The Recovery of the Polecat *Mustela putorius* in Great Britain

Submitted by Katherine A Sainsbury to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, July 2019.

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) ……………………………………………………………………………

We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we first started
And know the place for the first time.

TS Elliot
Little Gidding, 1942

Abstract

Many carnivore species are experiencing declines due to anthropogenic factors such as direct killing, habitat loss, secondary exposure to chemical control agents, and depletion of prey resources. Due to their top-down effects on the structure and function of ecosystems, carnivores are, however, increasingly the focus of efforts towards ecological restoration. To enable such restoration to take place, wildlife managers need to understand both the ecological processes and the social-ecological factors that may affect carnivore recovery and establishment.

In this thesis, I use the European polecat *Mustela putorius*, which is currently recolonising Great Britain following near extirpation in the nineteenth century, as a case study through which to explore the processes of carnivore recovery. I investigate social and ecological risks to the polecat's continuing range and population expansion, which may also be pertinent to the wider challenges of carnivore conservation.

In my introduction, I outline the importance of carnivores to ecosystem function and review the wide-ranging and cascading effects their reinstatement can have. I provide an overview of human-carnivore interactions and the anthropogenic processes that directly or indirectly lead to carnivore declines. I give a historical context to human-carnivore relations in Great Britain, introduce polecats, their biology and changing status and provide an overview of my research objectives and thesis structure.

I then carry out a detailed literature review of the changing status of the eight terrestrial mammalian carnivores native to Great Britain. I summarise the anthropogenic processes that have influenced their status. I find that polecats have recolonised Great Britain less quickly than otters *Lutra lutra* but more quickly than pine martens *Martes martes.* Badgers *Meles meles* have increased in abundance. Foxes *Vulpes vulpes* are experiencing a decline and wildcat are imperilled by hybridisation with domestic cats. Stoats *Mustela erminea* and weasels *Mustela nivalis* are data deficient, but evidence suggests that stoats may be increasing in number relative to weasels.

Next, I explore polecat resource use during a period of ecological change by analysing the stable isotopes of carbon and nitrogen from a museum collection of polecat whiskers. I find that variation in isotope ratios and isotopic niches indicate differences in resource use between polecats collected from the leading edge of the range compared to the established parts of the range and that this effect was greatest in the 1960s when rabbits *Oryctolagus cuniculus*—an important prey for polecats—were in low abundance. I also find that female polecats show greater variation in resource use than males, indicating that they may have different needs as part of conservation efforts.

Next, I carry out a study of polecat diets to assess responses to fluctuating abundance of rabbits. I analyse the stomach contents from polecat carcasses collected between 2013 and 2016. I compare my results with those from earlier polecat dietary studies and find that the proportion of lagomorphs increased in polecat diet between the 1960s and 1990s. Although rabbit populations have been declining since the 1990s, I find no difference in the proportion of lagomorphs in polecat diet between the 1990s and 2010s.

Secondary exposure to second generation anticoagulant rodenticides is a contemporary risk to polecat recovery that is also related to their diet, as polecats are likely exposed to rodenticides by eating contaminated rodents. In Chapter 5, I analyse the livers from polecat carcasses collected between 2013 and 2016 to measure current levels of secondary exposure and explore factors that may affect exposure. I find that the frequency of exposure to rodenticides was 79% in polecats and that this represents a 1.7 fold increase in exposure frequency over 25 years. I find that the probability of exposure increases with age and with increasing values of □^{15}N, suggesting that resource use influences polecat exposure to rodenticides.

I then explore the principles underpinning modern gamekeeping practices, by carrying out interviews with gamekeepers to find out what they do and why. In this qualitative study, I analyse gamekeepers' conception of The Balance, which is an overarching narrative that they have adopted to explain their approach to wildlife management. Although The Balance includes echoes of the heuristic of the 'balance-of-nature', it is most often employed in the context of maximising shootable game surpluses while providing opportunities to other wildlife that do not conflict with this objective. I find that keeping The Balance requires a ritualised, highly interventionist approach to producing game that presents both risks and rewards to predators. The multiplicity of The Balance—in which gamekeepers are stewards of both game and the countryside—creates an ambiguity that, when associated with the regular culling of predators and negative perceptions of sport shooting, may cause misunderstandings between gamekeepers and other publics.

In conclusion, I find that polecats have been able to recolonise most of southern Britain despite the risks of fluctuating rabbit populations, increasing exposure to rodenticides and predator controls. Polecat recovery has occurred with minimal direct conservation effort. It has also taken a long time: one hundred years after their population nadir, polecats are yet to fully recolonise their former range. More broadly, a low-intervention approach is unlikely to succeed, or be desirable, for all carnivores. In particular, those that are slower to mature, have lower reproductive rates, more specialised resource requirements and greater impact on anthropogenic practices, or where the potential ecological benefits that may be derived from a species' restoration necessitate an expedited recovery.

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count in the end, but I had the best of times with you all and the memories will stay with me forever.

