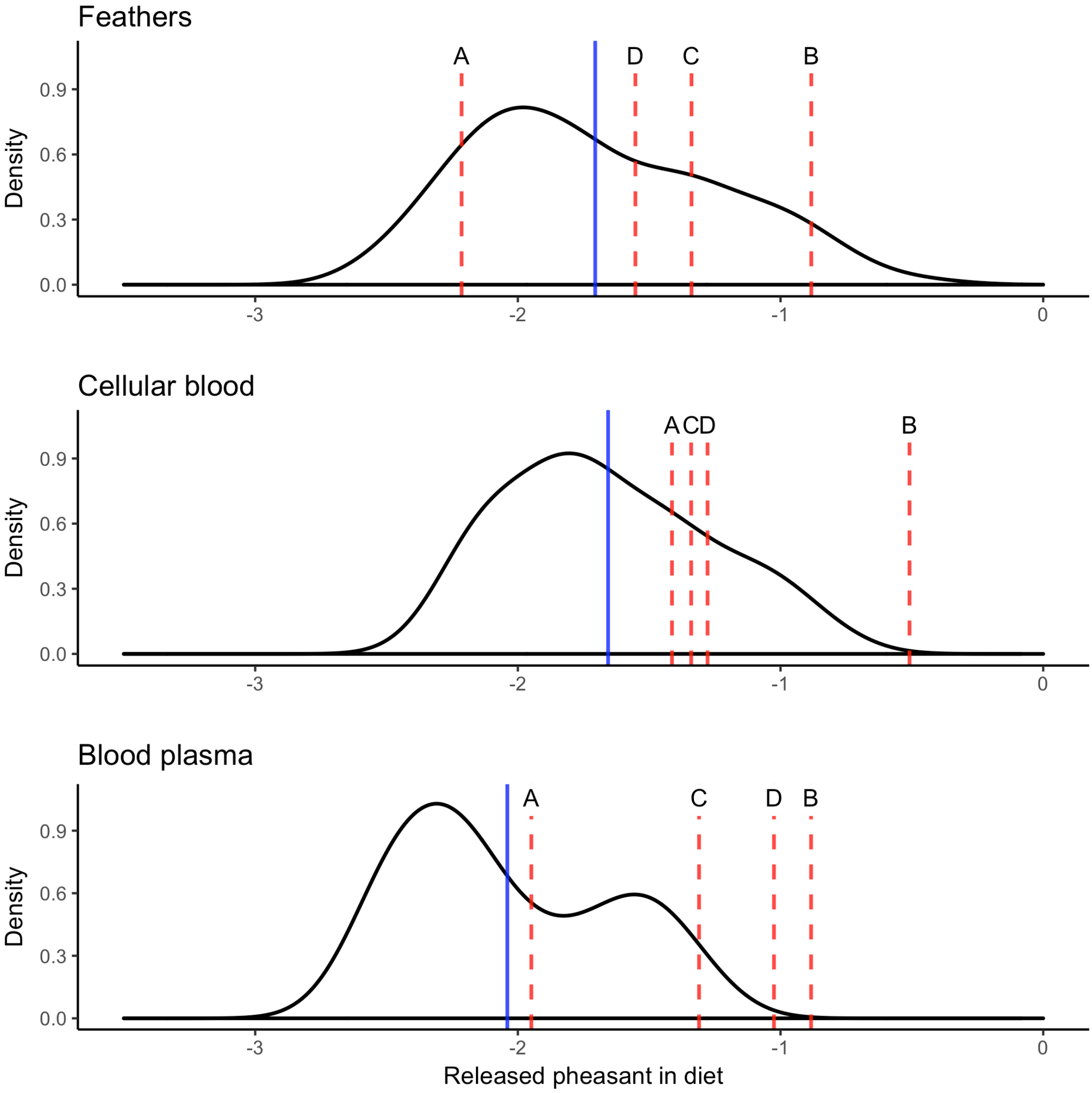


Figure 4.5: *Distribution of individual-level stable isotope mixing model estimates for the proportion of released pheasant in diet (logit-transformed). The mean of all non-problem buzzards (blue line) and the estimates for the four 'problem buzzards' (A: D) (red dashed lines) are shown.*

Table 4.3: *Results of one-sample t-test analysis comparing dietary estimates from 'problem buzzards' against those of non-problem buzzards.* P_{FDR} *denotes the P value corrected for False Discovery Rate due to multiple comparisons.*

Buzzard	Feathers			Red blood cells			Blood plasma		
	t value	*P* value	*P* FDR	*t* value	*P* value	*P* FDR	*t* value	*P* value	*P* FDR
A	1.107	0.271	0.542	-0.620	0.538	0.538	-0.238	0.821	0.821
B	-1.724	0.087	0.348	**-2.927**	**0.005**	**0.020**	**-2.891**	**0.006**	**0.024**
C	-0.754	0.452	0.603	-0.807	0.425	0.538	-1.824	0.076	0.101
D	-0.300	0.765	0.765	-0.966	0.340	0.538	**-2.537**	**0.015**	**0.030**

Discussion

For selective management to be effective in mitigating the impact of wildlife on human interests, the targeted subset of the animal population must be disproportionately responsible for these impacts (Linnell *et al.* 1999; Swan *et al.* 2017). The existence of this subset of 'problem' animals is central to current disputes and contested practices in relation to buzzard management in the U.K. (Parrott 2015). Using the stable isotope ratios of buzzard feathers and blood, this study has explored variation in consumption of released pheasants and provides three main strands of evidence. First, although the effect size was small, buzzards living in territories where gamekeepers identified a problem with buzzard predation consumed more released pheasants than those with no pheasant release pens in their territories, but did not consume any more pheasant than buzzards in territories with release pens that were not thought to experience problems. Second, three of the four buzzards caught within pheasant release pens, where gamekeepers had identified a problem, produced higher estimates of released pheasant consumption than other buzzards (two of which were statistically significant). Third, by analysing tissues assimilated over different time periods, there is some, limited evidence that individual buzzards caught in pens can be identified as frequent, recent consumers of released pheasants.

Dietary information from the preceding two years, stored in the metabolically inert keratin of buzzard feathers (Zuberogoitia *et al.* 2005; Inger & Bearhop 2008), identified significantly higher levels of released pheasant consumption in 'problem territories' relative to those territories without pens. This result supports the findings of Kenward *et al.* (2001) who observed a strong correlation in the number of pheasant depredation events between the two years of their study. My analysis did not find a significant difference between territories encompassing a release pen with problems and those encompassing a release pen with no problems. Instead, consumption of released pheasants in territories with a release pen with no problems was highly variable (Figure 4.3), raising the possibility that, alongside foraging specialisations, there was a highly variable opportunistic component to buzzard consumption of pheasants.

There is an alternative explanation as to why buzzards with territories encompassing pheasant release pens might produce higher estimates of released pheasant in diet; that the isotopic ratios of released pheasants are being assimilated indirectly though other prey due to changes to the 'iso-scape' around pheasant pens after annual release of gamebirds. Similar pathways have been documented in natural systems, such as the transfer of nutrients from immigrant Pacific salmon *Oncorhynchus spp.* into riparian ecosystems (Naiman *et al.* 2002). However, were this the case, I would have expected to see the results from nestling tissues (for whom direct consumption of released pheasants was not possible) to mimic the significant effects observed in the adult tissue.

Making statistical inferences about a foraging behaviour that is rarely expressed in a population is difficult as, by definition, I am measuring the behaviour of a small minority of distinctive individuals (Cerling *et al.* 2006; Yeakel *et al.* 2009; Graham *et al.* 2011). However, there is evidence to suggest that buzzards that consistently kill and eat released pheasants are such a distinctive subset of the population. In their study of 136 radio tagged buzzards in Dorset, U.K., Kenward *et al.* (2001: p813) observed that only 11 buzzards (8%) had "*significantly more association than other buzzards with pheasant pens*". Thus, while my sample of 'problem birds' is small, it represents an important opportunity to explore the rare expression of this behaviour, particularly as I was able to collect multiple tissue samples from each individual, each containing dietary information reflecting different time periods. When analysed as individual samples, feather tissue, grown over the preceding two summers (Dare 2015), did not suggest that released pheasants had been an important food source for these birds. Red blood cells identified a single buzzard (B; Figure 4.5, Table 4.3) as having particularly high poult consumption over the preceding weeks (Hobson & Clark 1993; Bearhop *et al.*

2002), though the greatest level of poult consumption, relative to the wider population could be observed in samples of blood plasma, where two problem individuals were distinguishable (Buzzards B & D; Figure 4.5, Table 4.3). The other two 'problem' buzzards trapped in pens did not produce significant results for any of the three tissue types, suggesting that their utilisation of poults in the pens was either a very recent development or pheasants contributed little to their overall diet (Hobson & Clark 1993; Bearhop *et al.* 2002). Given the small sample size of buzzards caught inside pheasant release pens it is not possible to draw firm conclusions on the prevalence or ecological correlates of 'problem buzzards'. However, these results do provide provisional support for individual behavioural variation playing a role in this conflict.

Using dietary stable isotope analysis to explore human-wildlife impact

I have shown how stable isotope analytical approaches can be applied to quantify the contribution of released pheasant poults to the diet of buzzards. By analysing the isotopic ratios of adult buzzard tissue I was able to explore their feeding ecology outside the nestling rearing period (Kenward *et al.* 2001), without the biases of alternative indirect methods associated with prey handling and digestibility that could potentially overestimate the frequency of predation of gamebirds (Francksen, Whittingham & Baines 2016).

Analysis of the isotopic ratios of the five food sources included in all BSIMMs provided clear evidence that the tissue of released pheasant poults is isotopically distinct from other buzzard foods. The ability of the models to provide separate dietary estimates for both wild and released pheasants makes this study a rare example of dietary isotope analysis that is able to discriminate among life stages within a species. However, the limitations of this study merit discussion. Primarily, the results presented here are relative dietary proportions that have not been converted into rates of predation. In other words, I have shown how important consumption of pheasants is to buzzards, but not how important consumption by buzzards is to pheasants.

Stable isotope analysis can provide valuable insights into resource depletion (Inger *et al.* 2006), however, in order to ascertain how depredation affects the number of gamebirds available to harvest, further data would be required. This includes the proportion of pheasants scavenged against those actively hunted and the extent to which predation is additive to other losses (Kenward *et al.* 2001).

Management implications

The presence of ‘problem buzzards’ was recently identified as a key knowledge gap in the debate over buzzard management (Parrott 2015). In response to licensing requests from those who perceive they are impacted, policy has allowed selective lethal control when impact was deemed to be severe. To date, such licences have included requirements that lethal control be targeted only at buzzards caught in release pens (Natural England 2016c; d; e). My results provide tentative evidence to support this approach, suggesting that some, but not all, of those individuals caught within pens are likely to be problem individuals expressing high levels of poult consumption, relative to the wider population.

For licencing authorities, this form of spatially and temporally concentrated, selective removal might represent a pragmatic solution to complaints about predation. In northern Scotland, a similar management strategy directed at ‘rogue seals’ (*Phoca vitulina* and *Halichoerus gypus*) has created a workable compromise between various stakeholders (Graham *et al.* 2011). Such targeted management, if undertaken at a small scale, is unlikely to threaten the conservation status of buzzards and the large number of non-breeding ‘floaters’ in the population suggests that birds will quickly be replaced (Kenward *et al.* 2000). However, little is known about the effects of culling raptor populations (Viñuela & Arroyo 2002) or the time-period over which benefits will be felt (Parrott 2015). Were such benefits to game rearing interests short-lived (or absent), it is likely that on-going selective removal could create a sink with local reductions in buzzard densities. Lees *et al.*

(2013) highlight the wider potential for this to have unintended negative consequences for game shooting interests, namely the competitive release of other medium-sized predators, such as corvids, whose populations may be regulated through predation by, or competition with, buzzards. It is also possible that the removal of adult buzzards might break down territorial structures, increasing any aggregative responses to pheasant releases. This effect has been observed in coyotes *Canis latrans,* where emigration into territories left vacant after the lethal control meant that no reduction of livestock losses was observed (Conner *et al.* 1998).

There are non-lethal options that could be refined using these findings, though these may not be as popular with impacted stakeholders (Harradine, Reynolds & Laws 1997; Treves & Naughton-Treves 2005). For example, buzzards holding territories encompassing a release pen with problems could be prioritised for diversionary feeding (Parrott 2015). Similar strategies have proved successful in reducing raptor predation of gamebirds in upland ecosystems (Amar *et al.* 2004). Alternatively, concentrating deterrent measures, already widely used by stakeholders (Harradine, Reynolds & Laws 1997), such that they lead to the aversive conditioning of individual buzzards, is possible, although not without technical difficulties. Although aversive conditioning has proved successful in field conditions at reducing predation of marbled murrelet *Brachyramphus marmoratus* eggs by a subset of Steller's jays *Cyanocitta stelleri* (Gabriel & Golightly 2014), studies on black bears *Ursus americanus* found that once an animal became 'food-conditioned' its behaviour was difficult to change (Mazur *et al.* 2010).

Further research that attempts to identify 'problem' buzzards and the proximate drivers of this behaviour should now be prioritised. Previous work that observed higher predation levels in pens with little shrub cover and high numbers of released poults provides a good starting point (Kenward *et al.* 2001). The application of dietary stable isotope analysis alongside more traditional methods of recording predation will strengthen this research, allowing for a more complete understanding of buzzard prey selection and the validity of management methods.

Although my sample of problem buzzards was small, the results raise the possibility of developing a diagnostic approach that could be used to inform or evaluate management on a case-by-case basis. In North America, for example, $\delta^{13}C$ in black bear hair can predict the risk of that bear being a ‘conflict bear’ (Kirby, Alldredge & Pauli 2016). Where licenced lethal control is conducted, stable isotope analysis might also provide a valuable tool by which to assess whether buzzards removed in culling operations were indeed problem buzzards or non-target individuals. Such data are rarely collected or evaluated, even where selective approaches form the mainstay of management (Swan et al., 2017), but could then be used to inform future licensing processes.

Chapter 5

BUZZARD FORAGING AND BREEDING ON LAND MANAGED FOR PHEASANT SHOOTING

Chapter 5: Buzzard foraging and breeding on land managed for pheasant shooting

Abstract

In the U.K. long-term increases in populations of common buzzards *Buteo buteo* have created disputes over their management. A concern expressed by shooting interests is that buzzards are able to reach higher densities and produce more young on land managed for pheasant *Phasianus colchicus* shooting. However, this perception, and any potential underlying causes, has never been fully examined. In this study I investigated how buzzard density, foraging and breeding success are influenced by the abundance of pheasants (birds that had survived previous shooting seasons) and two alternative prey items (rabbits *Oryctolagus cuniculus* and field voles *Microtus agrestis*) on, and around, shooting estates in southwest England. I found a significant effect of both pheasant and rabbit abundance on buzzard breeding density. However, when I studied prey brought to the nest for chicks, only rabbits were provisioned in relation to their abundance. Rabbits were also the only prey for which provisioning rate explained variation in the number of buzzard nestlings. Pheasants were rarely brought to the nest and no relationship was observed between pheasant abundance and provisioning rate at the nest. My results therefore suggest that although buzzards nest in closer proximity to one another in areas with more pheasants, pheasants are not a preferred prey item. I suggest that winter pheasant carrion or high densities of alternative prey due to habitat and predator management might explain this trend. The visibility of buzzards as a predator and the positive relationship between buzzard densities and pheasant abundance has potential to influence perceptions of impact and increase the social conflict over their management.

Introduction

Across Europe populations of many predatory species are recovering from the detrimental impacts of persecution and of toxic contaminants (Clements 2000; Chapron *et al.* 2014). Although such increases are usually seen as positive by conservation organisations, increased incidence of real or perceived predation can raise concerns with other land users (Amar *et al.* 2010). This is especially true where predators are thought to reduce prey that is either threatened itself or of economic importance (Park *et al.* 2008; Mattisson *et al.* 2011). A common response from those who observe negative impacts is to implement or request lethal control (Treves & Naughton-Treves 2005). However, this can be controversial, sometimes leading to social conflicts over wildlife management (Redpath *et al.* 2013).

In the U.K., one such conflict concerns the common buzzard *Buteo buteo* (Arraut, Macdonald & Kenward 2015). Buzzard populations have grown over 450% since 1970 (Hayhow *et al.* 2016) due to a reduction in killing by humans and the recovery of prey populations (Clements 2002; Dare 2015). This increase has been observed in annual standardised breeding bird surveys (Musgrove *et al.* 2013), and informally, by those working in the countryside and tasked with maintaining small game numbers (Ainsworth *et al.* 2016). Indeed, the majority of gamekeepers now believe that buzzard populations have reached a point where they are not only impacting on game, but also other wildlife (GWCT 2011). Animosity towards buzzards appears to be particularly strong on estates that rear and release pheasants *Phasianus colchicus* (Lees, Newton & Balmford 2013; Parrott 2015). There is provisional evidence that part of this animosity stems from gamekeeper perceptions that buzzards reach ‘unnaturally’ high densities (Chapter 6). However, the effect of gamebird releases on raptor biology has received little scientific attention (Bicknell *et al.* 2010).

Buzzard densities and breeding success are principally limited by the amount of available prey (Tubbs 1974; Swann & Etheridge 1995; Sim *et al.* 2001).

Therefore, land managed for driven pheasant shooting might influence buzzard breeding biology both directly, by supporting high densities of prey, and indirectly, by providing high densities of alternative, non-game, prey species arising from legal predator control or habitat management (Trout & Tittensor 1989; Oldfield *et al.* 2003). In order to investigate this in more detail, it is important to consider how buzzards respond to variation in the abundance of different potential prey species (Park *et al.* 2008; Smout *et al.* 2010; McKinnon *et al.* 2013). Buzzards are dietary generalists and able to hunt a wide variety of prey (Graham, Redpath & Thirgood 1995; Selås, Tveiten & Aanonsen 2007). This allows them to respond to increases in prey availability not just numerically, through increased breeding density and productivity, but functionally, by increasing how often they consume the prey (Francksen *et al.* 2017).

In this study, I examined how buzzard breeding ecology is influenced by the local abundance of pheasants, as well as alternative prey (rabbits *Oryctolagus cuniculus* and field voles *Microtus agrestis*), on, and around, shooting estates in Cornwall, U.K. Specifically, I address two hypotheses: (1) buzzards respond to increases in pheasant abundance numerically by increasing either their breeding density or breeding success; and (2) buzzards respond to increases in pheasant abundance functionally by increasing the proportion of pheasant in their diet. As the annual release of reared pheasant poults occurs when most buzzard chicks are well developed and mortality rates are low (Kenward *et al.* 2001; Hardey *et al.* 2013; Rooney & Montgomery 2013), it appears unlikely that poult releases in the same year will influence the density of buzzard nests or the number of nestlings or fledglings. Therefore, this research focuses on those pheasants that have either been released and survived the previous year's shooting season or have been hatched in the wild.

Methods

Study sites

Fieldwork was undertaken from April to August 2015 on three study sites in Cornwall, U.K. (50.35°N, 4.85°W). All three sites centred on separate private shooting estates that were managed for the purposes of pheasant shooting. On all, management included the killing of mammalian and corvid predators and the release of >10,000 pheasant poults annually.

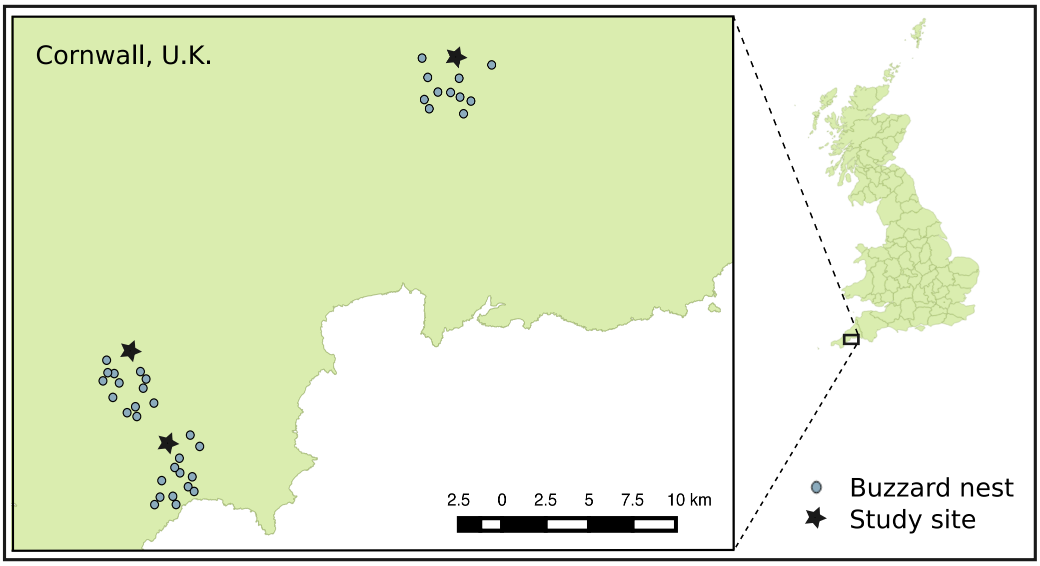


Figure 5.1: *The locations of three study sites and 37 common buzzard nest sites in Cornwall, United Kingdom.*

Territory mapping

Buzzard breeding territories were mapped by locating active buzzard nests through systematic searches of all woodland, tall hedgerows and lone trees during April and May 2015. A nest was considered active with the observation of an adult bird leaving the nest. Once all nests had been located, the nearest neighbour distance (NND) was calculated using QGIS. Following Swann & Etheridge (1995), NND was used as a proxy for territory size. The mean NND/2 was then used as the 'core territory' radius for all nests. Active nests were accessed three times during the nesting season: (i) to confirm clutch size during late incubation, (ii) to check hatching success and install nest cameras 7 days after hatching, and (iii) to ring the chicks at 18-25 days old. All work was conducted by trained and experienced personnel under licences from the British Trust for Ornithology (CO/6164) and Natural England (2015-7805-SCI-SCI).

Prey abundance

As buzzard pairs provision their chicks from prey hunted within established territories (Prytherch 2013), the area within the core territory of each nest was used to sample prey abundance. In addition to pheasants, the relative abundance of rabbits and field voles were quantified as these are known to be an important prey source from buzzards in the U.K. (Graham, Redpath & Thirgood 1995; Francksen, Whittingham & Baines 2016; Prytherch 2016).

This was achieved by surveying forty random points (assigned using QGIS) within each territory immediately after the nestlings had fledged (July – early August). At each point, appropriate sampling methods were employed to produce indices of relative abundance for the three prey types. For rabbits, an adaptation of the 'standing crop pellet count' (Fernandez-de-Simon *et al.* 2011) was followed. A 1m^2 quadrat was thrown and searched for evidence of rabbit droppings. The total number of quadrats per territory in which rabbit droppings were located was then used as a relative index of rabbit abundance. For field voles, the top right 25cm^2 of the same quadrat was examined for the presence or absence of field vole signs, specifically grass clippings. Following Lambin, Petty & Mackinnon (2000) this area was then scored 0, 1 or 2 depending on the deterioration of the clippings (fresh = 2, old = 1). This score was then summed for each territory to create a field vole sign index. To provide a measure of relative abundance of pheasants for each territory an adaptation of the timed point counts conducted by Selås, Tveiten & Aanonsen (2007) was employed. At each point, 'wild' pheasant (not released that year) observed within 100m over 2 minutes were recorded. I excluded juveniles in and around release pens as these were all assumed to be captive bred. Juveniles seen with a hen pheasants outside of pens were included. Distances were measured using a laser rangefinder (Rangemaster 1600, Leica). The total number of points in each territory from which pheasants were observed was then used as the index.

Sampling provisioning rate

Buzzard feeding data were collected using motion-activated remote cameras (CMOS 380 TVL, HandyKam, Cornwall) installed at nests. Recording provisioning by adults of chicks at the nest in this way represents the most accurate technique for determining food habits at raptor nests (Lewis, Fuller & Titus 2004). On detecting movement, the cameras recorded up to 5 minutes of continuous video footage. Videos of prey deliveries were watched by a single observer (GS) to reduce any effects of between-observer bias. Where possible, prey items were recorded at a species level. As pheasant releases occurred > 18 days into nestling development, it was assumed that they did not influence nesting density or productivity directly (Rooney & Montgomery 2013). All released poults were therefore excluded from further analysis.

Statistical analysis

To investigate whether there was a relationship between buzzard breeding density and the relative abundance of their prey, linear models were fitted with ‘nearest neighbour distance’ as the response and the abundance indices of rabbits, voles and pheasants as explanatory variables.

Using the dietary data from the camera footage the provisioning rates for rabbit, vole and pheasant prey were calculated for each nest. Provisioning rate was the total observations for each prey group divided by the number of hours the camera was running. To investigate how buzzards utilise rabbits, voles and pheasants in relation to their abundance (their functional response), linear models were fitted with provisioning rate for each of the three prey groups as the response variable and the index of relative abundance for that prey as the explanatory variable. Prior to inclusion in the model, the provisioning rates were log-transformed to meet assumptions of normality.

The relationships between provisioning rates and buzzard productivity were then tested using the number of nestlings, categorised as 1 or >1, as a measure of productivity. Nests containing two and three nestlings were grouped, as there were only two nests with three nestlings. A generalised linear model (GLM) was fitted with ‘nestling number’ as a binomial response. Different models were fitted with the provisioning rate of each prey (log transformed) as the explanatory variable.

Results

Nestling density and productivity

A total of 37 active buzzard territories were located and mapped (Figure 5.1). The average nearest neighbour distance was 690m (± 202m, n = 36) and thus core territories were assumed to be within a 345m radius from each nest. One nest was excluded from this calculation, as it was not possible to be certain that the nearest neighbour nest had been located.

26 nests (70%) successfully raised chicks to the point of fledging, with most failures occurring early in the nesting period (Figure 5.2A). The average number of nestlings per pair declined more slowly with a mean of 0.89 (SD = 0.70) nestlings surviving in each territory, two weeks after fledging had occurred (Figure 5.2B). The fact that there was minimal change in either measure of breeding success was observed across my sample after the nestlings had reached 18-25 days (the approximate time period at which that year’s released pheasants became available) adds weight to the assumption that buzzard breeding success was not significantly influenced by that year’s pheasant releases.

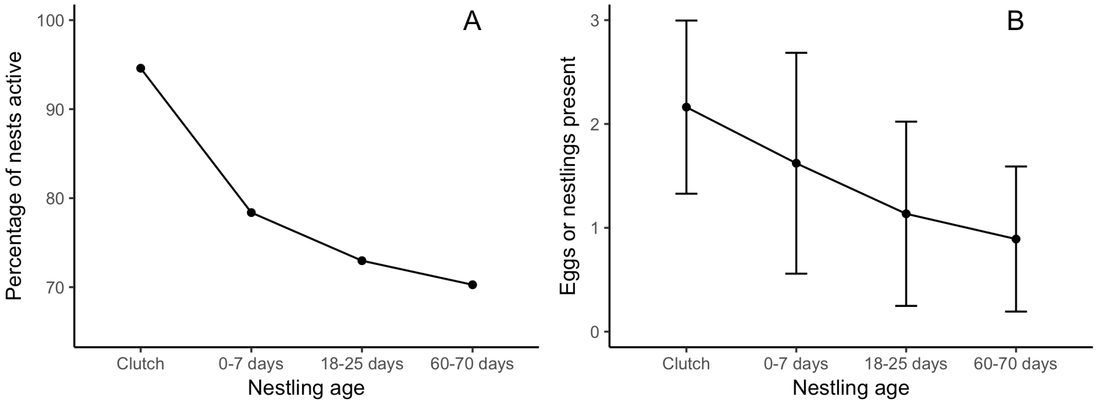


***Figure 5.2**: Decline in percentage of nests active (A) and the eggs or nestlings present (B) over the period of study.*

Provisioning observations

Using the nest cameras, a total of 4290 'hunting hours' were recorded at 24 nests. At nests, cameras were active over an average of 12.8 ± 6.4 days (mean ± SD) and encompassed an average of 178.8 ± 101.8 'hunting hours'. Within this footage, 1455 provisioning events were observed (mean per nest = 62 ± 35). Buzzards displayed a diverse diet that included mammals, birds, reptiles, fish and invertebrates. Voles (*Microtus agrestis* / *Myodes glareolus*) were the most important prey item by frequency (n = 365, 25.1% frequency, 6.9% biomass) and rabbits were the most important prey by mass (n = 195, 13.4% frequency, 39.1% biomass).

In total, 70 provisioning events involving pheasants were observed on the camera footage, of which, 39 (2.7% frequency, 7.3% biomass) were identified as released pheasant poults (identified by their clipped primary feathers) and 31 (2.1% frequency, 7.2% biomass) as 'wild' gamebirds. Of these 'wild' birds, 9 were pheasant chicks, 15 were young poults and 7 were adult birds.

Measures of relative prey abundance for each of the three prey groups (rabbits, field voles and pheasants) and nearest neighbour distance were recorded in 35 of the 37 territories (in one territory it was not possible to be certain that the nearest neighbour nest had been located, and in another it was not possible to adequately sample the core territory). There was a significant negative correlation between the indices of relative abundance for rabbits and voles (Spearman's rank-order correlation r_s = -0.342, P = 0.044), but no significant correlation between the abundance of pheasant and that of either rabbits or voles.

There was a significant negative relationship between nearest neighbour distance of buzzard territories and indices of relative abundance for rabbits ($F_{1,33}$ = 5.47, r^2 = 0.14, P = 0.026) and pheasants ($F_{1,33}$ = 4.68, r^2 = 0.23, P = 0.006), but not for voles ($F_{1,33}$ = 0.02, r^2 = 0.001, P = 0.88) (Figure 5.3).

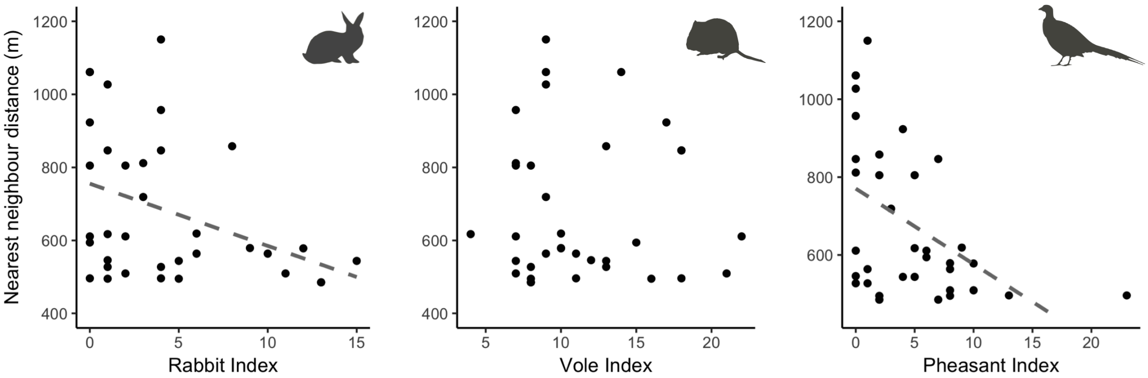


Figure 5.3*: The relationship between the nearest neighbour distance (m) between buzzard nests and indices of relative abundance for rabbits, voles and pheasants in 24 common buzzard territories. Dashed lines denote statistically significant relationships between nearest neighbour distance and indices of relative abundance for rabbits and pheasants.*

In those territories with cameras installed at buzzard nests (n = 24), there was a significant positive relationship for between provisioning rate at the nest and the abundance index for rabbits ($F_{1,22}$ = 8.80, r^2 = 0.29, P = 0.007), but not for voles ($F_{1,22}$ = 3.13, r^2 = 0.13, P = 0.09) or gamebirds ($F_{1,22}$ = 0.24, r^2 = 0.01, P = 0.63) (Figure 5.4).

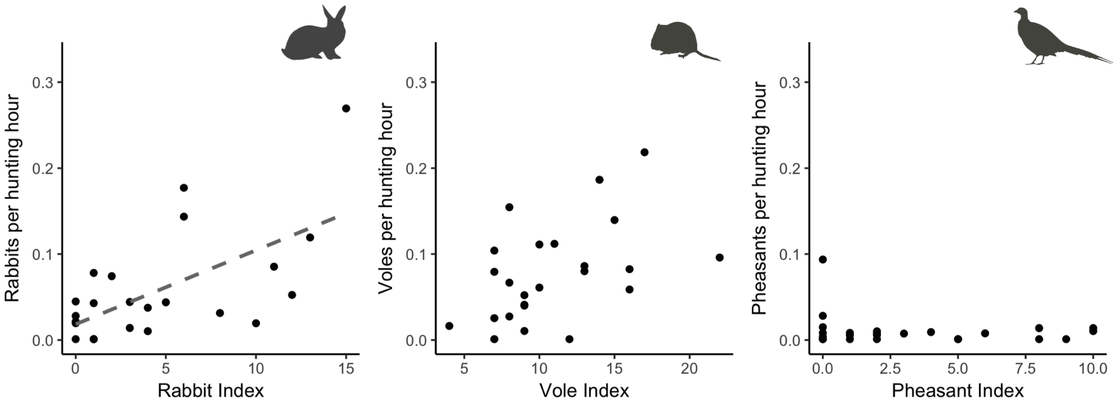


Figure 5.4*: Relationships between prey provisioning rates (provisioned items per hour of nest camera footage) at common buzzard nests and indices of relative abundance for rabbits, voles and pheasants in 24 buzzard territories. The dashed line denotes a statistically significant relationship between rabbits provisioned per hunting hour (log-transformed) and an index of relative abundance for rabbits.*

There were differences in the relationship between provisioning rate and nest productivity for the three prey groups. There was again a significant relationship between the provisions per hour of rabbits and nestling number ($\mathcal{X}^2{}_1$ = -7.98, P = 0.004) but the same relationship was not present for voles ($\mathcal{X}^2{}_1$ = -0.99, P = 0.319) or pheasants ($\mathcal{X}^2{}_1$ = -1.86, P = 0.172) (Figure 5.5).

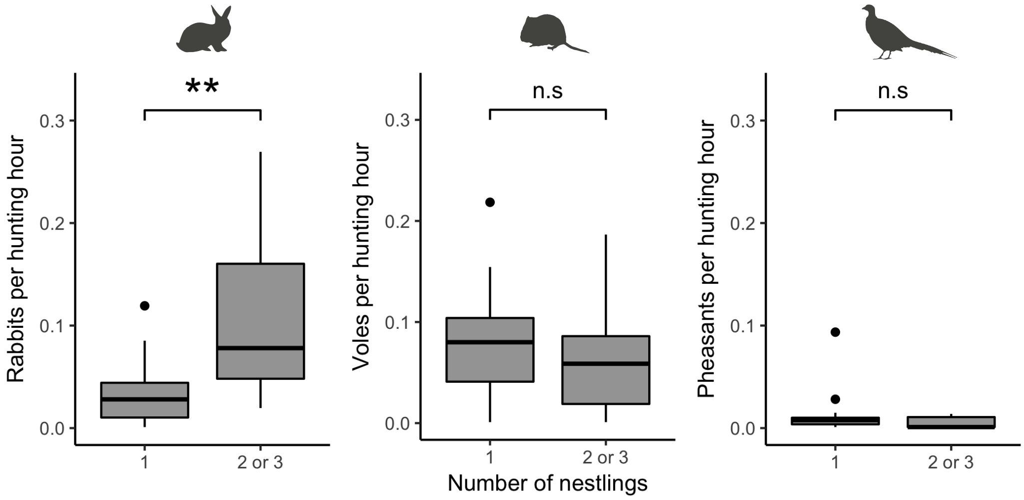


Figure 5.5. *Provisioning rates of prey items per hour of rabbits, field voles and pheasants in relation to the number of nestlings in 24 buzzard territories. Boxplots indicate the median and interquartile range, whiskers indicate largest/smallest observation + / - 1.5 x the interquartile range. The stars denote a significant difference in the number of rabbits provisioned per hour (log-transformed) in nests with 1 and >1 nestlings.*

Discussion

The results of this study suggest that buzzards nest at higher densities in areas where pheasants and rabbits are more abundant. However, only rabbits were provisioned to nestlings in proportion to their abundance, and it was only rabbit provisioning rate that predicted the number of nestlings. I therefore find evidence to support the first hypothesis that buzzards respond to increasing pheasant abundance numerically, in local breeding density but not productivity. I was able to reject the second hypothesis that buzzards exhibit a functional response to pheasant abundance, as there was no relationship between pheasant abundance and pheasant provisioning rate.