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Which brings me to my family. Mum, Dad, Pat and Phil, thank you for indulging us on our latest crackpot adventure. Cam, Rita, John, Peggy and Tony, thank you for forgiving us for leaving you to come and do this. Huw, Bernice, Tim and Helen—our Cornish family—made us feel so at home. Sarah, Andy and Matthew, thank you for housing me to and from various long trips up and down the country. Anna, thank you for listening and Gran for laughing. Barbie, thank you for letting me in and Diego, as the song says, ‘you make me smile’. I owe so much to Nigel that words fail me and only hope that one day I can repay the debt with the same amount of good humour, love and unrelenting faith in everything coming good in the end. And Chucho. We walked miles, climbed mountains, crossed oceans together. I really thought you’d be at my side until the end of this particular journey. So, this is for you and all animals out there—domestic or wild—that deserve a second chance.

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Authors declaration for co-authored manuscripts

Chapters 2, 3, 4, 5 and 6 have been published or written for publication as co-authored academic papers. I developed the direction and research design for chapters 2, 3, 4, 5 and 6 in conjunction with Robbie McDonald (RM), Richard Shore (RF) and Henry Schofield (HS).

For Chapters 3, 4 and 5, polecat carcass data from 2013 to 2016 was based on carcasses collected as part of the Vincent Wildlife Trust’s national polecat survey of Britain. Carcasses were collected from volunteers by Elizabeth Croose (EC) and associated metadata was documented by EC. The carcasses were catalogued and stored by Elaine Potter and Lee Walker at the Centre of Ecology & Hydrology as part of the Predatory Bird Monitoring Scheme until necropsy and sampling (of whiskers, teeth, liver, muscle tissue and stomach contents), which took place at the National Museums Scotland by Georg Hantke (GH) and Stephen Rogers with my and EC’s assistance. GH cleaned the teeth in preparation for them to be sent to Matson's Lab LLC, USA for age analysis. GH carried out the museum preservation process on the polecat skins and sampled whiskers from a subset of animals for the comparative analysis described in Chapter 3.

In Chapter 3, Lorna Drake (LD) sampled whiskers from pelts stored at the National Museums Scotland which had been added to the museum collection between the 1960s and 2000s. LD then processed the whiskers for stable isotope analysis, which was carried out using University of Exeter stable isotope facilities. Isabella Endicott and I processed the whiskers sampled from the 2013-2016 carcasses for stable isotope analysis (these are also used in Chapter 5), which was carried at Elemtex, UK. I collated the two sets of data and analysed them with the carcass metadata.

In Chapter 4, Megan Bruce and Maude Chappell (MC) cleaned the stomach contents from the 2013-2016 carcasses and MC carried out initial identification of hard parts and hair. I carried out further validation and analysed the data.

In Chapter 5, I processed the polecat livers for rodenticides analysis with assistance from Nicola Thompson and assistance and guidance from Gloria M Pereira (GP) and Darren Sleep (DS). I analysed the data.

In Chapter 6, I designed and carried out all of the fieldwork. I processed and analysed the data with advice from Caitlin DeSilvey (CD).

I wrote all five manuscripts, then amended and revised them in response to comments, suggestions and advice from RM, RS, HS and other co-authors (EC, GH, LD, GP, DS, CD, Andrew Kitchener, Ruiridh Campbell and Sarah Crowley).

Chapter 1

Introduction

Chapter 1: Introduction

The trophic downgrading of planet earth, through global declines of apex predators, is an insidious consequence of anthropogenically-induced loss of biodiversity (Estes et al. 2011). Extensive ecological research carried out over several decades finds that predators are important to the structure and function of ecological communities (Ripple et al. 2014). Predators cause a cascade of direct and indirect effects throughout an ecosystem (Trussell et al. 2006, Heithaus et al. 2008, Estes et al. 2011). Direct effects occur when predators reduce prey populations by eating them (Terborgh 1988) while indirect effects occur when prey behaviour is influenced through predation avoidance and can be as far reaching as to affect disease dynamics, invasive species establishment, carbon sequestration, atmospheric composition, wildfire frequency and extent, and species diversity (Estes et al. 2011).

In a review of evidence of the impacts of carnivores on ecosystems, Schmitz et al. (2000) found that removal of predators increased the numbers of herbivores, along with concomitant increases in plant damage and reductions in plant biomass in 75% of studies. Sustained increases in herbivory can dramatically change visual as well as functional aspects of ecosystems (Estes et al. 2011).