Although previous studies have address buzzard density and breeding in relation to abundance measures of alternative prey (Graham, Redpath & Thirgood 1995; Sim *et al.* 2001), to the best of my knowledge this is the first study that has examined how buzzard breeding variables relate to any measure of pheasant density. Although my results suggest that buzzard densities are highest where pheasants are abundant, I found that pheasants represent a small proportion of buzzard diet and that pheasant abundance was not correlated with provisioning rates. These findings suggest that pheasants are not preferred buzzard prey, at least pre poult release. Considering the current conflict over buzzard management on pheasant shooting estates this study therefore represents an important contribution to our ecological understanding of the problem.

Due to these conflicts, the positive relationship between buzzard densities and gamebird abundance is also worth brief discussion in a socio-ecological context. Buzzards are highly visible predators and, if seen frequently in proximity to pheasants, might generate a high level of concern (Naughton-Treves & Treves 2005) in comparison to other sources of mortality (Lees, Newton & Balmford 2013). This has the potential to influence levels of illegal killing by gamekeepers, an activity known to be a frequent occurrence in Britain (RSPB 2015b). Indeed, in their recent conceptual framework for understanding predator persecution, Carter *et al.* (2017) identified a link between predator abundance, interactions with people and poaching opportunity.

The significance of the relationship between pheasant abundance and the nearest neighbour distance between buzzard nests (Figure 5.3) is perhaps surprising, considering the relatively small contribution of pheasants to buzzard diet in the breeding season (Figure 5.5). A potential mechanism to explain this observation could be that pheasants are of greater dietary importance in late winter or early spring when nest sites are selected and territories defined (Tubbs 1974; Prytherch 2013). It is possible that buzzards increase their predation of pheasants over this period - gamekeeper records of raptor predation on grey *Perdix perdix* and red-legged *Alectoris rufa* partridges peak between February and May (Watson *et al.* 2007). An explanation that might be more plausible, however, is that areas with more pheasants provide more carrion during the winter and early spring period as a consequence of unrecovered hunting casualties (Watson *et al.* 2007) and vehicle collisions (Madden & Perkins 2017). In their study of wild grey partridge survival, Watson *et al.* (2007) estimate 10% of birds shot were not recovered. Were this estimate a similar percentage for pheasants this would represent a sizable biomass, potentially allowing pairs to maintain smaller territories. It is also possible that habitat management on land that is intended to hold pheasants over the winter provides buzzards with prey sources not quantified in this analysis. This could be either though maintaining hedgerows and woodland belts (Oldfield *et al.* 2003) or planting game crops intended to provide pheasants feed and cover (Sage *et al.* 2005). For example, Sage *et al.* (2005) observed over ten times more songbirds in winter game crops than on adjacent arable fields.

Of the three prey items investigated in this study, rabbits appear to have the most important influence upon buzzard breeding ecology. Specifically, I have shown that buzzards in areas with higher rabbit densities nest closer together, provision more rabbits and, consequently, are able to rear more chicks. The findings are therefore confirmation, not just of the importance of rabbits in buzzard diet (Swann & Etheridge 1995), but of the importance of rabbit abundance on buzzard density and productivity. This result has potential management implications for game estates as rabbits occur at higher densities on land where mammalian predators are removed (Trout & Tittensor 1989). Thus, the legal predator control commonly practised by gamekeepers (GWCT 2011; Martin 2011), might trigger the ‘competitive release’ of buzzard populations, allowing them to reach unusually high densities (Trewby *et al.* 2008; Bodey, McDonald & Bearhop 2009).

Although restricted by the necessity to sample across habitats, the rabbit, field vole and pheasant indices provided suitable approximations of the relative abundance of each of these prey items. One possible shortcoming of the analysis is that, while the vole sign index only reflects field vole abundance, I was unable to differentiate between field voles and bank voles *Myodes glareolus* during provisioning observations. However, the results of pellet and prey analysis of buzzard diet suggest that bank voles only constitute a small percentage of all vole prey (Graham, Redpath & Thirgood 1995; Dare 2015). Indeed, in Graham, Redpath and Thirgood's (1995) analysis of pellet and prey remains, of the 206 voles recorded, only 3 were identified as bank voles. Thus, while it might be assumed that some bank voles were recorded, any bias in the provisioning data would be expected to be small.

As my study sites were all pheasant shooting estates, this study used fine scale data on the relative abundances of pheasants in each territory. A useful further contribution would be to research how buzzard breeding densities vary at a landscape scale; comparing between sites where gamebirds are released and those where no releases occur. These results also highlight the need for data on buzzard winter diet on lowland shooting estates to help understand the relationship between buzzard breeding densities and pheasant abundance. This will necessitate methods that can be applied without the nest as a focal point such as direct observations (Redpath *et al.* 2002), collecting pellets at roosts (Francksen *et al.* 2016) or, if the tissue of birds can be successfully sampled, dietary stable isotope analysis (Inger & Bearhop 2008).

In conclusion, this study is the first to explore buzzard breeding density and success against a measure of pheasant abundance. The results show a positive relationship between pheasant abundance and buzzard breeding density. However, the ecological driver of this is currently unknown as pheasants, at least in the breeding season, made up a small proportion of overall diet and were not provisioned in relation to their abundance. Instead, I suggest that buzzards are able to nest in closer proximity in areas of high pheasant abundance as a result of either the availability of pheasant carrion over the winter or the abundance of alternative prey sources due to predator control and habitat management. The visible nature of buzzards as predators and the positive relationship between buzzard and pheasant densities may contribute to the apparent disconnect between the published evidence of buzzard predation of pheasants and the perceptions held by gamekeepers.

Chapter 6

GAMEKEEPERS' MOTIVATIONS FOR PREDATOR MANAGEMENT

Chapter 6: Gamekeepers' motivations for predator management

Abstract

Disagreements and disputes over the management of predatory animals are common factors in multiple conservation conflicts. In the U.K., there are long established conflicts surrounding the management of game species and the associated control of predator numbers. Despite the central role of game managers as stakeholders and actors in these activities, little attention has been paid to their perspectives and motivations. I conducted semi-structured interviews on the subject of predator control with 20 gamekeepers across the south of England, to explore the underlying beliefs, norms and information sources that motivated their behaviour. Six 'primary motivations' for predator management emerged: professional norms, personal norms, potential penalties, perceived impact, personal enjoyment and perceived efficacy. The influences of these motivations are discussed in detail and a conceptual model, incorporating the theory of planned behaviour, is developed. The findings have the potential to advance and inform wildlife management, and the conflicts with which it is associated, in three ways, by 1. characterising the information sources used to make decisions, 2. providing a basis for improved communication with stakeholders by detailing how the concepts of 'balance' and 'natural' are perceived and defined and 3. uncovering the interests and motivations behind predator control and illegal behaviour. I propose that, conflict mitigation will be more effective if efforts are tailored to address specific motivations of impacted stakeholders.

Introduction

When humans and predators share spaces, there can be social disagreements over how these animals are managed. Where conflict develops, this is often because of a disparity in how people differently value and perceive predators. Some view them as intrinsically valuable or ecologically beneficial (Lees, Newton & Balmford 2013; Ramp & Bekoff 2015) while others view them with fear or intolerance (Treves & Bruskotter 2014) that can be centred around perceived threats to human safety, livestock or game (Graham, Beckerman & Thirgood 2005; Woodroffe, Thirgood & Rabinowitz 2005b). Where stakeholders feel threatened by predators, responses can be made privately, through legal or illegal killing (Liberg *et al.* 2012), or more publicly through exerting political pressure to remove protections (Parrott 2015). Such actions can elicit strong opposition and conflict, particularly when killing actually or potentially threatens conservation objectives (Treves & Naughton-Treves 2005; Redpath *et al.* 2013; Ramp & Bekoff 2015).

Attempts to mitigate conflicts about predatory animals and their management have focused on the ecological and economic aspects of impacts (Dickman, Marchini & Manfredo 2013; Marchini 2014). This has included offering financial compensation, advising on animal husbandry or reducing populations (Graham, Beckerman & Thirgood 2005). Yet, such mitigation efforts can take for granted that the impact caused by wildlife is directly related to the response and that the level of impact elicits a proportionate response on the part of those affected (St John, Edwards-Jones & Jones 2010; Dickman 2010). This has been described as a ‘bio-rational’ understanding of the problem (Cavalcanti & Gese 2010), that ignores other possible social-psychological drivers behind stakeholder behaviour (Burton, Kuczera & Schwarz 2008; Cavalcanti *et al.* 2010). There is increasing evidence to suggest that management approaches based on a bio-rational understanding can be short-sighted; For example, Pohja-Mykrä (2016) observed that wolf killing in Finland was motivated not only by risk perception but by defiance of authorities, while Inskip *et al.* (2014) observed that tiger killing in Bangladesh is motivated by fear and by expected social rewards.

In this context, evaluating conflicts through a social-psychological lens appears a crucial step towards effective and lasting management (Madden & McQuinn 2014). Where pre-existing knowledge suggests possible predictors of behaviour, researchers can approach respondents with surveys or questionnaires designed to test *a priori* hypotheses (St. John *et al.* 2014). One social-psychological model that has been used for this purpose is the ‘Theory of Planned Behaviour’ (Figure 6.1) (Ajzen 1985). This framework has proven valuable in supporting analysis of both intentions and behaviour by addressing: (i) the attitude held toward a behaviour, (ii) the normative beliefs about what others expect and (iii), the degree that a person can control their behaviour (Armitage & Conner 2001; St John, Keane & Milner-Gulland 2013). It has also been successfully applied to understanding predator management. Marchini & Macdonald (2012) used this framework to demonstrate how perceived threats to livestock and human safety influenced rancher intent to kill jaguars in the Brazilian Pantanal.

Qualitative research has also yielded detailed data on motivations and preferences for wildlife management (Dandy *et al.* 2012; Maye *et al.* 2014; Pohja-Mykrä 2016). A qualitative approach investigates social-ecological systems through the perspective of respondents, permitting the identification of “insider viewpoints that could easily be missed using predesigned, structured surveys based on outsider perspectives” (Rust *et al.* 2017: p1305).

In this chapter, I explore predator management by gamekeepers using qualitative enquiry. I do so by investigating the norms, values and beliefs that create motivations for predator control. Although there is no broad consensus on how values are defined (Ives & Fischer 2017), I follow social-psychological definition that conceptualises values as “trans-situational goals and principles that guide human behaviour” (Manfredo *et al.* 2017: p773). Values are formed

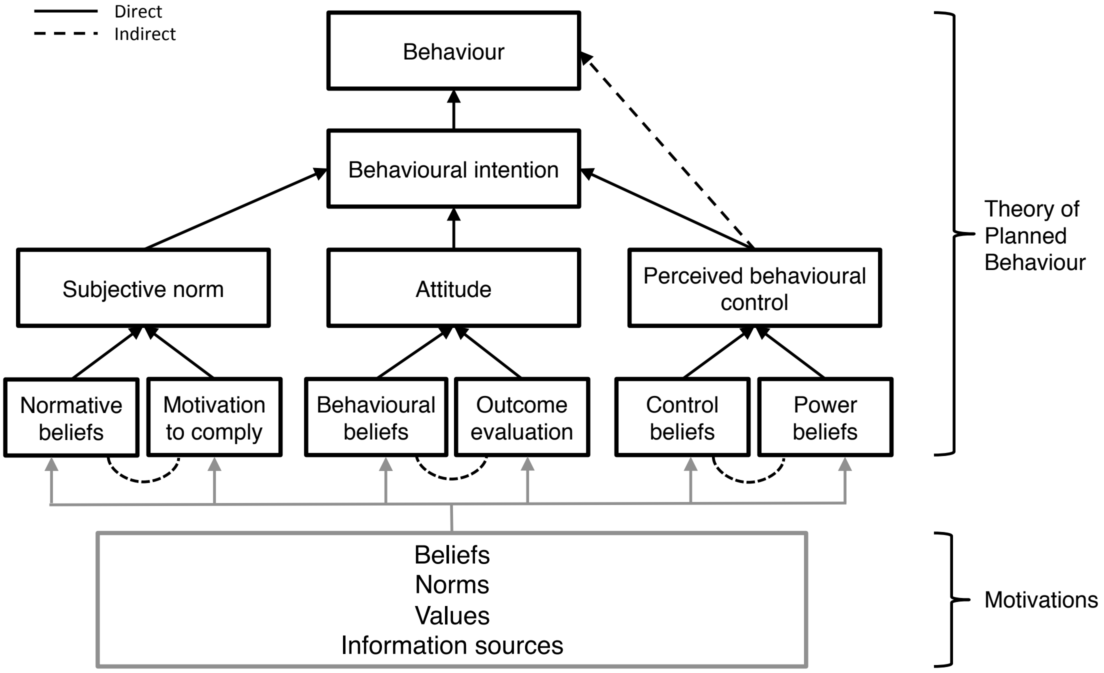


Figure 6.1: *Diagrammatical representation of the Theory of Planned Behaviour (Ajzen 1985) and potential motivation sources.*
Adapted from St. John et al. (2010). Solid lines represent direct links and dashed lines represent indirect links

during socialisation and influence how attitudes towards objects and actions are constructed and maintained (Stern & Dietz 1994). Following Dandy *et al.* (2012), I define 'beliefs' as "pieces of information, judgements or 'facts'… that the believer thinks to be true". As humans make decisions based on an evaluation of the information available to them (Ajzen & Fishbein 1980), I also attempt to highlight information sources that influence management decisions.

I use 'the theory of planned behaviour' to structure how individuals come to decisions. Here, the motivations can be seen as providing the "the basis for the corresponding attitude, norm or perception of control" (Manfredo & Dayer 2004: p318) (Figure 6.1). I first describe the background to these conflicts before presenting a qualitative assessment of the values and beliefs that shape decisions on predator control.

Background to gamebird hunting

The shooting of driven gamebird species is a widespread recreational activity in the U.K. and can play an important social, ecological and economic role within rural communities (Oldfield *et al.* 2003; Public & Corporate Economic Consultants 2006). In lowland landscapes, the majority of the birds hunted are ring-necked pheasants *Phasianus colchicus* of which ~28 million are released annually from captive-bred stock (BASC 2015). The spatial coverage of such releases is substantial (5 - 10% of the U.K.'s land area; Tapper 1999), and one in twelve woodlands in England is thought to contain a pheasant release pen (Sage, Ludolf & Robertson 2005). In order to rear gamebirds, conduct releases and oversee the shooting during the hunting season many shooting estates employ gamekeepers. Alongside habitat management, the majority of gamekeepers also conduct predator control in some form (Reynolds & Tapper 1996; GWCT 2011).

There is evidence that removing predators increases both the surplus of game and the density and breeding success of other native wildlife (Tapper, Potts & Brockless 1996; Fletcher *et al.* 2010; Reynolds *et al.* 2010). However, predator killing has created a social conflict centring on animal welfare and threats to conservation objectives (Lees, Newton & Balmford 2013; Elston *et al.* 2014). These conflicts are exacerbated by shooting interests being repeatedly linked to the illegal killing of protected predator species (Smart *et al.* 2010; Amar *et al.* 2012; Whitfield & Fielding 2017). Illegal killing not only threatens the conservation status of several predatory species (Etheridge, Summers & Green 1997; Whitfield & Fielding 2017) but also erodes trust between conservation organisations and shooting interests, making constructive dialogue on broader issues difficult (Redpath *et al.* 2013). Conflicts concerning game shooting and predator management are exemplified by the long-running conflict between hen harrier *Circus cyaneus* conservation and moorland managed for the purposes of red grouse *Lagopus lagopus scotica* hunting. Here, although there has been significant investment from stakeholders and scientists, a practical means of conflict mitigation remains elusive (Redpath & Thirgood 2009; Sotherton, Tapper & Smith 2009; Elston *et al.* 2014).

Despite the central role of gamekeepers in this conservation conflict (White *et al.* 2009), the spatial extent of game releases (Sage, Ludolf & Robertson 2005), and the participation of some gamekeepers in illegal predator killing (Nurse 2011), there is little published literature analysing their perspectives and motivations behind predator management. Such information might allow stakeholder groups to acknowledge, engage and respond to the deeper social and psychological drivers that might influence predator killing. The results of the few quantitative studies of practice, based on mailed questionnaires, suggest that gamekeeper effort to trap mustelids is higher following perceived predation (Packer & Birks 1999) and on estates that rely on 'wild' game (McDonald & Harris 1999). However, more detailed qualitative research on game managers in Spain provides evidence that, as well as perceived impact on hunting opportunities, intentions to control predators are influenced by broader social factors (such as tradition) and ecological factors (such as predator population size) (Delibes-Mateos *et al.* 2013). In the context of these findings and the apparent impasse over predator management, it seems pertinent to evaluate the social drivers of predator management in the U.K.

Methodology

I conducted 20 semi-structured, one-to-one interviews with gamekeepers in five counties across the south of England (Table 6.1) between September and November 2016. Eleven interviews were conducted while the gamekeepers carried out their daily activities, while nine were sedentary discussions. 'Go-along' interviews were used in conjunction with static interviews as they provide "a unique means of obtaining contextually based information about how people experience their local worlds" and the consequences these experiences have on actions (Carpiano 2009: p271).

To recruit interviewees, I employed a ‘snowball sampling’ method whereby gamekeepers known to the research team were contacted first and then asked to recommend others. In selection I sought individuals currently employed as gamekeepers, with a diversity of experience and backgrounds (rather than a sample that was representative of broader variation in the industry at national or regional scales). This approach was chosen to maximise access to research subjects. The use of known individuals, rather than cold-calling, also served to build a foundation of trust, which was particularly important as the research topic contained inherent sensitivities (predator control is controversial and illegal behaviour persists within the profession). Prior to interviews, all participants were supplied with information on the research and provided written consent. This project received ethical approval from the University of Exeter College of Life and Environmental Sciences Ethics Committee. To provide anonymity, participant names are replaced with numbers (e.g. G1). Position is noted to distinguish:

- Headkeepers (HK), who were ultimately responsible for all gamekeepers and game management on the estate. These also had their own ‘beat’ (a section of the estate that was their primary responsibility).
- Single-handed keepers (SHK), who were ultimately responsible for all game management on the estate.
- Beatkeepers (BK), who had their own beat that was their responsibility.
- Underkeepers (UK), who had their own beat but reported regularly to the Headkeeper.

With the exception of a single ‘wild bird’ shoot, all respondents annually supplemented gamebird populations with juvenile pheasants reared in captivity. These releases varied in size but could be substantial; several estates released over 50,000 pheasant poults each year. Several also released smaller quantities of red-legged partridges *Alectoris rufa*. Shoots were run commercially, by a private family or by syndicates of hunters (often the distinction between these types was blurred). Seventeen of the respondents were employed full time, while three had part-time positions. Within the sample, six respondents were second or third generation gamekeepers. Collectively, my data represented over 400 years of gamekeeping experience (range 4 – 45 years).