The return of predators can trigger trophic cascades that reinstate ecosystem functions. When grey wolves *Canis lupus* were reintroduced to Yellowstone National Park, female elk *Cervus elaphus* and female bison *Bison bison* increased their vigilance levels and modified their foraging patterns and use of the landscape (Laundré et al. 2001, Ripple & Larsen 2000, Ripple & Beschta 2007). By regulating prey and their behaviours, carnivore controls cascade further down to plant communities and beyond. Wolf recovery in Yellowstone National Park increased the aspen *Populus tremuloides* overstory (Ripple & Beschta 2007), plant diversity and songbird abundance (Hebblewhite et al. 2005). In the Aleutian Islands, reduced herbivory following sea otter *Enhydra lutris* recovery resulted in a reduction in herbivorous sea urchins *Strongylocentrotus polyacanthus* which lead to the restoration of kelp forests (Estes et al. 1978). However, the later arrival of a top predator, in the form of killer whales *Orcinus orca,* changed the ecological dynamics. The killer whales predated on the sea otters, reducing sea otter populations, allowing sea urchins to increase in number again and the kelp forest biomass declined once more (Estes et al. 1998). These wolf and sea otter examples underline the importance of taking a long-term view in assessing species recoveries and trophic interactions (Estes et al. 1998, Miller et al 2001, Ripple & Beschta 2007). They also highlight that top predators can affect mesopredator populations. The removal of top predators can cause mesopredator release (Crooks & Soulé 1999), which can then lead to declines in prey species (e.g. Palomares et al. 1995, Rogers et al. 1998). This has been demonstrated in a study of dingoes *Canis dingo* in Australia, which were found to control numbers of invasive non-native red fox *Vulpes vulpes* (Letnic et al. 2012). The reduction in foxes then led to increased numbers of endangered small mammals (Letnic et al. 2012). Cascades can also affect multiple species among guilds with a ripple effect of consequences. For example, in the United States, elevated coyote *C. latrans* abundance had been associated with increasing songbird and small mammal diversity through suppressing mesopredators such as domestic cats *F. catus* and foxes. Returning wolf populations in North America have reduced coyote numbers, but this has subsequently released foxes from top down control by coyotes (Levi & Wilmers 2012).

While there is a substantial body of literature in support of the “top-down” effects of predators on ecosystems, historically popular “bottom up” paradigms of trophic flows still pervade (Estes et al. 2011). These assume that plant and herbivore communities regulate population densities through competitive interactions (Polis & Strong 1996, Miller et al. 2001). In the “bottom up” paradigm, carnivores are situated at the top of the chain. Carnivores may act as indicators of the state of the ecosystem as a whole, but play a largely passive role in ecosystem function and as such may be viewed as ‘passengers’ in an ecosystem (Estes et al. 2001, Estes et al. 2011). The perception of a lack of functional role played by carnivores may legitimise management approaches that aim to reduce carnivore populations as part of prioritising human needs (Miller et al. 2001).

Of course, both “top-down” and “bottom-up” models simplify ecological systems. In reality, energy flows may be multi-directional and simultaneous, although the size of the effects may be greater in one direction than another in different scenarios (Power 1992) and therefore the extent to which “top-down” or “bottom-up” effects are more important is context-dependent. Regardless of the model adopted, these examples illustrate the importance of carnivores to ecosystem function and the cascading impacts of their declines or recoveries. The consequences of changing carnivore abundance may not only affect wildlife. In West Africa, declines in lions *Panthera leo* and leopard *P. pardus* coincided with increases in olive baboons *Papio anubis* and decreases in small ungulate and small primate populations. Olive baboons are a species that consume agricultural crops (Brashares et al. 2010) and so the potential for conflict between baboons and humans also increased as a result of reduced carnivore numbers.

Carnivore-human interactions

Carnivores and humans share a long history of complicated interactions (Kruuk 2002). Carnivores pose a very real threat to human life, livelihoods and recreational activities and anti-carnivore attitudes in the interests of self-preservation are a commonplace human sentiment (Kruuk 2002). But humans have also domesticated carnivores and have long exploited them for their fur, sport, guardianship, aesthetic beauty, or company in the home environment. Consideration of the social implications of carnivore presence therefore adds value to any wildlife management planning that involves them (Breitenmoser 1998).

Although it is now clear that carnivores play an important role in ecosystem function, many carnivores have experienced population declines as a result of interactions with anthropogenic processes. Some carnivore declines have been due to direct killing via overexploitation (tigers *P. tigris* - Walston et al. 2010; African lions - Packer et al. 2009) or predator controls (wolves– Mech 1998). Other risks to populations are indirectly the result of human activity and include prey depletion due to human activity (snow leopards *P. uncia* – Berger et al. 2013, tigers – Chapron et al. 2008), environmental contamination (European otter *Lutra lutra* - Mason & Macdonald 1993), habitat destruction (Sumatran tiger *P. t. sumatrae* – Linkie et al. 2003) and introduction of domestic species with which they may hybridize (wolves – Andersone et al. 2002, European wildcat *Felis silvestris* – Driscoll et al. 2007). In the case of the wildcat, genetic extinction as a result of hybridisation is now a very real threat (Breitenmoser 2019).

Effective conservation of threatened species requires an understanding of both the contemporary threats to a species recovery and the ecological processes that may support a species' recolonisation. Species range expansions can be likened to simple diffusion models (Skellam 1951). Increases in the population of a recovering species lead to a 'wave-front' of individuals who move the leading edge of the population's range outwards (Skellam 1951). As recoveries among threatened carnivores are relatively rare, invasive species provide a potential source of information about the processes for recolonising native species. Invasive species usually display behavioural and dietary flexibility (Ehrlich 1989, Sol & Lefebre 2000, Sol et al. 2002, Jeschke & Trayer 2006, Ibarra et al. 2009, Bodey et al. 2010). Whether species that successfully recover former native ranges exhibit similar ecological flexibility is of interest as it may inform conservation policy and the extent of management intervention required in support of recolonisation.