Table 6.1: *Research participants categorised by position and size of pheasant shoot. Shoot size was defined by the gamekeepers themselves as the number of birds released was found to be a sensitive question.*

Shoot size	Headkeeper	Single-handed keeper	Beatkeeper	Underkeeper
Small		4 [c]		
Medium	6 [a]	2 [d]	3 [e]	2 [g]
Large	2 [b]		1 [f]	
Total	8	6	4	2

Notes: [a] 2 West Sussex, 1 Cornwall, 1 East Sussex, 1 Kent, 1 Devon; [b] 1 West Sussex, 1 Cornwall; [c] 2 East Sussex, 1 Cornwall, 1 Kent; [d] 1 Cornwall, 1 West Sussex; [e] 3 West Sussex; [f] 1 West Sussex; [g] 2 East Sussex.

Interviews followed a schedule of themes, beginning with personal background and professional development before moving on to predator impact and management decisions (Appendix 15). I asked general, open questions structured around subjective norms, perceived behavioural control and attitude in accordance with the theory of planned behaviour. Specific predatory species were not introduced by the interviewer to avoid specific preconceptions biasing results. Instead, respondents were encouraged to discuss their attitudes to any species that they perceived killed or ate gamebirds or their eggs. By allowing respondents to consider a diversity of predatory species I aimed to uncover the broader motivations for predator control. Discussions were developed during the process to expand on concepts or statements brought up in previous conversations (Appendix 15). The introduction of statements from other keepers into our conversations created an indirect dialogue aimed at producing a more nuanced discussion.

During discussions I focused on how respondents used legal methods to control predators and did not seek to identify those conducting illegal behaviour. However, as I was interested in the context in which illegal behaviour is rationalised I used 'projective' questioning (whereby respondents were asked about how they suspect others rationalise their behaviour) to shed further light on gamekeepers' motivations behind this behaviour (Nuno & St John 2014).

Analysis

Interviews were digitally recorded and fully transcribed. One respondent asked not to be recorded but allowed detailed notes (including direct quotes) to be taken. Transcripts were then analysed using *NVIVO 11* (QSR International Pty ltd 2015) software for qualitative analysis. This was achieved in two stages. In the first stage, transcripts were analysed by identifying underlying and unprompted patterns in language, subject or content concerning predators and their management. Themes were aggregated into six 'primary motivations'. I understand these to be the key drivers of predator control but acknowledge that there are additional, less common, motivations that are not discussed. By analysing the text in this way motivations emerged both from the questions in the interview guide but also inductively from the gamekeepers' reasoning and experience. In the second stage, motivations were restructured within the theory of planned behaviour based on whether they related to subjective norms, attitudes, or perceived behavioural control.

Results

Gamekeeping was viewed as a "*way of life*" (G13, HK) or a "*vocation*" (G14, HK) rather than an occupation. On a day-to-day basis, gamekeepers described themselves as largely solitary[1] and autonomous[2], making their own

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[1] "*Keepers are usually quite isolated, they don't like other peoples company, they don't like to talk to people*" (G2, SHK)

[2] "*I keep myself to myself and do what I've got to do*" (G14, HK)

decisions on much of the detail concerning game releases and predator management[3]. A total of 24 mammals and birds (11 and 13 respectively) were implicated in predation of pheasants or their eggs on the estates visited. Twelve of these 24 species could be subject to legal lethal control without prior application for a licence. Although I observed variation in the way participants viewed specific predators and mitigated perceived impact, broad patterns in motivations and perceptions emerged. I discuss their influence below using the theory of planned behaviour to structure my findings.

Normative beliefs and motivation to comply

Social normative pressures were evident through expected behavioural conformity within the gamekeeping profession (e.g. "*Any gamekeeper worth his salt would control…*": G13, HK). The normative beliefs regarding predators meant that the abundance of some predatory species could be seen as a personal reflection of the gamekeepers' capabilities. In other words, these beliefs could be considered as professional norms. For instance, gamekeepers talked of the presence of certain predators on their beat as being "*like a stigma*" (G4, UK) and finding it "*ridiculously embarrassing*" (G2, SHK) if they were seen during a shoot day[4]. Another talked about how he controlled magpies, in part, because other gamekeepers "*take the micky*" (G7, HK) when they see them (magpies) on his shoot. Such responses suggest not only that professional norms have an influence on predator control, but also that they might affect the instinctual and emotive responses gamekeepers feel toward predators (e.g. "*I bloody hate seeing magpies*": G2, SHK).

In my projective questioning, professional norms and what it meant 'being a gamekeeper' were used to explain illegal behaviour. A prevalent attitude "*I'm a gamekeeper, therefore I have to kill absolutely everything*" (G6, BK) was ascribed by some to the older generation, while others perceived that some of

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[3] "*There's no bureaucracy, there's no red tape, there's no paperwork*" (G11, SHK)

[4] "*If a fox runs out on a shoot day, it's like, fuck there's a fox here, but you can't kill every single one*" (G20, BK)

the younger generation thought such killing was how a ‘good’ gamekeeper behaved[5]. This is not to say they felt that such norms were static, and many made references to a perception of change within their profession. For some[6], this professional change ran parallel to a personal change:

> “*I think that gamekeepers* [now] *are hugely more aware… my thinking has definitely changed over my lifetime… I’m far more lenient and far happier to let live and not overreact… I think most people have grown up with the idea that there has to be acceptance, of really reaching a balance. Which is where we are. And I think that there is a greater acceptance now that we must be more lenient in our approach to say, for instance, birds of prey, because those old days have gone*.” (G17, HK).

The motivation of individuals to comply with their own normative beliefs appeared to be largely structured around an individual’s moral beliefs about what was right and wrong. These can be described as ‘personal norms’ (Carter *et al.* 2017) and their influence on predator control appeared as a complex composite of professional/social norms, perceived impact and conformity to the law. Gamekeepers described the responsibility they felt to protect both game and non-game wildlife by controlling predators in moral terms[7]. For example one gamekeeper, in describing why he killed predators, used the metaphor of a pet that had been left in his care:

> “*It’s like if you dropped a dog off at me to look after, it’s my responsibility to make sure that dog comes back to you in perfect health. It’s the same with pheasants come the* [start of the shooting

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[5] In reference to what the younger generation of gamekeepers think the profession entails: “*they think that it’s to kill everything*” (G2, SHK)

[6] “*Years gone by I might have thought about doing it* [illegal predator control] *but now I don’t*” (G9, SHK)

[7] *“If I didn’t shoot a single fox all year, you’d never have a nesting pair of skylarks on the top of the downs*” (G6, BK)

> season]. *Not only is my boss expecting it, but I'm expecting it*" (G2, SHK).

A moral obligation to protect game was also used during projective discussions as to why other gamekeepers might decide to break the law and kill protected predators:

> "*If you spent 12-14 hours a day, from when they're little chicks, keeping something alive and then it's getting attacked every day by something and you've tried your scarecrows and you've tried your bangers and you've tried all that sort of thing, then I think it could push some people over the top*" (G8, HK)

One gamekeeper expressed frustration in how illegal behaviour was framed by the media and conservation organisations: "*We're not bird of prey killers. We're game protectors*" (G17, HK). For many of the keepers within the sample, however, the responsibility they felt for their pheasants appeared not to outweigh the moral cost of breaking the law and removing protected predators: "*I'm sure my percentages are not as good as other keepers, I don't give a fuck, at least I can live with myself*" (G11, SHK).

Behavioural beliefs and outcome evaluations

As the primary purpose of gamekeeping is to produce gamebirds for recreational hunting[8], perceived impacts, in the form of gamebird losses to predators, was a key motivation in predator removal. Gamekeepers considered that predation resulted in reductions in the number of gamebirds available to shoot and, thereby, created a threat to their job security[9]. This

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[8] "*Our primary purpose is to produce shoot days. That's what we're paid to do.*" (G9, SHK)

[9] "*Christ, if I drop down to 60% everybody would notice. The boss would say, 'Oh we haven't had a very good season really' even though we've shot 60%. So there's still pressure, there's still a pressure but its all relative*" (G9, SHK)

"*pressure to produce*" (G16, HK), was often referenced during in the projective discussions on the illegal behaviour of others.

"You're forced to break the law, or some people are, if you're under a lot of pressure. Luckily we don't head for massive percentages here, and we allow for enough in the pens, so that I can lose 30-40 (individuals) *and it doesn't matter*" (G5, BK)

Impact and risk appeared to be ascribed mainly through daily interactions with predators (or predation) and through the occasional transfer of knowledge with other gamekeepers. Individuals frequently recounted instances where they had witnessed predation events or their aftermath first hand, making the harm done by a species thereafter self-evidently valid[10]. When predators were not observed directly, predation could be attributed to specific species through detailed personal ecological knowledge such as smell, tracks, or in-field necropsy examinations[11]. References to other sources of information were less common, though information sourced from scientific studies, the shooting press and various shooting NGOs was specified[12].

Gamekeepers' descriptions of predation suggested that perceived impact was influenced both by experiential and analytical systems (Epstein 1994). Analytical processing (the cognitive and deliberate evaluation of information; Wilson 2008) was observed when individuals rationalised losses to predators by framing them in relative terms. This was observed in sentences such as *"You expect to lose 10% whether it's disease* [or] *predators"* (G2, SHK) and

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[10] "*Hedgehogs will kill poults. I've proved that. I watched a hedgehog one morning, there was a poult in the pen in the track, nothing wrong with it, just tucked down, and the hedgehog actually went on top of it and actually bit the back of its neck and he killed that poult". (G14, HK); "I've seen it, it happens*" (G19, SHK)

[11] "*Fox, you'll always know, you can smell it.*" (G10, HK); "*I could generally see tracks going around the pen*" (G11, SHK); "*You'll just see a skeleton, there's no head or neck but the wings, just the rib cage and feet left. That's a buzzard*" (G10, HK)

[12] *"I know there have been environmental studies…"* (G1, SHK); *"I know from reading the shooting press…"* (G5, BK)

"*When you've got livestock in the number we've got them, you're going to get dead-stock*" (G14, HK). Often, however, evidence of experiential processing (instinctive, involuntary and largely produced by affect; Wilson 2008) was clear[13]. For example, one gamekeeper described losses of pheasant poults as "*heart-breaking*" (G13, HK), while another asserted "*every one hits me like an arrow*" (G17, HK). The instantaneous reaction that individuals had to predator appearance and behaviour was also evident. Peregrine falcons *Falco peregrinus*, for instance, had an obvious "*killer mentality*" (G12, BK) while red kites *Milvus milvus* did not "*have that sort of killer-ness about them*" (G6, BK).

Incidents where predators were able to kill tens, or sometimes hundreds, of gamebirds were recounted to justify attitudes or behaviours[14]. Gamekeepers commonly ascribed these events to specific 'problem' animals that transgressed the limits of tolerated behaviour. These were either animals having a disproportionate impact, such as a fox that had "*figured out it can get under the electric fence*" (G11, SHK) or they were animals that had developed what they saw as a malicious agency, such an animals that will "*kill for the sake of killing*" (G12, BK). In some cases it was both:

> "*You'll get one buzzard that might not kill a pheasant in its life. It'll be sat around eating worms and voles and that sort of stuff. Then you'll get one that'll be switched on and it'll just kill pheasants all day for fun*." (G20, BK).

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[13] "*To my boss that's a £38 pound loss. To me, I'm more disappointed that that pheasant is dead. I've spent all summer keeping it alive." (G20, BK); "I don't really see it as money at all. Not at all… no it's a life at the end of the day... You hate the fact that you weren't there and this bastard fox has gone chasing round and killed one of your poults."* (G5, BK)

[14] "*It's that point when you outside a pen in a morning and you pick up 109 dead pheasants. And I've done that twice in the 16 years I've been here*" (G14, HK); "*I've had mass kills where you get there in the morning and there's bodies everywhere... It's very demoralising.*" (G16, HK)

Gamekeepers considered that, if left, the behaviour might continue indefinitely, being passed on to offspring[15]. Thus, experiencing multiple losses and/or the perception of such 'problem' animals translated into a preference for more intense, reactive and direct management[16].

Personal ecological knowledge was also used to determine what was, or wasn't, 'natural'. Here, gamekeepers followed an 'appeal to nature' argument, positing that because something is perceived as more 'natural' than something else, it is therefore of higher worth and more valid (Moore 1903). Indeed, they saw their own role as to provide a surplus of gamebirds but also to monitor, and when appropriate, correct that which was unnatural[17].

Thus, what individual gamekeepers view as 'natural' and how they define it are both important questions. The threshold appeared largely structured around the benefit, or cost, produced from anthropogenic disturbances[18]. The perception of predators being 'unnatural' was most clearly demonstrated in attitudes to invasive predators - animals that were entirely a product of human actions and therefore, "*not supposed to be here*" (G14, HK). For this subset of species no observational checks and balances were required to guide attitudes or management, as one respondent put it when discussing grey squirrel control: "*you know you're doing good because they're an invasive species*" (G5, BK).

The concept of predators being 'unnatural' was further developed by the idea, shared by five of the respondents, that some individuals of native predatory species were the result of secret reintroductions or releases. The behaviour of

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[15] "*She will take a brood into a pen to teach them how to hunt"* (G9, SHK)

[16] "*If I've got one killing them then I'll sit up there until I get it*" (G12, BK); "*A lot of gamekeepers are quite perfectionist and regimented and if something cocks up they take it, I take it, personally … Like when those mink attacked for instance, I sat out for three days before I trapped all those ... I didn't go home*" (G2, SHK).

[17] "*Everything has to be at a certain balance"* (G3, HK); *"why persecute they* [sic] *when there's plenty of natural food, like rabbits, for them?*" (G14, HK).

[18] *"Buzzards have learnt to follow that tractor and they hammer the leverets*" (G1, SHK)

individual animals or observations of rapid population rises was used as evidence for these theories[19]. One gamekeeper talked of having a particular problem with "*released*" buzzards predating pheasant pens because pheasants were "*easy pickings*" (G3, HK) implying that released predators were unable to hunt 'naturally'. There were also those species whose rapid population increase was *"not a true representation of a natural success story*" (G19, SHK) because of a belief that they were being artificially fed.

References to maintaining 'balance' were common and appeared to influence how observations were converted into management intentions. This was interpreted through personal ecological knowledge of abundance: "*balance is when you go out your backdoor and you don't see loads of predators*" (G10, HK). This concept seemed to be analogous to what was, and what wasn't, 'natural' in that it helped identify species that were "*over-populated*" (G3, HK) as a consequence of anthropogenic disturbances:

> "*I guarantee, the way the world is now, that if you didn't control any predators, things would go extinct. Not maybe nationally or worldwide but within areas they would. So yes,* [gamekeepers] *have to balance it.*" (G6, BK)

When viewed through the lens of 'balance', management preferences for predators could be decided. A perceived increase in population therefore increased negative attitudes towards the species: "*Badgers, they've become a pest and that's simply because there are too many of them*" (G7, HK). Accordingly, keepers spoke about their enjoyment, or at least tolerance, of predators they perceived to be rare[20].

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[19] "*They would be sitting there like dogs, not even caught and we could just walk up to them and shoot them. It was quite bizarre … it's what we call 'fluffy foxes.' It's almost like they're not wild animals, they've been living in someone's shed or something*" (G16, HK)

[20] "*…because it isn't something you see everyday"* (G14, HK)

For some, however, the very concept of a 'balanced' population of predators on game shooting estates was an oxymoron. To these keepers, the release of game or the control of other predators had, to continue the metaphor, tipped the scales[21] and therefore justified direct interventions to restore equilibrium[22]. They had, by their own actions, made predator populations unnatural[23]. They feared that "*if left, predator levels would build and build and build*" (G9, SHK) to a point where they would reduce both game and non-game prey. This belief effectively shifts the focus from an economic impact to a more powerful platform of environmental damage, creating moral incentives to act. Thus, keepers used most or all legal methods[24] to "*keep on top of*" (G2, SHK) predator populations. As one respondent put it, gamekeepers "*should keep everything on level playing field*" (G17, HK). The belief that there was a constant source of new predators being drawn in from areas not under game management was also used as evidence that predator control was unlikely ever to threaten conservation objectives[25]. Furthermore, when keepers were not legally able to control species that they perceived to be over abundant (principally badgers and buzzards) there was a belief that environmental harm would continue and increase[26].

For several gamekeepers, predator control was not only to reduce predation but also for personal enjoyment. This was mentioned only in relation to fox

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[21] "*Gamekeepers are the reason why the birds of prey are at the biggest population that they've ever been"* (G17, HK)

[22] "*If you provide a food source, something will turn up to eat it"* (G8, HK)

[23] "*There's no natural predator for a badger is there? So if nothing is there to control them, but you're controlling other species, then you're just going to get a massive boom of one species and it's just that balance isn't it?"* (G12, BK)

[24] "*We use every legal method that we can to be honest*" (G16, HK)

[25] "*You'd be mad to think you could ever wipe something out on one estate*" (G4, UK); "…*buzzards and kites and things like that for every one you kill you'd get another ten move back in"* (G12, BK) This was in reference to why the respondent felt licences would not work.

[26] "*The protected status should be lifted and in doing so, very quickly there will be a rebalancing of populations*" (G1, SHK); *"There'll come a time when there's going to be so many buzzards that something will have to be done about them.*" (G16, HK)

control: "*If I didn't have this job where I could go lamping and shoot foxes, I would probably pay to go lamping"* (G20, BK).

Power and control beliefs

Gamekeeper perceptions of their ability to perform predator control were linked to the efficacy of the control method. A variety of methods were utilised including shooting, trapping and poisoning (the latter used for rodents only) usually as part of a yearly cycle linked to opportunity and availability[27]. The efficacy of these methods were largely self determined[28] and judged both directly by the number of predators killed and indirectly by the absence of observations of predation. Trapping allowed low efficacy methods to be implemented with little cost. For instance, one gamekeeper explained that he hadn't caught a stoat in his Fenn traps for over 8 months but still set them because "*it's that one time you don't* [that] *something is going to happen*" (G2, SHK). As a consequence of access to guns, traps and poison, gamekeepers described it as technically easy to kill most predators, including (they imagined) those protected by law, however, perceived behavioural control could be overwritten by an evaluation of the expected penalties: "*If I* [kill a protected predator] *I'm going to lose my job, lose my livelihood, lose my car, lose my house and, more than likely, lose my missus*." (G2, SKH).