Carnivores in Britain

Britain is a microcosm for the effects of different approaches to wildlife management on carnivores. There are eight mammalian carnivores native to Britain that are currently extant: European wildcat, red fox, European otter, European badger *Meles meles*, European pine marten *Martes martes*, stoat *Mustela erminea*, weasel *Mustela nivalis,* and European polecat *Mustela putorius.* Top predators such as wolves, Eurasian lynx *lynx lynx* and brown bear *Ursus arctos* were extinct as a result of human controls by the Middle Ages (Yalden 1999). The loss of these top predators means that there is an absence of "top down" population regulation on medium and small carnivores in Britain, which would otherwise have been exerted by these species (Tapper 1995). Foxes, otter and badgers are the largest of Britain's native mammalian carnivores and may have some regulatory effects on smaller carnivores. For example, intraguild predation is documented between foxes and stoats (Mulder 1990) and foxes and pine martens (Strachan et al. 1996), but has not been reported between foxes and polecats, or otters and polecats, or polecats and stoats. There are intraguild effects between carnivores of similar size. For example, reductions in badger numbers have led to local increases in fox abundance (Trewby et al. 2008). Among the mustelids, coexistence has been theorized to be facilitated by the partitioning of resources, i.e. size of mammalian prey (Dayan & Simberloff 1994). While there is empirical evidence of resource partitioning between the sexes of some mustelids, there is no evidence to support a theory of resource partitioning by prey size between species (McDonald 2002).

That being said, abundance of stoats and weasels does fluctuate with the abundance of their prey: rabbits (stoats) and voles (weasels) in a dynamic system where rabbit numbers impact vole populations through affecting the amount of grass sward and cause fluctuations in stoat and weasel populations as a result. Studies on the behaviour of sympatric polecats and American mink *Neovison vison* in Britain indicate that the two species adjust their activity patterns to reduce competition, with mink becoming more active in daytime (Harrington and Macdonald 2008). This change in behaviour coincided with the return of otters *Lutra lutra* to the study area, and changes in mink activity may have been influenced by the presence of otters rather than polecats. Analysis of studies from across Europe has found that polecat sex ratios can be affected by the presence of non-native American mink (Barrientos 2015). The consequence of a lack of large carnivores in Britain, and the presence of non-native additional carnivores such as American mink and the feral ferret *Mustela furo,* is that wildlife managers in Britain have to decide whether to intervene and control mesocarnivores (Tapper 1995).

Thousands of years of human activity on mainland Britain have meant that there are ‘few, if any, nooks’ unaffected by human hand (Simmons 2001). Even the landscape in the Scottish Highlands, considered by some as the ‘last wilderness’ in western Europe, is a result of anthropogenic environmental degradation (Coates 1998). Early attitudes and actions towards wildlife, based on Judeo-Christian traditions concerning humankind’s role in nature, were informed by judgements on the relative utility of plants and animals to people (Thomas 1983). The resulting combination of centuries of habitat conversion and widespread state-sponsored culling initiated by the Tudor Vermin Act 1566 (which placed bounties on all wildlife species that were classified as agricultural pests (Lovegrove 2007)), followed by predator controls to protect sporting interests, were instrumental in causing the decline, of many of Britain's native mammalian carnivores. By the turn of the twentieth century the pine marten, polecat and wildcat had been almost eliminated from Great Britain (Langley & Yalden 1977, Lovegrove 2007).

Although a less anthropocentric view of nature now prevails, anthropogenic processes continue to affect carnivores in Britain. In the twentieth century, organochlorine compounds used as agricultural pesticides were associated with catastrophic declines of the otter population in Britain (Chanin & Jefferies 1978). Similarly, all mammalian carnivores examined to date have been found to have been secondarily exposed to second generation anticoagulant rodenticides (McDonald et al. 1998, Shore et al. 2003; Shore et al. 2015, Ruiz-Suárez et al. 2016). Agricultural intensification in general has been associated with reductions in farmland biodiversity with broad implications for the prey availability for carnivore species (Tattersall & Manley 2003).

In last 100 years there has been a change in cultural emphasis towards carnivore protection (Reynolds & Tapper 1996). Legal protections were put in place for some species in 1970s, 1980s and 1990s. In Britain, badgers, otters, pine martens, polecats and wildcats are protected – albeit to varying degrees - by law. Lethal predator controls may only be used legally on stoats, weasels and foxes without specific licenses. Examples of predator controls that wildlife managers may employ include lethal and non-lethal methods. Lethal approaches include trapping, snaring and shooting, or a combination thereof. Use of chemical control agents to manage predators, such as poisons, may have been widespread in the past, but are now regulated. Non-lethal deterrents include use of electric fencing and scent, visual and auditory deterrents. There is little information on the uptake or efficacy of non-lethal controls. There is evidence to suggest that bird populations can and do benefit from implementation of appropriately applied lethal controls (e.g. Côté & Sutherland 1997, Tapper et al. 1996, Fletcher et al. 2010).

Translocation programs have been carried out for some carnivore species, such as pine marten and otter, to support population recovery. Otters, polecats, pine martens, badgers and foxes have all increased in distribution and / or number since the 1960s (Aebischer et al. 2011, Birks 2015, Birks 2017, Judge et al.

2017). The growth in salience of environmental issues has placed the British countryside under increasing pressure to provide for competing cultural interests and requirements. For example, it is required to provide adequate food for humans, as well as the necessary habitat for protected flora and fauna, or to provide the background to recreational field sports, such as fox hunting and game shooting, which are central to elements of its aesthetic identity (Franklin 2002), while simultaneously supporting increasing numbers of carnivores. Given these current competing pressures, it is timely to understand the status of Britain's carnivore species and what the contemporary ecological and anthropological processes affecting carnivores in Britain might be.

The European polecat *Mustela putorius*

The European polecat is a medium-sized member of the mustelid family with a pan-European distribution (Skumatov et al. 2016). Genetically it is most similar to the Steppe polecat *Mustela eversmanii* and is the ancestor to the domestic ferret *Mustela furo* with which it can produce fertile hybrid offspring (Costa et al. 2013). Ferrets were introduced to Britain for the purpose of rabbit (*Oryctolagus cuniculus*) hunting at some point between the Norman Conquest and the fourteenth century AD (Thomson 1951, Davison et al. 1999). Scattered records of ferrets have appeared regularly in national polecat surveys, probably due to the continued widespread use of domesticated ferrets for rabbiting leading to lost working animals, escapees and / or releases (e.g. Birks & Kitchener 1999, Birks 2008, Kitchener & Birks 2008, Croose 2016). There is no evidence to suggest that feral ferrets are widely established on mainland Britain beyond isolated populations in North Yorkshire, Speyside, Renfrewshire, Argyll and Caithness, although they have become established on some islands of Britain, including Isle of Man, Jersey, Arran, Benbecula and South Uist, Bute, Islay, Lewis, Mull, North Uist, Shetland, Rathlin Island, and Northern Ireland (Bodey et al. 2011, Mathews et al. 2018).

The polecat has dark brown fur with a paler undercoat and distinctive white facial markings above the eyes, under the chin and on its ear tips (Fig. 1.1). Polecat-ferret hybrids usually possess a preponderance of paler fur, less distinctive facial markings and are often smaller in size, although the ability of physical characteristics to identify hybrid animals without genetic analysis is limited (Costa et al. 2013).

Figure 1.1. *The European polecat* Mustela putorius*. With kind permission from A. Newton*

The polecat releases a malodorous stink when alarmed, much like a skunk (Blandford 1987). Males are larger than females such that a large male may weigh several times that of a small female (Blandford 1987). A single male polecat usually occupies the territory of multiple females (Lodé 1996). They breed once a year in the spring. The polecat is a generalist obligate carnivore with a diverse diet across its range although, in Britain, rabbits are an important food source (Blandford 1986, Birks & Kitchener 1999). Polecats also frequently make use of rabbit burrows as den sites (Birks & Kitchener 1999). They utilise a wide range of habitats, and although they are described elsewhere in their range as semi-aquatic, in Britain they show a preference for woodland edge, field boundaries, and wetlands (Birks & Kitchener 1999). They also make use of agricultural premises such as farmyard buildings and barns (Birks & Kitchener 1999).

Once common across Britain, the polecat was hunted for its fur, for sport and culled as vermin as part of statutory controls and by gamekeepers (Lovegrove 2007). No creature was more unpopular than the polecat:

> 'The polecat has earned for itself a most unenviable fame, having been long celebrated as one of the most noxious pests to which the farmyard is liable. Slightly smaller than the marten, and not quite so powerful, it is found to be a more deadly enemy to rabbits, game, and poultry, than any other animal of its size.' (Wood 1885).

The polecat's distribution extent reached a nadir *c.* 1915, when it persisted in only central Wales and northern Scotland (Langley & Yalden 1977). Only the population in Wales proved viable. Since then, the polecat has expanded its distribution out of its Welsh refugium and is now present across most of central, southern and eastern England (Croose 2016). Much of this expansion into England occurred after the 1970s (Langley & Yalden 1977, Birks & Kitchener 1999). Reductions in predator controls, the banning of the gin trap (a leg-hold trap commonly used to control rabbits) in 1958 and the recovery of rabbit populations post-myxomatosis are all thought to have contributed to its recovery in Britain (Birks 2015). More recently, research suggest that the polecat is declining across much of the rest of its European range (Croose et al. 2018).