Incorporating motivations into the theory of planned behaviour

To summarise, the gamekeepers in my sample articulated multiple drivers of predator control that connected and interacted to influence behaviour. Predation was rarely framed as an economic loss, although concerns about job security might make this an important indirect influence. Instead respondents described a duty of care over the gamebirds and non-predatory wildlife on the land they managed. This required them to maintain the 'natural

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[27] "*We use tunnel traps, we snare, we poison the rats, Larsen cages, letterbox cages…*" (G16, HK); "*We'll go after* [corvids] *in the spring … foxes we got after all year. Stoats and weasels, we go after autumn and spring* (G7, HK)

[28] "*You can read as many books as you like and they'll all tell you something different. The only way to do it is to do it the way that you know works*" (G14, HK)

balance', removing animals that were 'unnatural' or 'overpopulated'. This included predators that were perceived to benefit from gamebird releases. For many, predator management was a moral obligation as well as a professional responsibility.

Of the empirical results detailed above, I identified six 'primary motivations' for predator management: professional norms, personal norms, potential penalties, perceived impact, personal enjoyment and perceived efficacy. In Figure 6.2 I present these within the theory of planned behaviour to illustrate their potential influence on predator management. Of these motivations, perception of impact appeared to have the most salient influence and thus, I detail an additional three 'secondary motivations' that appear to influence how this was determined: maintaining 'balance', 'appeal to nature' and 'problem' animals (Figure 6.2). I observed that gamekeepers discussed predator control as being reactive or proactive. In Table 6.2 I provide indicative extracts to illustrate how various motivations might determine these specific actions.

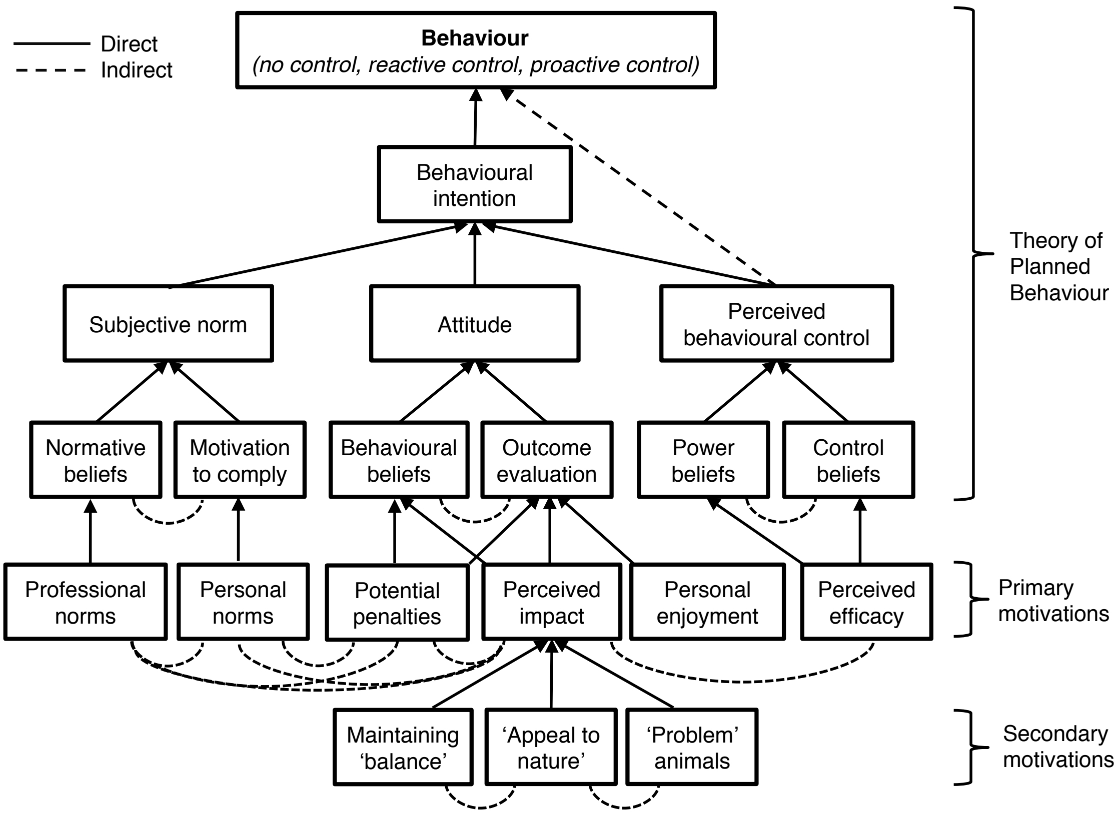

Figure 6.2: *Diagrammatical representation of the Theory of Planned Behaviour (Ajzen 1985) with primary and secondary motivations for predator control on game shooting estates in the south of England. Direct influences are denoted with a black line, indirect influences are denoted with a dashed line. Adapted from St. John et al. (2010).*

***Table 6.2**: Management preferences for predators on gamebird shooting estates with underlying motivations and examples taken from qualitative interviews.*

Management intention	**Motivation**	**Examples**
No control	• Perceived impact	"*I'm not going to put down Fenn traps, which arbitrarily kill mustelids, if they're not doing any harm*" (G11, SHK)
	• Maintaining balance	"*I know they take some birds but they're rare*" (G7, HK)
	• Personal norm	"*I wouldn't* [kill] *something just because they're there*" (G17, HK)
	• Potential penalties	*"It's not worth getting caught, I like my job too much to risk losing everything"* (G20, BK)
Reactive control	• Perceived impact	"*Generally it's best to leave stuff alone unless it's an actual major problem"* (G3, HK)
	• 'Problem' animals	"*You'll get rogue foxes and they'll just kill for the sake of killing … they're the ones that you need to try and get on top of*" (G12, UK)
	• 'Appeal to nature'	"*I just think it's Mother Nature. It adapts and overcomes. That's why the populations have increased*" (G19, SHK)
Proactive control	• Perceived impact (game)	"[I'm] *controlling small pests and predators … all the things that are going sneak under the fence and take a poult or two"* (G18, SHK)
	• Perceived impact (wildlife)	"*If I didn't shoot a single fox all year, you'd not have a single pair of nesting skylarks"* (G6, BK)
	• Maintaining balance	"*Everything has to be at a certain balance. When something becomes overpopulated…*" (G3, HK)

• ‘Appeal to nature’	*“Something definitely needs to happen with the buzzard population. … you see as many buzzards some days as you do pigeons flying around. Which isn’t natural”* (G12, BK)
• Professional norms	*“We all have a duty to try and keep the number of foxes down”* (G4, UK)
• Personal enjoyment	*“I enjoy fox shooting”* (G11, SHK)
• Perceived efficacy	“*When we hadn’t got Larsen traps, magpies were actually quite difficult… but then the Larsen trap come along and absolutely revolutionised catching magpies*” (G1, SHK)

Discussion

My study has revealed the interacting factors that directly and indirectly motivate predator management by gamekeepers. My results can advance and inform wildlife management and the human conflicts it creates in at least three ways. First, they characterise the information sources used to make decisions. Second, they might improve communication with external stakeholders by detailing how specific concepts are perceived and defined. Finally, they uncover previously unrecognised motivations behind both legal and illegal predator control.

Characterisation of information sources

I observed that personal observation dictated much of how gamekeepers think about, and respond to, predators. This is perhaps unsurprising considering the strong power of direct experience in shaping attitudes (Maye *et al.* 2014; Eriksson, Sandström & Ericsson 2015). Furthermore, as perceptions of abundance are linked directly with control preferences through concepts like ‘balance’, there appeared to be an interaction between the number of encounters a gamekeeper has with a predator, and management preferences due to perceptions of population trends. Indirect feedbacks between predator population size and motivation to control have also been observed in Swedish wolverine *Gulo gulo* management (Carter *et al.* 2017). This presents a potential challenge where the objective is improving coexistence between gamekeepers and predators, as evidence suggests that those that rely on ‘local knowledge’ (such as personal experiences) might estimate predator populations to be increasing significantly faster than those who rely on ‘scientific knowledge’ (such as academic articles) (Ainsworth *et al.* 2016).

Defining concepts for improved communication

Discussions over conservation conflicts have encountered problems where terms or concepts mean different things to different stakeholders. For example, while stakeholders discussing predator management in the uplands of Scotland could agree their broad goal was “to establish and maintain balanced and healthy populations”, the concepts of balance and health within this statement translated into different ecological realities depending on associated conservation-management objectives (Ainsworth *et al.* 2016: p14). I therefore take this opportunity to describe how gamekeepers in my sample perceived ‘balance’ and ‘nature’, concepts central to how they managed predators and the natural world.

While broader publics might define ‘natural’ as “*that which is not under the control of humans*” (Clayton & Myers 2009: p16), gamekeepers appeared to perceive the concept as that which has not been affected, for better or worse, by human activities. The differences in these definitions have real management implications, allowing gamekeepers to rationalise much predator control as corrective. In this sense, there was evidence that some predator management was viewed as hybrid (Latour 1993), a product of a socio-natural landscape: “*We live in a managed environment, everything needs managing*” (G16, HK). In a similar way, gamekeepers viewed ‘balance’ in the predator populations as a point where the perceived benefit or cost to a species from human activities (including the activities of the gamekeepers themselves) was countered. Therefore, ‘keeping the balance’ was framed as both a professional and moral duty. This result can be seen as a version of the ‘outrage effect’ where individuals are more willing to pay to correct environmental problems presented as man-made than those presented as ‘natural’ (Bulte *et al.* 2005).

By identifying and exploring narratives concerning ‘balance’ and ‘nature’, this study joins a small body of literature that has investigated how underlying philosophies about the natural world influence wildlife management (Buller 2008; Eden & Bear 2011; Maye *et al.* 2014). Such philosophies can have significant sway over decision making (Adams 1997; Buller 2008). For example, when ecosystems are thought able to regulate themselves, minimal interference might be advised (for example 'the land ethic': Leopold 1949). However, when important components are thought to be under or over-represented, direct intervention might be preferred. Intervention can take the shape of introductions (for example ‘rewilding’: Nogués-Bravo *et al.* 2016) or population control. Where the intervention involves lethal management, there is evidence that other rural stakeholders share this perspective, viewing lethal management as necessary to ‘rebalance’ nature (Campbell & Mackay 2009; Maye *et al.* 2014).

Representation of motivations

Although several of the older respondents in this study perceived that attitudes to predators in their profession had changed and were changing, attempts to fundamentally alter the way that individuals think is difficult over short timescales (Manfredo *et al.* 2017). Instead, there is potential to “recognise and work within the boundaries of existing values” (Manfredo, Teel & Dietsch 2016: p287). In this context, that would mean asking the question: how do we best conserve predators, given the values and beliefs of gamekeepers? Although my study provides a strong foundation from which to consider this, such a question might best be answered by addressing the relative strength of the motivations I outlined (St. John *et al.* 2014). Following others (Marchini & Macdonald 2012), this could be analysed (semi)quantitatively to uncover the relative power of each motivation in predicting behavioural intention or behaviour. Data on the strength of the various motivations would then encourage targeted interventions aimed at fostering higher levels of coexistence (St John, Edwards-Jones & Jones 2010). Take, as an example, an initiative working to reduce the illegal killing of birds of prey: quantifying the respective strengths of ‘perceived impact’ and ‘potential penalties’ at predicting behavioural intention would allow the direction of effort towards either disseminating information emphasising the consequences of being caught or, alternatively, methods for preventing predation of gamebirds. Thus, testing the strength of my findings should be considered an important step towards the development of communication and engagement strategies within conflicts.

Study limitations

The geographic focus of this research involves some limitations for broader application of these findings. Chiefly, these concern the absence of any large carnivores in the U.K. As a consequence, factors that can significantly influence management preferences, such as risk to high value livestock (e.g. horses) or to human safety (Frank, Johansson & Flykt 2015) are missing from this study. It should also be stressed that, although I have reported negative attitudes to protected predators, that are not at all equivalent to illegality (Delibes-Mateos 2013). That said, the repeated identification of links between some gamekeepers and illegal predator killing (Whitfield *et al.* 2003; Whitfield 2004; Smart *et al.* 2010; Amar *et al.* 2012; Whitfield & Fielding 2017) will certainly make these findings relevant to those wishing to understand this behaviour. With Delibes-Mateos (2013), I call for further research that attempts to understand when negative attitudes towards protected predators result in illegal activities.

Conclusions

Using qualitative research methods and analysis I have provided a detailed exploration of a question central to multiple conservation conflicts: why do gamekeepers kill predators? By contextualising this behaviour within broad motivations my findings suggest that predator control in the U.K. is not simply a consequence of impact perception, but rather complex and interacting social, personal and ecological perceptions. Furthermore the findings indicate that gamekeepers are not simply motivated by financial rewards but are knowledgeable stakeholders with emotional ties to both wildlife and the game they release. Conservationists, policy makers and scientists will benefit from acknowledging perspectives and motivations, beyond those relating to ecology or economics.

Chapter 7

DISCUSSION

Chapter 7: Discussion

As human populations continue to expand, it seems inevitable that pressures on wildlife and ecosystems will intensify (Cardinale *et al.* 2012). The loss of predatory species that compete with humans for space and resources has been identified as a particular concern (Ritchie & Johnson 2009; Ripple *et al.* 2014), causing disruption to ecological processes and the degradation of ecosystems (Estes *et al.* 2011). Nonetheless, living alongside predators can prove challenging. They can pose a direct threat to conservation objectives, human livelihoods and even human safety (Thirgood, Woodroffe & Rabinowitz 2005; Festa-Bianchet *et al.* 2006; Neff & Hueter 2013). Therefore, a key test for conservation in the 21st century is to find ways to sustain predators in human dominated landscapes (Chapron & López-Bao 2016). This will require the successful mitigation of the ecological impacts as well as the management of the social conflicts they can create (Redpath *et al.* 2013). The broad aim of this thesis is to contribute to human-predator coexistence by exploring the perceptions of impacted stakeholders from ecological and social perspectives.

I have done so by concentrating on conservation conflicts around predation and gamebird shooting in the UK. This is a system in which predation, and predator management, have taken a central place since the 17th century (Munsche 1981; Martin 2011), dictating the fortunes of British wildlife for better and worse (Lovegrove 2008). Yet while gamebird shooting has remained, for the most part, very traditional (Reynolds & Tapper 1996), wider publics have begun to value wildlife differently (Teel, Manfredo & Stinchfield 2007). This value change has matched an increase in non-consumptive wildlife use (Treves & Naughton-Treves 2005; Walpole & Thouless 2005; Booth *et al.* 2011). Indeed, while there is evidence that the number of people interested in gamebird shooting is rising (Martin 2011), bird hunters now find themselves greatly outnumbered by bird watchers (Treves & Naughton-Treves 2005). Thus, disagreements over predator management might be seen as symptoms of a larger underlying conflict between ‘traditional’ forms of land management (i.e. farming and shooting) that value wildlife in a more utilitarian way and more urban populations that prioritise animals' rights, welfare and conservation (Manfredo, Teel & Henry 2009; Dickman, Marchini & Manfredo 2013). This societal divergence has, perhaps, made conflicts over wildlife management inevitable.

As highly visible predators, birds of prey enjoy an elevated position in the public consciousness, in conservation efforts and in considerations of land management (Galbraith, Stroud & Thompson 2003). Yet, for those with interests in gamebird hunting, the positive value of these birds can be outweighed by their perceived negative impact. The disparity in how various parties perceive these birds has created particularly acute disagreements over their management (Park *et al.* 2008; Thirgood & Redpath 2008; Lees, Newton & Balmford 2013). These have developed into conservation conflicts where the 'sides' tend to believe that their interests are being dismissed or ignored by the other (Redpath & Thirgood 2009; Sotherton, Tapper & Smith 2009; Thompson *et al.* 2009). Such conflicts are exacerbated by illegal killing, which serves to build distrust and animosity (Redpath *et al.* 2013). Some of these conflicts, namely that over hen harrier conservation (Thirgood *et al.* 1997), have now been on-going for several decades, potentially adding specific, contemporary meaning and emotion to somewhat unrelated disagreements about wildlife management.

Ecology can play a vital role in informing these debates and providing robust, objective evidence that enables those involved in the conflict to negotiate solutions (Messmer 2000; Ormerod 2002). This could be by uncovering the scale of perceived impacts (Kenward *et al.* 2001), identifying the underlying causes (Francksen *et al.* 2017) and testing potential solutions (Redpath, Thirgood & Leckie 2001). However, the social context in which these conflicts are enacted should not be overlooked (Manfredo & Dayer 2004; Madden & McQuinn 2014). Addressing any underlying social drivers is particularly important as fundamental differences in values and attitudes can cause misunderstandings (Ainsworth *et al.* 2016) and a breakdown of communication (O'Rourke 2014), even where aspects of underlying ecology might be agreed.

In this thesis, I have addressed both ecological and social aspects of a conflict surrounding predation and game shooting interests. This has involved detailed investigation of two perceptions that appear central in how gamekeepers view and manage predators. Specifically these are 1, that certain animals are disproportionately responsible for impacts and 2, that the release of gamebirds creates high densities of protected predators. These studies have required the application of dietary stable isotope analysis as well as more conventional means of collecting ecological data, such as point counts and prey abundance sampling. I have also contributed to a more detailed understanding of gamekeeper motivations for predator control. This is a stakeholder group who, despite having a central role in conservation conflicts, has been the subject of little academic attention. This was facilitated by the application of inductive, qualitative methods to explore complicated reasoning through the perspective of those that conduct predator control.

I now revisit the original aims of this thesis before reviewing how my findings relate to each one:

1. Review the literature for evidence of the existence of 'problem' animals in human-wildlife impacts and assess if 'selective removal' is a generally viable policy from social and ecological perspectives.
2. Evaluate the use of dietary stable isotope analysis as a potential method for studying the diet of wild predators.
3. Assess the ecological evidence that, within buzzard populations, there is a limited number of 'problem' buzzards that disproportionately feed on released gamebirds.
4. Investigate the numerical and functional responses of buzzards to gamebird abundance on shooting estates.

5. Explore the motivations behind predator management from the perspective of those that conduct it, the gamekeepers.

In this discussion, I synthesise the key findings of this study in relation to these original aims. I then go on to discuss their management implications within conflicts over game management and human-predator conflicts more widely. Finally, this thesis concludes with a review of outstanding questions and recommendations for future research.