The principal contemporary risks to polecats include: secondary exposure to second generation anticoagulant rodenticides (Shore et al. 2003), predator controls (Packer & Birks 1999), hybridisation with feral domestic conspecifics (Costa et al. 2013) and changing food availability as rabbit populations continue to fluctuate (Harris et al. 2018). These risks are representative of those that may affect other carnivores as a result of anthropogenic processes. As such polecats are a useful proxy for the wildlife management challenges facing carnivores in Great Britain and more widely.

The thesis

My work has aimed to understand some of the ecological aspects of a species recovery as well as the broader context in which this particular case study species is situated. To investigate all of the potential ecological aspects of polecat recovery and all of the contemporary risks associated with the species is beyond the scope of this thesis. For example, I do not address the prevalence of polecat-ferret hybridisation here as this has already been explored extensively by Costa (2014). My research objectives were focussed on the following areas:

1. To assess the current status of polecats in Great Britain and to relate this to the changing status of other British mammalian carnivores.
2. To elucidate mechanisms relating to resource use that may influence polecat recovery.
3. To understand contemporary risks to polecat recovery, including:
    a. Secondary exposure to second generation anticoagulant rodenticides.
    b. Fluctuations in rabbit populations.
    c. The practices of modern gamekeeping.

Thesis structure

Following this introduction, the thesis is structured into five original research chapters, each comprising an individual academic paper, and a concluding general discussion. The research chapters focus on two themes. Chapters 2 and 3 explore what we know about and can learn from polecat recovery. Chapters 4, 5 and 6 examine some of the ecological and anthropogenic processes that may have influenced polecat recovery in Britain. Specifically, the chapters comprise the following:

- Chapter 2: I review the changing status of all of Britain’s terrestrial mammalian carnivores between the 1970s and 2010s. I gather together all available survey data from systematic monitoring of British carnivores to plot their range and / or population changes. I examine the anthropogenic processes that have influenced, and continue to influence, carnivore distributions and densities in Britain.
- Chapter 3: I explore polecat resource use through the past 40 years using stable isotopes of carbon and nitrogen. I examine whether isotopic signatures differ between males and females and whether such differences have varied over time and space. I particularly focus on

potential differences between polecats at the core of their expanding range compared to those at the frontline of expansion.

- Chapter 4: I analyse polecat diet using stomach contents from road casualty carcasses to see how this may have changed with varying availability of a key food source for polecats in Britain–rabbits. I contrast current consumption levels of lagomorphs with historical levels recorded in dietary studies from the 1960s, 1980s and 1990s.
- Chapter 5: I examine current levels of secondary exposure to second-generation anticoagulant rodenticides in polecats and examine whether there are key factors that determine likelihood and extent of exposure. I also examine whether levels of exposure have changed in the last 25 years, a significant period in which polecats have expanded into regions of heavier use of rodenticides.
- Chapter 6: I explore the principles underpinning twenty-first century gamekeeping, in the words of gamekeepers themselves. Gamekeepers were implicated in the original declines of polecats and are important agents of wildlife management in Great Britain. The profession remains controversial, primarily due to conflicts relating to raptor persecution, but little has been written in the academic literature about gamekeepers' approach to wildlife management, their relationship with carnivores and the implications of their actions for carnivores.
- Chapter 7: I conclude this thesis with a general discussion of the implications of my research for understanding the changing status of polecats in Great Britain and for the management of carnivores in general.

Data collection approach

In the course of writing this thesis I carried out a combination of desk research (Chapter 2), lab work using samples from polecat carcasses (Chapters 3, 4 and 5) and fieldwork (ecological: see "Polecat fieldwork" section below, and ethnographic: Chapter 6) to generate data for analysis.

In Chapters 3, 4 and 5, polecat carcasses collected as part of the Vincent Wildlife Trust's National Polecat Survey 2013-2016 (Croose 2016) were sampled to represent polecats collected during the 2010s decade. The varied condition of the carcasses (which were predominantly road casualties) meant that different samples were available from each specimen. While there was some overlap of the polecat specimens collected 2013-2016 utilised in each chapter, the degree of overlap was limited due to the availability of samples from each animal (for example, some contained gut contents but not livers, others had teeth and whiskers but no liver or gut contents for analysis). Chapter 3 also includes samples taken from polecats that are part of the National Museum of Scotland's full polecat collection. Chapter 5 utilises historical analyses of secondary exposure to rodenticides in polecats collected in two earlier polecat rodenticide survey periods (Shore et al. 2003). Some of the analyses in these chapters are necessarily limited by the metadata available for these historical datasets. The covariates analysed in each chapter were determined by the research objectives for each individual chapter. As a result, some variables (e.g. polecat age) were analysed in Chapter 5, but not in Chapters 3 or 4 (Table 1.1).