Addressing the aims of this thesis

Aim 1: *Assess the evidence of the existence of 'problem' animals in human-wildlife impacts and evaluate if 'selective removal' is a generally viable policy.*

There is much anecdotal evidence from those suffering human-wildlife impacts that specific animals are disproportionately responsible (Linnell *et al.* 1999). Indeed, this perception is central to recent licences that allow the killing of specific birds of prey in the UK. However, as yet, there had been no synthesis as to whether this was a viable and effective management policy. In Chapter 2, I conducted a literature review that assessed the ecological evidence for 'problem individuals' playing a role within human-wildlife impacts.

There is now substantial evidence that within-population behavioural variation is common in wild animals, influencing a suite of natural processes. In wildlife management I found evidence that 'problem' animals were involved in many human-wildlife impacts, with the clearest examples in generalist species with high behavioural plasticity. Often, mitigation measures appear to take this into account, yet the accuracy of methods to identify and target these individuals is variable and species specific. I highlighted that three approaches were available for those adopting 'selective' management, focused on identity, location and demographic class. Lethal control of these animals was often the only practical option for wildlife managers. Indeed, translocations can, on occasion, make impacts worse.

In Chapter 2, I also acknowledged the human aspects of wildlife management by exploring whether problem individual removal met social objectives. Removing specific individuals can generally be seen as more socially acceptable than generalised population control, though this prospect is still likely to receive opposition from some quarters. Evidence for selective management increasing tolerance towards species, though assumed, is uncertain and requires further investigation. Despite successes, I identified that targeting problem individuals should not be seen as a long-term solution. The behaviour these animals exhibit, though often rare in population terms, seldom appears to be truly unique. Consequently, any benefits of removal might be short-lived as problem animals are quickly replaced. As these strategies often involve on-going lethal management, I highlight the need to consider the indirect effects of ‘selective’ management such as skewed sex ratios, breakdown in social systems and, in the long term, trait selection.

The findings from Chapter 2 formed the foundation of two further chapters of my thesis. First, this work highlights the importance of precision in determining between-individual variation in diet, leading to my investigation in Chapter 3 of stable isotope analysis as a tool in quantifying individual variation in diet. Second, my review highlighted that, although ‘selective management’ and problem animal removal is common in wildlife management, it is rarely specifically evaluated with ecological evidence, leading to my work in Chapter 4 on an ecological basis for identifying problem individuals.

Aim 2: *Evaluate the use of dietary stable isotope analysis as a potential method for studying the diet of wild predators.*

In conflicts over animal management, the diet of predators is often of specific interest. Yet collecting the necessary fine-scale dietary data is tricky, conventionally relying on indirect methods (such as analysing faeces, prey remains or regurgitated pellets) that are known to contain unpredictable biases. In Chapter 3, I evaluated the performance of dietary stable isotope analysis at quantifying buzzard diet using the $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios from the feathers and blood of buzzard nestlings. I studied dietary composition determined with multiple Bayesian stable isotope mixing models (BSIMMs) run with various trophic discrimination factors (TDFs) and with/without informative priors. These were then compared to estimates of diet collected from direct observations using remote cameras of prey provisioned to nestlings in the same nests. My results show that BSIMMs with different TDFs varied markedly in their performance, though I highlight a recently developed statistical package (SIDER; Healy *et al.* 2016) as producing BSIMMs with the greatest similarity to the observed diet. These models produced strong agreement at the population level and, for the main prey of buzzards, at the individual nest level. I use the provisioning data to show how the inclusion of informative priors from conventional analysis of prey remains, markedly reduced model performance. The results of this chapter show that BSIMMs can provide highly accurate assessments of diet in wild animals at population and finer scales.

In recognition of the findings in Chapter 3, I utilised dietary stable isotope analysis in Chapter 4 to assess the diet of adult birds over a broader time period. These results also gave me a confidence that my selection of model inputs, specifically TDFs and keeping informative priors absent, would yield reliable data.

Aim 3: *Assess the ecological evidence that, within buzzard populations, there are a limited number of 'problem' buzzards that disproportionally feed on released gamebirds.*

In Chapter 4 I bring together the findings of Chapters 2 and 3 by applying dietary stable isotope analysis to assess the existence of 'problem buzzards' that are disproportionately feeding on gamebirds. In so doing I also evaluated the efficacy of recent mitigation methods that have licensed the killing of specific birds. I analysed the stable isotope ($\delta^{13}C$ and $\delta^{15}N$) ratios of adult buzzards and their known food sources using BSIMMs to estimate the relative contribution that released pheasant poults make to buzzard diets. This was possible as released pheasants were isotopically distinct from other buzzard prey, including wild pheasants, as a result of their distinctive anthropogenic diet pre-release. I observed significantly higher released pheasant consumption by buzzards from territories with a release pen that had a perceived predation problem than those in territories with no release pen. However, variation in the released pheasant consumption in buzzards from territories with a release pen and no perceived predation problem suggests that in some pens, pheasant consumption is going undetected or unremarked as a problem. Analysis of the tissue of a small sample of alleged 'problem buzzards', caught and released under license within pheasant release pens, suggested that buzzards caught within pens consumed more released pheasants than their conspecifics. However, this was only apparent in tissue formed in the preceding days and weeks (red blood cells and blood plasma) suggesting that 'problem' behaviour might not be consistently expressed over long time periods. Although these results suggest that released pheasant consumption is not limited to buzzards in territories around 'problem pens', they provide evidence that the current management strategy (only removing those birds found feeding within pens) can target these individuals somewhat effectively.

Aim 4: *Investigate the numerical and functional responses of buzzards to gamebird abundance on shooting estates.*

In Chapter 5 I sought to investigate buzzard ecology on shooting estates. Shooting interests perceive that buzzards respond to high local abundance of pheasants both numerically, in the form of increased population densities and/or productivity, and functionally, by increasing the contribution of pheasants to their diet. To examine these hypotheses, I studied how the relative abundance of pheasants, as well as two alternative prey items (rabbits and field voles), correlated with buzzard density, foraging and breeding success on, and around, pheasant shooting estates in southwest England. I provided evidence that nearest neighbour distance between buzzard nests, a proxy for buzzard breeding density, decreased as the abundance of both pheasants and rabbits increased. However, the provisioning data from the nest cameras showed that only rabbit provisioning rate was related to nestling number. Of the three prey groups, rabbits were also the only prey for which there was a significant positive relationship between abundance and provisioning rate, strongly suggesting that rabbits, not pheasants or field voles, are preferred buzzard prey. My results provide evidence that the provisioning of pheasant prey during the nestling period does not significantly influence the productivity of buzzard pairs. However, the positive relationship we observed between pheasant abundance and buzzard density has the potential to influence perceptions of impact by association. This feedback between encounter rate and perception of impact is further explored during Chapter 6.

Aim 5: *Explore the motivations behind predator management from the perspective of those that conduct it, the gamekeepers.*

Predator killing, both legal and illegal, is a frequent cause of conservation conflict. This is particularly true of conflicts over game management in the UK where disagreement over predator control is common and shooting estates are often linked with illegal killing. Despite the central role of game managers as stakeholders and actors in this activity, surprisingly little attention has been paid to their perspectives and motivations. In Chapter 6 I sought to address this by conducting semi-structured interviews on the subject of predator control with 20 gamekeepers across the south of England. I explored how various aspects of predator ecology (including those investigated in Chapters 2, 4 and 5) were perceived. The results suggest that, while predator control is structured around perceived impacts, there are a number of currently unacknowledged factors that influence how management decisions are made in practice. Six separate motivations for predator management emerged: professional norms, personal norms, potential penalties, perceived impact, personal enjoyment and perceived efficacy. I illustrate how these might influence actions using the Theory of Planned Behaviour to structure a conceptual model. The results of this chapter not only uncover potential underlying drivers of predator control but also characterise the information sources used to make decisions and detail how specific concepts are perceived and defined. I use the discussion to outline how this work could be taken forward to identify the predictors with the greatest influence over specific predator conflicts. Tailoring conflict management in such a way has the potential to address conflicts at their root leading to more effective mitigation.

Synthesis of key contributions

In this section I will discuss the themes of my thesis and how my findings link together. My objective is to synthesise the key results and discuss how they might be used to address both conflicts over predator management generally and gamebird predation specifically.

Addressing the ecological aspects of predator management

For the removal of problem individuals to be effective in mitigating human-wildlife impacts, the targeted subset of the animal population must be disproportionately responsible (Linnell *et al.* 1999; Swan *et al.* 2017). This makes the data presented in Chapter 4 particularly pertinent to the current methods used to reduce buzzard impact at pheasant pens. The results present a mixed picture. On the one hand, I show that buzzards living near problem pens do indeed consume significantly more pheasants than those living away from pens and, that of our subsample of four ‘problem’ buzzards, two had been consuming enough released pheasants to make then distinct from the wider population. On the other hand, I observed no significant differences in released pheasant consumption between those buzzards with territories including ‘problem pens’ and other buzzards with pens in their territories. I suggest that, when taken together, these results provide tentative evidence to support current mitigation methods (licensed removal of buzzards observed in pens). However, it might be considered that this approach represents a trade off between sensitivity and specificity of the detection method (i.e. catching in pens), in that it suggests that not all the buzzards consuming pheasants will be identified but, of those that are, most will be correctly identified as pheasant killers. I recommend that, if further licences are granted to remove individuals, dietary stable isotope analysis be applied to evaluate this assumption. This stable isotope method proved an efficient and readily applicable method to studying the predation of released gamebirds.

Another key finding of this thesis that advances our understanding of buzzard ecology was the significant relationship between buzzard nesting densities and the abundance of ‘wild’ (pheasants that had either survived the previous shooting seasons or had hatched in the wild) game. Drawing on this result, and the frequent references to buzzard populations being above their ‘natural’ carrying capacity in the discussions presented in Chapter 6, I suggest that positive relationship between buzzard and pheasant abundance might serve to increase perceptions of impact through the association of the two species. However, the dietary data presented in Chapter 5 indicates that pheasants generally represent a relatively small proportion of diet (at least in the buzzard nesting season), despite being abundant in many territories. Instead, the majority of buzzard diet is comprised of prey such as rabbits, small rodents and amphibians. Of these (non-game) prey, rabbits were the most important prey in terms of overall nutritional contribution (Chapter 3) and determining buzzard productivity (Chapter 5).

Although I have provided evidence that some buzzards disproportionately feed on released pheasant poults, the results from Chapters 4 and 5 suggest that the contribution that pheasants make to the diet of the ‘average’ buzzard is low. This is in keeping with previous studies (Kenward *et al.* 2001; Valkama *et al.* 2005). However, recent work on buzzards and grouse has highlighted that, while predation is relatively rare, the cumulative effect of high densities of buzzards has the potential to have “*a considerable impact*” under certain conditions (Francksen 2016: p 172). Ultimately however, the question of whether buzzards are having a significant impact on the number of pheasants available to shoot cannot be answered yet. This is partly because neither of the two dietary assessment methods (stable isotope analysis and nest cameras) used in this study permitted a clear differentiation between predated and scavenged food sources. This is a common problem for studies that examine small game predation (Allen 2001; Turner & Sage 2004; Francksen *et al.* 2016). We know from an extensive radio tracking project of released pheasants that approximately 10% of mortality is ‘accidental’ (e.g. vehicle or fence collisions) (Turner 2007). And, although there is little published evidence to support Sim’s (2003) assertion that the majority of gamebirds in buzzard diet are scavenged, we did observe clear signs of scavenging (e.g. maggots within the carcass) on some, but not all, of the larger pheasants brought back to the nest.

There are other ecological mechanisms by which the impacts of predation might not carry through into a reduction in pheasants available to shoot. For example, it is possible that some predators kill more sick birds that would not have survived to the shooting season. Disproportionate raptor predation on parasitised gamebirds has already been observed in upland ecosystems (Hudson, Dobson & Newborn 1992). Such a loss would not be additive to mortality experienced without predation and would thus have little influence on shooting returns (Redpath & Thirgood 2003). It is also possible that high densities of buzzards might moderate predation of pheasants by other predators; recent research has raised the prospect that buzzards might serve to reduce the densities of alternative predators, such as foxes *Vulpes vulpes* or carrion crows *Corvus corone*, through direct predation or competitive suppression (Lees, Newton & Balmford 2013; Rooney & Montgomery 2013).

Addressing the social aspect of predator management

There is a conviction among conservation scientists that wildlife management should guided by a systematic appraisal of the evidence rather than more traditional knowledge, perceptions, anecdotes and "myths" (Sutherland *et al.* 2004). While this is generally laudable, "*robust scientific evidence alone is not sufficient to manage predators effectively*" (Woodroffe & Redpath 2015: p1313). Social factors can have direct implications for conservation objectives, especially when conflicts involve predator killing (Goldman, de Pinho & Perry 2013; O'Rourke 2014; Inskip *et al.* 2014; Verissimo & Campbell 2015; Pohja-Mykrä 2016). Indeed, the influences of social factors (perceptions, values, beliefs, etc.) on predator control have been outlined in this study. While I recommend that conservation practitioners should attempt to understand and engage with gamekeeper perspectives, translating this into successful conservation objectives is not a trivial undertaking.

One avenue that appears particularly relevant to promoting coexistence with predators is attempting to increase tolerance toward these animals (Treves & Bruskotter 2014). This might be possible if the value of predators to broad publics is translated into tangible benefits to those impacted (Dickman, Macdonald & Macdonald 2011). Tolerance for predators has been facilitated through financial payments (Nelson 2009), however, there is no precedent for government based compensation for predators in the UK (Wilson 2004).

If we accept, possibly controversially, that protective legislation alone will not be sufficient to prevent predator killing (Thirgood & Redpath 2008). A pertinent question in relation to this thesis would be whether allowing the removal of a limited number of buzzards would increase gamekeeper tolerance towards the species as a whole? Although this question has been explored in general in relation to 'problem individual' removal in Chapter 2, I take this opportunity to highlight some key findings. There is good evidence that affording individuals control over an activity or threat will make them more likely to accept risks (Starr 1969; Dickman 2010). There is also evidence that, when people see animal populations as individuals, they compartmentalise their bad behaviour as being the fault of an individual rather than a species (Lescureux & Linnell 2010; Dorresteijn *et al.* 2016). We also know that some wildlife authorities might opt to kill, or allow the killing of, animals as a mechanism to increase tolerance (Hoare 2001). Whether this translates into tolerance for predators remains uncertain. The acceptance capacity toward brown bears in Croatia appears to have declined when local residents were not able to remove individuals through hunting (Majić *et al.* 2011). However, the results of Chapron and Treves (2016) suggest that policies that allowed the culling of some animals (intended to increase tolerance for the species as a whole) actually increased illegal killing.

In Chapter 6, I provide evidence that tolerance (in the form of motivation to control) is partly a function of the professional norms and values of the gamekeeping profession. Despite questionable attempts by conservationists to impose certain values to save threatened species (Dickman *et al.* 2015), changing the way that individuals think about the natural world is difficult over short timescales (Manfredo *et al.* 2017). Instead, there is potential to develop initiatives that are consistent with values that are already present (Manfredo, Teel & Dietsch 2016). In the context of predator killing and game management it would mean identifying the motivations that have the most influence on behaviour and tailoring mitigation efforts specifically to address them. There are examples where this has worked to protect predators. In Maasailand, Kenya, young men were motivated to kill lions by strong cultural drivers such as the opportunity to increase their social status (Hazzah *et al.* 2014). By employing these men as ‘Lion Guardians’, these cultural drivers appear to have been maintained alongside the desired effect of greater coexistence between lions and the Maasai (Hazzah *et al.* 2014).

Although attempting to build such a model that is relevant to gamekeepers and birds of prey is beyond the scope of this thesis, I suggest that there are motivations described in Chapter 6 that might provide the foundations for considering such a strategy. For example, despite the killing of wildlife being a common aspect of their profession, gamekeepers articulated a strong personal responsibility towards protecting both game and other wildlife, including predators that were perceived as rare. I hypothesise that designing mitigation strategies that incorporate and work with such values or beliefs will have greater acceptability and longevity. Mitigation efforts that focus solely on financial or ecological impacts without considering stakeholder acceptability may fail, despite their sound evidential foundations. For instance, despite studies showing that diversionary feeding is remarkably successful in reducing red grouse predation by hen harriers (Redpath, Thirgood & Leckie 2001), the uptake of this mitigation method has been poor, due possibly to the strongly negative views toward it, expressed by key stakeholders (Milner & Redpath 2013).

Incorporating both predator ecology and stakeholder motivations

In this thesis, I have explored not only the ecological aspects of predation and predator behaviour but also the social-psychological drivers that influence predator management. Yet, the behaviour and presence of wild animals and the responses of humans to these stimuli, feed back jointly into social–ecological systems (Sjölander-Lindqvist, Johansson & Sandström 2015). There is growing interest in multidisciplinary management frameworks that account for both of these drivers concurrently (White *et al.* 2009; Dickman 2010; Redpath *et al.* 2013; Carter *et al.* 2017). In this section of the discussion I fit the results of this thesis into one such framework, illustrating how predator management occurs simultaneously within social and ecological contexts.

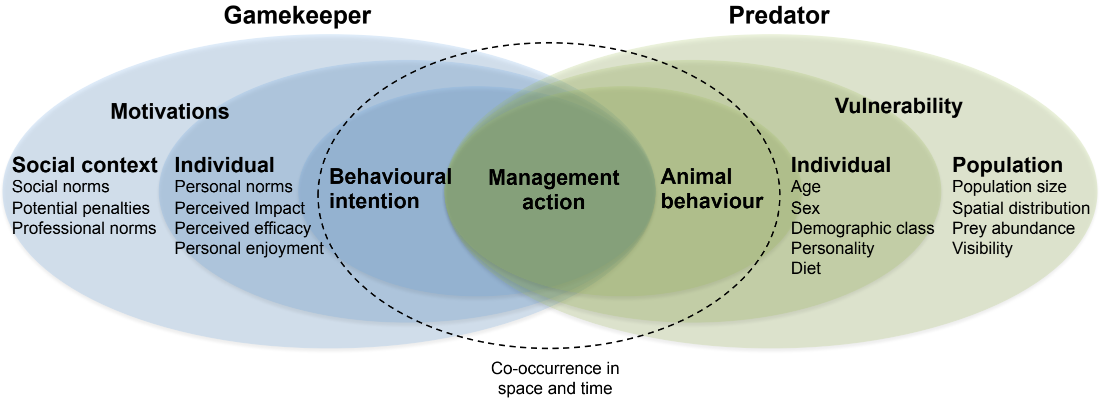

Figure 1. *Social-ecological system framework for predator control on gamebird shooting estates. The area within the dashed circle indicates the co-occurrence of gamekeepers (or their traps, snares and poisons) and predators in space and time. Factors shown here are taken from the findings of this thesis and from relevant literature. The social-ecological framework is adapted from Carter* et al. *(2017)*

I adapted a nested social-ecological system framework originally developed by Carter *et al.* (2017) to explore carnivore poaching (Figure 1). In this figure the two innermost shells illustrate that control is only possible when predators and humans (or their tools) co-occur in space and time. The two middle shells detail the individual attributes of both people and predators that might influence human tolerance. I draw from the findings of Chapters 2 and 4 to populate the individual predator characteristics. For instance, I include 'sex' as a factor here, as there is a general trend for males to be overrepresented in human-wildlife impacts (Königson *et al.* 2013; Mutinda *et al.* 2014; Moseby, Peacock & Read 2015). Individual factors on the human side are principally those personal motivations outlined in Chapter 6. Here, overlapping shells illustrate the feedback mechanisms that influence how decisions are made. For instance, predator visibility might serve to increase the perceptions of impact. The outer-most levels of this framework detail the broad factors that determine how gamekeepers as a 'community of practice' interact with predatory species (Carter *et al.* 2017). This includes social influences such as professional norms (outlined in Chapter 6) but also characteristics of the predator species, such as its spatial distribution and dietary breadth (outlined in Chapter 5).