Table 1.1 *Overview of covariates included in statistical models by chapter*

Chapter	Response variable	Explanatory variables
2	Distance from central point in 1960s range for pine martens, polecats and wildcats	Time (decade)
3	Stable isotopes of carbon and nitrogen, individual whisker variation in carbon and nitrogen	Time (decade) Position in range Distance from the centre of the polecats 1915 refugium in Wales Sex
4	Presence or absence of lagomorph in polecat gut contents	Sex Season Region
5	Extent of secondary exposure to rodenticides	Age Fat score

		Land class (arable or pastoral) from which the polecat was collected Sex Season Stable isotopes of carbon and nitrogen Region Time of year (first half or second half) that the polecat was collected Survey period that the polecat was collected from. Position in range (in relation to the 1990s polecat range)

Statistical methods

I use generalised linear models (glm) to estimate the effects of variables in chapters 2, 3, 4 and 5. All statistical analyses were carried out in R (R Core Team 2013). In Chapter 2, I fit a glm using range extent statistics for polecats, pine martens and wildcats in order to calculate the rate of range expansion for each species for decades with available distribution data between 1960 and 2018. In Chapters 3 and 5, I use an information-theoretic approach (Burnham & Anderson 2004) to identify top models using AIC to evaluate model performance and determine which variables should be included in average models to explain isotopic variation and rodenticides exposure respectively. In both of these chapters, the relative complexity of both the underlying systems being explored and the number of variables being examined for inclusion indicate that an information-theoretic approach would be most appropriate. Adopting an information-theoretic approach can help to minimise type II errors (false negatives) during the model simplification process and in doing so may aid the inclusion of all larger biological effects that are present (and detectable given the level of statistical power in the model). In Chapter 4, I fit a binomial glm to explore the determinants of lagomorph detection in polecat gut contents. Due to the relatively low number of variables included in this model and simplicity of the system, I opted to use step-wise deletion using p-values to determine the most parsimonious model. I analyse the data in Chapter 6 using qualitative methods. In all chapters using statistical models I report confidence intervals to assess biological and statistical significance.

Polecat fieldwork

Between June 2016 and December 2016, I planned and executed a licensed polecat trapping exercise in Herefordshire and Gloucestershire. The aim of this study was to evaluate how polecats use their home ranges given the anthropogenic risks present in the landscape (including but not limited to rodenticide use, predator controls and roads). Eight 1x1km squares were selected in areas of high polecat presence, which was determined by records reported in the Vincent Wildlife Trust's 2014-2016 National Polecat Survey of Britain (Croose 2016). Trapping followed the protocol defined in Birks & Kitchener (1999). Six polecats were successfully caught, anaesthetised, PIT tagged, sampled for whiskers, fitted with radio collars and released. Unfortunately due to the low number of polecats caught and poor rates of radio collar retention, it was not possible to analyse the data that was collected as part of this study and I decided not pursue a second field season.

Chapter 2

Recent history, current status, conservation and management of native mammalian carnivore species in Great Britain

Chapter 2: Recent history, current status, conservation and management of native mammalian carnivore species in Great Britain

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Abstract

After historical declines in population sizes and ranges, we compare and contrast the recent history and contemporary variation in the status of Great Britain's eight native mammalian carnivore species from the 1960s to 2017.

Wildcat *Felis silvestris* conservation status is unfavourable and is masked by hybridisation with domestic cats *Felis catus*. Red foxes *Vulpes vulpes* remain widespread but are currently declining. European otter *Lutra lutra*, European pine marten *Martes martes* and European polecat *Mustela putorius* populations are characterised by rapid recovery. Otters have almost completely recolonised Great Britain, polecats have expanded their range throughout southern Britain from refugia in Wales and pine martens have expanded their range from the Scottish Highlands. European badgers *Meles meles* have generally increased in population density. Status assessments of stoats *Mustela erminea* and weasels *Mustela nivalis* are data-deficient but available evidence suggests that stoats may have increased while weasels may have declined.

Anthropogenic processes influencing carnivore status include legal protections, habitat quality, reintroductions, predator control, pollutants, hybridisation and diseases and their associated control practices. Population effects of contaminants, such as anticoagulant rodenticides, remain poorly characterised. The widespread interface with domestic and feral cats makes the wildcat's situation precarious. Recent declines in rabbit *Oryctolagus cuniculus*

populations are a concern, given that several carnivore species depend on them as food.

We conclude that, with the exception of the wildcat, the status of Great Britain's mammalian carnivores has markedly improved since the 1960s. Better understanding of the social aspects of interactions between humans and expanding predator populations is needed if conflict is to be avoided and long-term co-existence with people is to be possible.