Future research directions

My work has highlighted a number of social and ecological questions that would advance the field of conservation conflicts, particularly those concerning predator impacts or selective management. By highlighting these areas for future research I also acknowledge a few of the limitations of this thesis and key caveats. Due to the propensity for scientific evidence to be contested or dismissed in conflicts (Woodroffe & Redpath 2015), it is crucial that such studies are not perceived by any of the parties concerned to be biased (Kenward et al. 2001).

(I) What are the ecological drivers of problem behaviours, and can proactive management of such drivers alleviate impact?

This question is at the core of the ecological side of problem animal management, yet few studies have addressed it explicitly. While tackling the ecological drivers requires an analysis of the correlates of certain behaviours (such as Artelle *et al.* 2016), finding proactive mitigation measures for behaviours that are rarely expressed could prove potentially costly. In this instance, wildlife managers need to weigh up social, financial and ethical costs of both reactive animal removal or proactive mitigation. In the case of buzzard predation on released pheasants, the work of Kenward *et al.* (2001) that highlights specific release pen characteristics provides a cost effective start. Experimental manipulation of pen characteristics with the simultaneous application of carcass recovery and dietary isotope analysis of buzzard tissue would provide the data to test this properly.

(II) Does removing ‘problem buzzards’ reduce impacts and how long are benefits apparent?

There is a lack of randomised experiments that investigate whether predator control meets its stated objectives (Woodroffe & Redpath 2015; Treves, Krofel & McManus 2016). Although evidence suggests that removing 'problem' buzzards will pose little threat to long-term conservation objectives (Kenward *et al.* 2000, 2007), little is known about the effects of culling raptor populations (Viñuela & Arroyo 2002). Buzzard pairs maintain exclusive territories (Prytherch 2013) and there is growing evidence that removing territorial predators as a livestock protection measure can create indirect negative feedbacks such as increasing populations and impacts (Peebles *et al.* 2013; Minnie, Gaylard & Kerley 2015). That said, Parrott (2015) provides anecdotal evidence that the removal of a single adult 'problem' buzzard at a free-range chicken farm was enough to stop all predation problems.

(III) Is pheasant provisioning influenced by the abundance of alternative prey sources?

The ecological data presented in this thesis come from a detailed study of a single year. However, the reliability of the findings would be increased by a more extensive study. There are also questions that arise from the findings that warrant investigation over a wider temporal period. Specifically, while I provide evidence in Chapter 5 that pheasants were not provisioned in proportion to their abundance, it would be particularly interesting to explore if the rate of pheasant provisioning changed in relation to prey densities in that territory. Buzzards are generalist predators and therefore it is possible that they might increase predation of gamebird prey in response to declines in primary prey species (rabbits). This is known as the alternative prey hypothesis (APH) (Angelstam, Lindström & Widén 1984). There is conflicting support for the APH influencing gamebird predation. Studies from Finland show that as the abundance of mammals declined, the proportion of gamebirds in predator diets increased (Reif *et al.* 2001, 2004). However, recent research by Francksen *et al.* (2017) looking at buzzard diet in the uplands did not observe an increase in grouse consumption when the primary prey declined.

(IV) What are the relative influences of the various motivations for predator control?

Where specific behaviours are being investigated, a quantitative analysis of the conceptual model provided in Chapter 6 would not only allow researchers to calculate the overall probability of a behaviour (Marchini & Macdonald 2012), but also highlight the differential influence of the various motivations (St John, Keane & Milner-Gulland 2013). Potential options include a structured questionnaire that includes Likert-type answers where respondents are given a spectrum of tick boxes between strongly agree and strongly disagree (St. John *et al.* 2014), or Q-methodology, in which participants sort relevant statements about the issue into an order that best reflects their viewpoint (Watts & Stenner 2005). Having such data could allow any intervention measures to be specifically targeted at the motivation most likely to influence behaviour.

(V) Does framing human-wildlife impacts as a consequence of individual-level behaviour create more or less disparity between stakeholder preferences to mitigation methods?

While there would be great utility in predicting the behaviours of certain actors (e.g. those where objectives are to change behaviours), managing conservation conflicts requires compromise between two or more parties (Redpath *et al.* 2013). Here, value may lie in investigating stakeholder preferences towards certain mitigation measures (Don Carlos *et al.* 2009). Of specific interest to this thesis would be research that measures whether changing the framing of impacts from populations to individuals would create more or less disparity between stakeholder preferences to mitigation methods.

Conclusions

Finding effective methods to manage conservation conflicts is a daunting task with few examples of successful resolution. Instead, conflicts need to be managed through dialogue and compromise. This requires an interdisciplinary perspective that investigates the motivations of key stakeholders, the reality of the perceived impacts and the efficacy of any methods intended to remedy them. By exploring conflicts surrounding predation and game management in the U.K., this thesis makes a contribution to our academic understanding of all three of these levels. It is clear that predator management (both legal or illegal) on game shooting estates is not simply a consequence of perceived financial risk, rather a complex combination of different motivations that include professional norms, personal moralities and interpretations of the natural world during daily observation. I highlight that within these motivations there are interactions and feedbacks that require consideration. While addressing such social-ecological drivers represents a challenge for those who wish to increase tolerance, mitigation measures that incorporate and work with these motivations have the potential to achieve lasting benefits.

APPENDICES

Appendices

Appendix 1: *Summary of studies examining buzzard diet in the U.K. and across Europe.*

N = Number of dietary samples, NT = Number of territories/nests, Units percentage by frequency (%) unless otherwise stated, (*) denotes U.K. studies whose area was known to contain shooting estates, † = unpublished studies, (?) *unknown, (-) unrecorded*

Reference	**Country**	**Dietary analysis method**	***N***	***NT***	**Unit**	**Mammals**	**Birds**	*Gamebirds*	**Herpetofauna**	**Invertebrates**	**Carrion**	**Others/ Unidentified**
Francksen *et al.* (2016)*****	Langholm, South Scotland (*winter*)	Pellet analysis	2100	44	%	73.3	7	***2.6***	-	19.6	-	-
Francksen, Whittingham & Baines (2016)*****	Langholm, South Scotland (*summe*r)	Video records	1005	32	%	58.9	13.1	***2***	14	0.5	-	13.5
		Prey remains	486	32	%	34	58	***21.6***	5.3	2.7	-	-
		Pellet analysis	476	32	%	60.7	14.5	***4.9***	1.1	23.7	-	-
Prytherch (2016)	Avon, Southwest England	Prey remains	301	108	%	40.0	58.9	***3.6***	0.7	-	0.3	-
Graham et al., (1995)*****	Langholm, South	Pellet analysis	581	19	%	74.0	16.9	***-***	2.6	6.4	0	0.2

	Scotland											
		Prey remains	365	19	%	48.8	46.6	***15.1***	1.4	0.2	0	0.2
Newton, Davis & Davis (1982)	Cambrian Mountains, Wales	Pellet analysis	1297	91	%	43.1	15.7	***0***	0.3	23.7	17	0.2
Kenward *et al.* (2001)*	Dorset, Southwest England	Prey remains	233	61	%	?	?	***2.6***	?	?	?	?
Sim *et al.* (2001)*	West Midlands, England	Prey remains	253	77	%	61.2	35.6	***5.1***	0.4	0	0.4	0
Dare (2015)*	Dartmoor, Southwest England	Pellet analysis	214	?	%	69	2	***-***	29	-	-	-
		Prey remains	508	?	%	67.1	14.4	***-***	14.8	?	?	?
Jardine (2003)	Colonsay, Scotland	Prey remains	313	?	%	61.7	37.7	***0.6***	0.3	-	-	0.3
				?	% (wt)	87.8	12.1	***2.6***	0.1	-	-	0.0
Swan (2011)* †	Central Scotland	Prey remains	170	38	%	57.6	35.3	***5.3***	4.1	-	2.9	0
		Pellet analysis	118	38	%	75.4	15.3	***-***	9.3	-	0	0
		Video records	263	6	%	41.8	11.8	***1.9***	37.6	-	0	8.7
Rooney & Montgomery (2013)*	Northeast Ireland	Prey & pellets	1194	61	%	41	41.2	***2.3***	0.5	17.3	-	-

Zuberogoitia *et al.* (2006)	Northern Spain	Prey remains	158	?	%	42.4	27.2	***0.6***	30.4	0	-	-
	Southern Spain	Prey remains	167	?	%	38.3	38.3	***5.4***	37.1	2.4	-	-
Reif *et al.* (2001)	Western Finland	Prey & pellets	1906	113	%	54.7	36.1	***7.4***	6.5	-	-	2.8
					% (wt)	38.3	55.2	***30.3***	4.1	-	-	2.4
Selås (2001)	Southern Norway	Prey & pellets	839	22	%	46.0	30.3	***2.5***	23.7	-	-	-
Selås *et al.* (2007)	Southern Norway	Video records	82	11	%	36.6	31.7	***0***	31.7	-	-	-
		Prey & pellets	148	11	%	29.7	35.8	***0***	34.5	-	-	-
Manosa & Cordero (1992)	Northeast Spain	Prey remains	598	80	%	69.6	16.1	***5.0***	14.0	-	-	-
		Pellet analysis	201	80	%	49.8	12.4	***-***	35.8	2.0	-	-
		Stomach contents	240	69	%	18.8	1.25	***0.4***	6.7	73.0	-	-
Sergio *et al.* (2002)	Northern Italy	Prey remains	142	25	%	28.9	46.5	***0***	23.9	-	-	0.7
Goszczynski *et al. (*2005)	Central Poland	Prey & pellets	747	80	% (wt)	38.5	60.7	***1.0***	0.6	-	-	-
Tornberg & Reif (2007)	Northern Finland	Prey remains	23	7	%	43.4	47.8	***34.7***	8.6	-	-	-
		Video records	104	7	%	52.8	16.3	***9.6***	5.8	-	-	24.9
Skierczyński (2006)	Northeast Poland	Prey & pellets	328	12	%	80.2	13.2	***0***	0	6.6	-	-

Appendix 2: *Remote camera setup*

The nest surveillance cameras were set up as follows. A bullet camera (black & white CMOS 380 TVL) with a waterproof covering was positioned ~1m from the nest up with a ball and socket mount. A mobile screen allowed a second observer on the ground to direct the climber to position the camera until the majority of the nest cup was both in the frame and in focus. The camera was connected to a DVR (digital video recorder) with motion activation technology at the base of the tree via a 20m AV cable. DVRs were programmed to record 5 frames a second for a maximum of 5 minutes when movement was detected. A 32 GB SDHC memory card allowed for < 8 days of footage. The system was powered by 12V leisure battery (33Ah or 120Ah). Cameras were installed on nests during the first or second nest visit. SD cards and batteries were changed every 5-6 days until the chick was > 40 days old. This cut off point was to ensure chicks did not fledge early due to disturbance, however, cameras were left recording and collected once fledging had occurred.

Appendix 3: *Assigning weights to provisioning observations*

Within a prey type or species, raptors may show selectivity; predating certain age (Hoy *et al.* 2015) or weight (Gotmark & Post 1996) classes disproportionately to their relative abundance. For example, Gotmark & Post, (1996) observed a decrease in relative predation risk for sparrowhawk *Accipiter nisus* once they had passed a threshold of body mass (in this instance 40g). This could be the result of underdeveloped predator avoidance strategies in juvenile prey (Hoy *et al.* 2015) or difficulties in catching and killing larger prey (Gotmark & Post 1996). I attempted to account for this in my study reviewing the footage and listing all species where size of buzzard prey indicated that juveniles were selected. We, like Resano-Mayor *et al.* (2014), also noted that large prey carcasses were often brought onto the nest partly eaten. As a result the footage of all prey items >100g were re-watched and the proportion of the carcass available on arrival to the nest was estimated. This value was then multiplied by the prey weight for that size category in order to gain the best possible estimate of mass available to the chick(s). On the rare occasions that carcass proportion could not be estimated, e.g. if the whole carcass could not be observed before consumption, the average carcass proportion of that prey type was used. For prey that could not be identified from the camera footage, e.g. eaten while the bird is facing away, two approaches were taken to approximate the weight of the item; either the item was given the weight of a recently identified item consumed within a similar timeframe or, the amount of minutes it took to consume was used as a proxy for mass (this was judged to be ~20g per minute).

Appendix 4: *Ethics statement for buzzard catching, ringing and sampling*

All animal procedures used in this study were conducted under the U.K. Home Office project licence #30/3274 and conformed with the U.K. Animals (Scientific Procedures) Act, 1986. All research received prior ethical approval from the University of Exeter Animal Welfare and Ethics Committee. Animals were handled by trained and experienced personnel under further licences from both the British Trust for Ornithology (CO/6164) and Natural England (2015-7805-SCI-SCI).

Appendix 5: *Buzzard diet from conventional methods (prey and pellet analysis) at 20 buzzard Buteo buteo nests in Cornwall, U.K. Data are presented showing frequency (N), percentage total frequency (% N), the estimated mean biomass (Est. mean BIO), the total biomass (Total BIO) in weight (g) and percentage (%)*

	Taxon	**Prey group**	**Species**	**Method**	**N**	**% N**	**Est. mean BIO (g)***	**Total BIO (g)**	**% total BIO**
Mammals	Lagomorpha	Rabbits	Rabbit *Oryctolagus cuniculus*	Prey	74	22.2	185.6	13733	28.1
				Pellet	37	11.1	185.6	6867	14.0
		n/a	Hare *Lepus europaeus*	Prey	1	0.3	185.6	186	0.4
	Rodentia	Small rodents	Vole *Microtus agrestis / Myodes glareolus*	Prey	18	5.4	17.9	323	0.7
				Pellet	28	8.4	17.9	502	1.0
		Small rodents	Wood mouse *Apodemus sylvaticus*	Prey	1	0.3	21.3	21	0.0
		n/a	Brown rat *Rattus norvegicus*	Prey	1	0.3	142.2	142	0.3
		n/a	Grey squirrel *Sciurus carolinensis*	Prey	9	2.7	367.4	3306	6.8
				Pellet	4	1.2	367.4	1469	3.0
	Soricomorpha	Shrews & moles	Mole *Talpa europaea*	Prey	2	0.6	86.8	174	0.4
				Pellet	8	2.4	86.8	694	1.4
		Shrews & moles	Shrew Soricidae	Prey	2	0.6	7.1	14	0.0
				Pellet	1	0.3	7.1	7	0.0

		n/a	Fox *Vulpes vulpes*	Prey	1	0.3	100.0	100	0.2
		n/a	Sheep *Ovis aries*	Pellet	1	0.3	100.0	100	0.2
Birds	Galliformes	Gamebirds	Pheasant *Phasianus colchicus*	Prey	43	12.9	192.0	8256	16.9
		n/a	Released pheasant	Prey	18	5.4	198.4	3570	7.3
		Gamebirds	Partridge *Alectoris rufa*	Prey	2	0.6	228.0	456	0.9
	Passeriformes	n/a	Thrush Turdidae	Prey	4	1.2	76.3	305	0.6
		n/a	Other Passeriformes	Prey	16	4.8	15.2	238	0.5
				Pellet	11	3.3	15.2	168	0.3
		Corvids	Magpie *Pica pica*	Prey	3	0.9	157.3	472	1.0
		Corvids	Jay *Garrulus glandarius*	Prey	1	0.3	157.3	157	0.3
		Corvids	Unidentified Corvidae	Prey	29	8.7	157.3	4562	9.3
				Pellet	2	0.6	157.3	315	0.6
	Columbidae	n/a	Woodpigeon *Columba palumbus*	Prey	7	2.1	236.5	1656	3.4
	Rallidae	n/a	Moorhen *Gallinula chloropus*	Prey	1	0.3	230.0	230	0.5
Amphibians	Anura	Frogs & toads	Common frog *Rana temporaria*	Prey	1	0.3	26.0	26	0.1
				Pellet	2	0.6	26.0	52	0.1
Unidentified		n/a	Unidentified reptile	Pellet	1	0.3	55.6	55	0.1
		n/a	Unidentified small mammals	Prey	1	0.3	17.9	18	0.0
		n/a	Unidentified large bird	Pellet	4	1.2	192.0	768	1.6
Total					334	100	4026	48941	100
Total identified					328	98	3760	48099	98
Total in 6 prey groups					254	76	1717	36630	75

Notes: * the mean biomass per item is taken from direct observations of chick provisioning from analysis of video footage.

Appendix 6: *Buzzard diet from direct observations of chick provisioning (frequency) from analysis of video footage at 20 buzzard nests in Cornwall, U.K.*

Data are presented showing frequency (N), percentage total frequency (% N), frequency of each size grouping (N size group).

	Taxonomic grouping	**Prey group**	**Species**	**N**	**% N**	**N size group**		
						S	**M**	**L**
Mammals	Lagomorpha	Rabbits	Rabbit *Oryctolagus cuniculus*	178	12.6	139	37	2
	Rodentia	Small rodents	Voles *Microtus agrestis / Myodes glareolus*	359	25.5	24	211	124
		Small rodents	Wood mouse *Apodemus sylvaticus*	49	3.5	11	22	16
		n/a	Brown rat *Rattus norvegicus*	22	1.6	7	10	5
		n/a	Grey squirrel *Sciurus carolinensis*	9	0.6	1	8	0
	Soricomorpha	Shrews & moles	Mole *Talpa europaea*	59	4.2	6	43	10
		Shrews & moles	Shrews Soricidae	66	4.7	8	34	24
	Mustelidae	n/a	Weasel *Mustela nivalis*	6	0.4	0	5	1
Birds	Galliformes	Gamebirds	Pheasant *Phasianus colchicus*	30	2.1	9	14	7
		n/a	Released pheasants	39	2.8	0	30	9
	Passeriformes	n/a	Thrushes Turdidae	26	1.9	2	19	5
		n/a	Unidentified *Passeriformes*	39	2.8	12	27	0
		Corvids	Corvidae	30	2.1	2	19	9
	Columbiformes	n/a	Woodpigeon *Columba palumbus*	7	0.5	1	4	2
	Accipitriformes	n/a	Buzzard *Buteo buteo*	1	0.1	1	0	0
	Gruiformes	n/a	Moorhen *Gallinula chloropus*	1	0.1	0	1	0

Amphibians	Anura	Frogs & toads	Common frog *Rana temporaria*	104	7.4	32	47	24
		Frogs & toads	Common toad *Bufo bufo*	108	7.7	16	56	36
Reptiles	Squamata	n/a	Slow worm *Anguis fragilis*	2	0.1	0	2	0
		n/a	Grass snake *Natrix natrix*	5	0.4	0	2	3
		n/a	Adder *Vipera berus*	1	0.1	0	0	1
Fish	Anguilliformes	n/a	European eel *Anguilla anguilla*	2	0.1	0	1	1
Invertebrates	Megadrilacea	n/a	Earthworms	9	0.6	4	2	3
Unidentified			Unidentified small mammals	104	7.4	21	80	3
			Small prey *(est. <50g)*	138	9.8	-	-	-
			Medium prey *(est. 50-150g)*	10	0.71	-	-	-
			Large prey *(est. >150g)*	5	0.35	-	-	-
Total				1409	100			
Total identified				1152	82			
Total in 6 prey groups				983	70			

Appendix 7: *Buzzard diet from direct observations of chick provisioning (weight) from analysis of video footage at 20 buzzard nests in Cornwall, U.K.*

Data presented show the mean percentage of carcass provisioned in each size group (mean % carcass), the mean biomass for each species (mean BIO) in weight (g) and the total biomass for each species (total BIO) in weight (g) and percentage (%).

	Taxonomic grouping	**Prey group**	**Species**	**Mean % carcass**			**Mean BIO (g)**	**Total BIO (g)**	**% total BIO**
				S	**M**	**L**			
Mammals	Lagomorpha	Rabbits	Rabbit *Oryctolagus cuniculus*	0.7	0.6	0.4	185.6	33161.1	37.4
	Rodentia	Small rodents	Voles *Microtus agrestis / Myodes glareolus*	-	-	-	17.9	6427.0	7.2
		Small rodents	Wood mouse *Apodemus sylvaticus*	-	-	-	21.3	1044.0	1.2
		n/a	Brown rat *Rattus norvegicus*	0.8	0.5	0.5	142.2	3196.2	3.6
		n/a	Grey squirrel *Sciurus carolinensis*	0.2	0.7	-	367.4	3306.2	3.7
	Soricomorpha	Shrews & moles	Mole *Talpa europaea*	-	-	-	86.8	5108.8	5.8
		Shrews & moles	Shrews Soricidae	-	-	-	7.1	470.0	0.5
	Mustelidae	n/a	Weasel *Mustela nivalis*	-	-	-	58.7	352.0	0.4
Birds	Galliformes	Gamebirds	Pheasant *Phasianus colchicus*	1	0.5	0.2	192.0	5760.2	6.5
		n/a	Released pheasants	-	0.4	0.2	192.0	7836.4	8.8
	Passeriformes	n/a	Thrushes Turdidae	-	-	-	76.3	1984.0	2.2
		n/a	Unidentified Passeriformes	-	-	-	15.2	594.0	0.7
		Corvids	Corvidae	0.8	0.5	0.5	157.3	4719.0	5.3
	Columbiformes	n/a	Woodpigeon *Columba palumbus*	1	0.7	0.6	236.5	1626.8	1.8
	Accipitriformes	n/a	Buzzard *Buteo buteo*	1	-	-	50.0	50.0	0.1
	Gruiformes	n/a	Moorhen *Gallinula chloropus*	-	1	-	230.0	230.0	0.3

Amphibians	Anura	Frogs & toads	Common frog *Rana temporaria*	-	-	-	26.0	2704.0	3.0
		Frogs & toads	Common toad *Bufo bufo*	-	-	-	29.6	3196.0	3.6
Reptiles	Squamata	n/a	Slow worm *Anguis fragilis*	-	-	-	13.2	26.4	0.0
		n/a	Grass snake *Natrix natrix*	-	-		70.6	353.0	0.4
		n/a	Adder *Vipera berus*	-	-	-	83.0	83.0	0.1
Fish	Anguilliformes	n/a	European eel *Anguilla anguilla*	-	1	1	300.0	600	0.7
Invertebrates	Megadrilacea	n/a	Earthworms	-	-	-	4.1	36.83	0.0
Unidentified			Unidentified small mammals	-	-	-	14.7	1524.0	1.7
			Small prey *(est. <50g)*	-	-	-	16.2	2236	2.5
			Medium prey *(est. 50-150g)*	-	-	-	104.0	1040	1.2
			Large prey *(est. >150g)*	-	-	-	200.0	1050	1.2
Total								88715	100
Total identified								82865	93
Total in 6 prey groups								62590	71

Appendix 8: *Weights used for buzzard prey size categories and their sources.*

	Species	**Estimated weight (g)**			**Weight source**		
		S	M	L	S	M	L
Mammals	Rabbit *Oryctolagus cuniculus*	200	558	915	[1[a]]	[1[a], 1[b]]	[1[b]]
	Voles *Microtus agrestis* or *Myodes glareolus.*	15	17	20	[2[a]]	[2[a]]	[2[a]]
	Mouse *Apodemus sylvaticus*	18	21	24	[2[b]]	[2[b]]	[2[b]]
	Brown rat *Rattus norvegicus*	200	241	282	[3]	[3, 4]	[4]
	Grey squirrel *Sciurus carolinensis*	483	544	588	[5]	[5]	[5]
	Mole *Talpa europaea*	74	85	102	[6]	[6]	[6]
	Shrews Soricidae	6	7	8	[2[c]]	[2[c]]	[2[c]]
	Weasel *Mustela nivalis*	36	54	82	M - $^{1}/_{3}$	L - $^{1}/_{3}$	[7[a]]
	Stoat *Mustela erminea*	124	188	285	M - $^{1}/_{3}$	L - $^{1}/_{3}$	[7][b]
Birds	Pheasant *Phasianus colchicus*	44	489	1363	[8[a]]	[8[b]]	[8[c]]
	Thrushes Turdidae.	49	74	96	M - $^{1}/_{3}$	[9[a]]	[9[b]]
	Unidentified small passerine	9	18	22	[9[c]]	[9[d]]	[9[e]]
	Corvids Corvidae spp.	150	225	469	M - $^{1}/_{3}$	[9[f]]	[9[g]]
	Woodpigeon *Columba palumbus*	207	314	524	M - $^{1}/_{3}$	L - $^{1}/_{3}$	[9[h]]
	Moorhen *Gallinula chloropus*	na	230	349	n/a	L - $^{1}/_{3}$	[9[i]]

Amphibians	Common frog *Rana temporaria*	17	25	40	M - $1/3$	[3[b]]	[10]
	Common toad *Bufo bufo*	23	28	35	[11[a]]	[11[a]]	[11[a]]
Reptiles	Slow worm *Anguis fragilis*	11	13	17	[12]	[12]	[12]
	Snake spp.	35	52	83	[11[b]]	[11[b]]	[11[b]]
Fish	European eel *Anguilla anguilla*	n/a	300	n/a	n/a	[12]	n/a
Invertebrates	Earthworm spp.	2.8	4.3	5.7	M - $1/3$	[13]	M + $1/3$

Notes: Where a complete dataset of weights is available I took the median to be medium, the first quartile to be small and the third to be large. Where two sources are presented I took the mean of both to be the medium weight. **Sources:** [1] Harris & Yalden (2008): [a] the average weight of a juvenile *Oryctolagus cuniculus*, [b] the average weight of an adult *Oryctolagus cuniculus*; [2] R. A. McDonald, P. Cooper & L. Furness unpublished data from small mammal trapping in Cornwall, U.K: [a] weights of *Microtus agrestis* and *Myodes glareolus* (n = 21), [b] weights of *Apodemus sylvaticus* (n = 160), [c] weights of *Sorex araneus* (n = 15); [3] Dare (2015): [a] weight of juvenile *Rattus norvegicus* found on buzzard nests, [b] weight of average *Rana temporaria* on found on buzzard nests; [4] Jones et al. (2009); [5] R. A. McDonald, unpublished data: weights of *Sciurus carolinensis* in Northern England (n =409); [6] F. Stoker, unpublished data: weights of *Talpa europaea* trapped as part of on going pest control across Cornwall (n = 55); [7] McDonald et al. (1998): [a] average weight of an adult *Mustela nivalis*, [b] average weight of an adult *Mustela erminea*; [8] M. Whiteside & J. Madden unpublished data weights from an on-going study on released *Phasianus colchicus* in southwest England: [a] mean weight of week old chick (n = 50), [b] mean weight of six week old male (n = 483), [c] mean weight of adult female (n =25); [9] Cramp & Simmons, 1980: weights are from adult [a] *Turdus merula*, [b] *Turdus philomelos*, [c] *Troglodytes troglodytes,* [d] *Erithacus rubecula,* [e] *Fringilla coelebs,* [f] *Corvus monedula*, [g] the average of *Corvus corone, Corvus frugilegus, Pica pica*, [h] *Columba palumbus,* [i] *Gallinula chloropus*.; [10] Petty (1999); [11] C. Reading unpublished data: [a] weights of *Bufo bufo* collected as part of on-going studies in the south of England (n = 17985), [b] weights of *Natrix natrix* collected in the south of England (n = 372); [12] Stumpel (1985); [13] Kruuk (1978)

Appendix 9: *The stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of species frequently recorded in the diet of buzzards in Cornwall, U.K. The table gives the sample size (n), as well as the mean and standard deviation for both isotopes. When multiple species have been sampled within a taxonomic Order, the average is also presented in bold. Muscle tissue was sampled from fresh dietary items found in buzzard nests. Additional tissue was collected opportunistically for frogs, toads and released pheasants.*

Order	**Species**	**n**	**$\delta^{13}C$**		**$\delta^{15}N$**	
			Mean	**SD**	**Mean**	**SD**
Lagomorpha	*Oryctolagus cuniculus*	24	-28.76	0.52	6.11	1.69
Rodentia	All	**17**	**-28.33**	**1.49**	**4.19**	**2.59**
	Apodemus sylvaticus	3	-27.29	3.05	5.08	2.37
	Microtus agrestis & *Myodes glareolus*	14	-28.56	1.00	4.00	2.68
Eulipotyphia	All	**7**	**-25.77**	**1.01**	**9.02**	**1.73**
	Sorex araneus	2	-26.53	1.51	8.47	0.98
	Talpa europaea	5	-25.47	0.75	9.23	2.01
Passeriformes	Corvidae spp.	5	-24.97	0.58	8.60	1.53
Galliformes	All	**19**	**-25.05**	**1.37**	**4.90**	**1.46**
	Phasianus colchicus (Wild)	8	-24.34	1.94	6.45	0.69
	P. colchicus (Released)	11	-25.57	0.11	3.78	0.42
Anura	All	**7**	**-26.54**	**0.44**	**6.25**	**1.47**
	Rana temporaria	4	-26.63	0.58	5.70	1.81
	Bufo bufo	3	-26.42	0.21	6.99	0.46

Appendix 10: *Difference in the isotopic ratios of ‘wild’ putative buzzard prey from the isotopic ratios of released pheasants in Cornwall, U.K.*

Differences were analysed using general linear models. Separate models were applied for $\delta^{15}N$ *and* $\delta^{13}C$ *with released poult set as the intercept (df = 75).*

	$\delta^{13}C$				$\delta^{15}N$			
Dietary source	**Est.**	**S.E**	**t value**	***P***	**Est.**	**S.E.**	**t value**	***P***
Released pheasant	-25.57	0.315			3.78	0.558		
Wild pheasant	1.23	0.485	1.74	0.086	2.56	0.832	3.08	0.003
Amphibian	-0.97	0.505	-1.92	0.058	2.48	0.895	2.77	0.007
Corvid, shrew & mole	0.13	0.436	0.30	0.765	5.07	0.773	6.56	< 0.001
Rabbit & rodent	-3.01	0.354	-8.50	< 0.001	1.54	0.629	2.45	0.017

Appendix 11: *Estimates of the proportional representation of food sources consumed by buzzards, estimated by Bayesian stable isotope mixing models.*

Values are means ± SD.

BSIMM tissue	Nestling feathers	Nestling blood	Adult feathers	Problem buzzard feathers	Problem buzzard blood
Dietary category					
Rabbit & rodent	0.576 ± 0.057	0.680 ± 0.042	0.252 ± 0.072	0.222 ± 0.126	0.263 ± 0.107
Corvid, shrew & mole	0.111 ± 0.057	0.047 ± 0.029	0.332 ± 0.066	0.162 ± 0.096	0.115 ± 0.067
Wild pheasant	0.048 ± 0.031	0.025 ± 0.016	0.096 ± 0.056	0.189 ± 0.134	0.129 ± 0.084
Released pheasant	0.055 ± 0.034	0.039 ± 0.025	0.080 ± 0.045	0.182 ± 0.109	0.262 ± 0.119
Amphibian	0.211 ± 0.100	0.210 ± 0.066	0.239 ± 0.151	0.245 ± 0.163	0.231 ± 0.142

Notes: The number of samples included in models differed (nestling feathers = 41, nestling blood = 82, adult feathers = 86 and adult blood =8). For blood samples both red blood cell samples and blood plasma for each buzzard were included in the models.

Appendix 12: *Results of the linear mixed effects model analysis for released poult consumption by territory category.*

The significant P value indicates a significant reduction in the goodness of model fit between model structures 2 and 3.

Model	d.f.	AIC	Log Lik	χ^2	*P*
Random effects structure					
Random = ~ 1 | territory					
Fixed effects structure					
1. Released pheasant in diet ~ territory category * age + feather type + site	117	120.2	-49.1		
2. Released pheasant in diet ~ territory category * age + site	**118**	**118.5**	**-49.2**	0.2489	0.6179
3. Released pheasant in diet ~ territory category + age + site	120	123.3	-53.6	8.7964	0.0123 *

Random effects on the slope and intercept were determined at the level of replicates nested within ‘territory’. The results of the model selection procedure on the fixed effect terms are given and the most parsimonious model is highlighted in bold.

Appendix 13: *Post hoc comparisons between the 'territory category' factor levels (calculated using least-squares means, with Satterthwaite's approximation for degrees of freedom) on model structure 2 (Appendix 12). (i) denotes no release pen, (ii) denotes a release pen with no problems and (iii) denotes a release pen with problems.*

Pairing	**Estimate**	**SE**	**d.f.**	**t. ratio**	***P* value**
Adults					
i - ii	-0.0161	0.0150	33.11	-1.074	0.5367
I - iii	-0.0468	0.0169	23.05	-2.768	0.0284 *
Ii - iii	-0.0307	0.0190	23.05	-1.616	0.2591
Nestlings					
I – ii	0.0237	0.0182	52.79	1.303	0.3997
I – iii	0.0211	0.0199	52.79	1.063	0.5409
Ii - iii	0.0026	0.0229	64.28	-0.114	0.9928

Notes: Results are averaged over the levels of site

Appendix 14: *Results of the linear mixed effects model analysis for released poult consumption by 'problem buzzards'.*

The significant P value indicates a significant reduction in the goodness of model fit between model structures 1 and 2.

Model	d.f.	AIC	Log Lik	Chisq	*P*
Random effects structure					
Random = ~ 1 | territory					
Fixed effects structure					
1. Released pheasant in diet ~ problem buzzard * tissue + site + age	207	135.4	-56.7		
2. Released pheasant in diet ~ problem buzzard + tissue + site + age	209	137.9	-59.9	6.4493	0.0398*

Random effects on the slope and intercept were determined at the level of replicates nested within 'territory'.

Appendix 15: *Example of semi-structured interview schedule.*

Questions were not necessarily asked in the order presented. Questions were asked generally (about all predators) and specifically (about specific species once they had been introduced by the respondent)**.**

Background

- What attracted you to gamekeeping? Current position?
- How did you learn your skills? Who taught you most?
- What are the best parts/ challenges?
- What type of shoot is it? Size? Habitat type?

Background to predation

- Which predators are legally controlled?
- Which predators take pheasants or their eggs? And on this estate?
- Which cause most problems? Does this change over the year?
- What loss is small enough to tolerate?
- Would you stop if you perceived a sudden decline?
- Are there any species whose population growth would concern you?

Behavioural beliefs / Outcome evaluation:

- What are the costs/benefits of predator control?
- What do you think would happen if there was no predator control?
- Does killing predators matter?
- Do you think there are indirect impacts of predators?
- What benefits of predators have you observed?
- Do you think other gamekeepers overlook/unfairly target some predators?
- (Projective) Why do you think some keepers kill protected predators?

Normative beliefs/ Motivation to comply:

- Who would you ask for advice on predator management?
- How do you feel when others see predators on this shoot?

- Do you ever ask others for their advice on predator management?
- (If relevant) How does it affect you having a neighbouring shooting estate(s)?
- Do you think its important to behave how [name of group previously mentioned by respondent] expect you to behave?

Power beliefs / Control beliefs:

- How are decisions on predator management made?
- What would prevent you from killing a predator that was having an impact?
- How easy is it to control predators?
- Would you consider applying for a licence to remove predator that was legally protected?

Examples of statements from previous interviews that gamekeepers were asked their opinions on:

- *"A gamekeeper is solely responsible for protecting birds on his own beat."*
- *"If a predator's a nuisance, it needs thinning out"*
- *"Gamekeepers could never wipe any species out."*
- *"I get a sense of pride having a rare predator on my estate"*
- *"Putting older birds into pens means you have to kill less predators"*
- *"You can judge predator impact by the number that you see about."*
- *"Everything has to be in a certain balance"*

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