Introduction

Eight species of terrestrial mammalian carnivore are native to, and extant in, Great Britain (defined here as England, Scotland, Wales and their islands): wildcat *Felis silvestris*, red fox *Vulpes vulpes*, European otter *Lutra lutra*, European badger *Meles meles*, European pine marten *Martes martes*, stoat *Mustela erminea*, weasel *Mustela nivalis,* and European polecat *Mustela putorius*. Since their arrival 5000–20000 years ago (Montgomery et al. 2014), they have had mixed fortunes, depending in part on whether they were reviled as vermin, used for sport, valued for fur, appreciated as rodent-catchers, or combinations thereof, during their shared histories with humans (Lovegrove 2007). Langley and Yalden (1977) illustrated the eighteenth and nineteenth century declines of what they termed Britain's ‘rarer carnivores’ (wildcat, pine marten and polecat), which they attributed largely to intensive predator control by gamekeepers, leading to persistence only in refugia where control was least intensive. Badger and otter populations were also greatly reduced but did not experience such pronounced range contractions (Cresswell et al. 1989, Jefferies 1989), despite local pressures from digging (Cresswell et al. 1989) and hunting (Jefferies 1989). By the twentieth century, only fox, stoat, and weasel appeared unaffected by control (Tapper 1992). The advent of World War I, cessation of sporting activities and the loss of a generation of gamekeepers led to a reduction in predator control (Langley & Yalden 1977). Contemporaneous reports suggest that the most affected species showed signs of recovery almost immediately (Lovegrove 2007). By the 1970s, there was evidence that the wildcat, pine marten and polecat were beginning to recolonise their former ranges (Langley & Yalden 1977). Otters, however, were experiencing catastrophic decline (Jefferies 1989), later ascribed primarily to exposure to organochlorine pesticides (Chanin & Jefferies 1978).

Since the 1970s, legal, social, and practical developments have altered the anthropogenic pressures faced by Britain's carnivores. Management practices have changed, with bans on certain traps and toxicants, and greater reliance on rearing and releasing pheasants *Phasianus colchicus*, as opposed to fostering wild gamebirds (Tapper 1992). Legal protections have been put in place internationally (e.g. the European Union's Habitats Directive 1992) and nationally for conservation (e.g. Wildlife & Countryside Act 1981) and on animal welfare grounds (e.g. Protection of Badgers Act 1992). Land use change (Swetnam 2007) and agricultural intensification have been associated with biodiversity loss (Robinson & Sutherland 2002). The mechanisms and implications of exposure to some contaminants are now better understood (Shore & Rattner 2001), advances in genetics have revealed the extent of hybridisation between wild and domestic species (Driscoll et al. 2007, Costa et al. 2013), and developments in epidemiology have enhanced knowledge of carnivores as disease reservoirs (Delahay et al. 2009).

A century after the rarest of Britain's carnivores reached their nadir and 40 years after the publication of the paper by Langley and Yalden (1977), it is timely to compare and contrast the status of the eight species. We have gathered literature from the 1960s to 2018 and include the latest population estimates. We review processes that affect carnivores, positively and negatively. Although two non-native carnivore species, feral ferret *Mustela furo* and American mink *Neovison vison*, have become established in Great Britain, they are not considered here, other than as an influence on native species.

Methods

We searched Scopus, Google Scholar, and Google using scientific and common names (wildcat, [red] fox, [European] otter, [European] badger, [European] pine marten, stoat, weasel, [European] polecat) and the keywords ‘Britain’, ‘England’, ‘Scotland’ or ‘Wales’ and ‘distribution’, ‘density’ and ‘monitoring’. Publications until 5 October 2018 comprising systematic surveys of distribution and abundance were catalogued. Further publications were added from their citations. *Ad hoc* records were not included because of the difficulty of distinguishing hybrids (wildcats and polecats) and because our objective was to assess status using large-scale accounts.

Distribution data were digitised (QGIS Development Team 2009) and scaled to hectads. Range expansion, if any, was modelled following Preuss et al. (2014), using R v3.5.1 (R Core Team 2013). Only surveys using comparable approaches, i.e. nationwide surveys using carcass collection and verifiable sightings, were included. Central points of the 1960–1975 core ranges (Langley & Yalden 1977) were used as the starting point from which later expansion was measured. For wildcats the starting point was Scotland, for pine martens it was northern Scotland, and for polecats it was central Wales. Range change was measured between starting points and range margins in each decade. Distances from central points were measured to the centre of each hectad in which presence was confirmed in later surveys. Outliers unlikely to be part of a contiguous population were removed. Range margins were estimated by fitting a gamma distribution to distance to central point data, using the 95th quantile to represent the location of the range edge. This approach was preferred as it is less sensitive to sampling variation (Preuss et al. 2014). The slope of the regression with time was taken as the rate of expansion.

Population change and current status

Wildcat Felis silvestris

The wildcat's range diminished earlier than those of pine marten or polecat. In 1915, wildcats were limited to the Scottish Highlands, showing the most restricted distribution of Langley and Yalden's (1977) rarer carnivores. By the 1970s, wildcats could be loosely grouped into two populations: a south-western population in the southern Highlands and Argyll and Bute; and a north to north-eastern population stretching from the north-central Highlands to the Grampians (Langley & Yalden 1977). Three distribution surveys using carcass collection, live trapping, and sightings were undertaken between the 1980s and 2010s (Fig. 2.1). An intensive camera-trapping survey was also carried out by Kilshaw et al. (2016) to assess wildcat occupancy with habitat covariates. It is difficult to assess changes in wildcat distribution, or to model range expansion, owing to the presence of, and changes in reporting of, hybrids (Fig. 2.1). Our model of wildcat range change was inconclusive (expansion rate 0.2 km per year over 30 years, 95% confidence interval: −4.4 to 4.9, Appendix 2.1b).

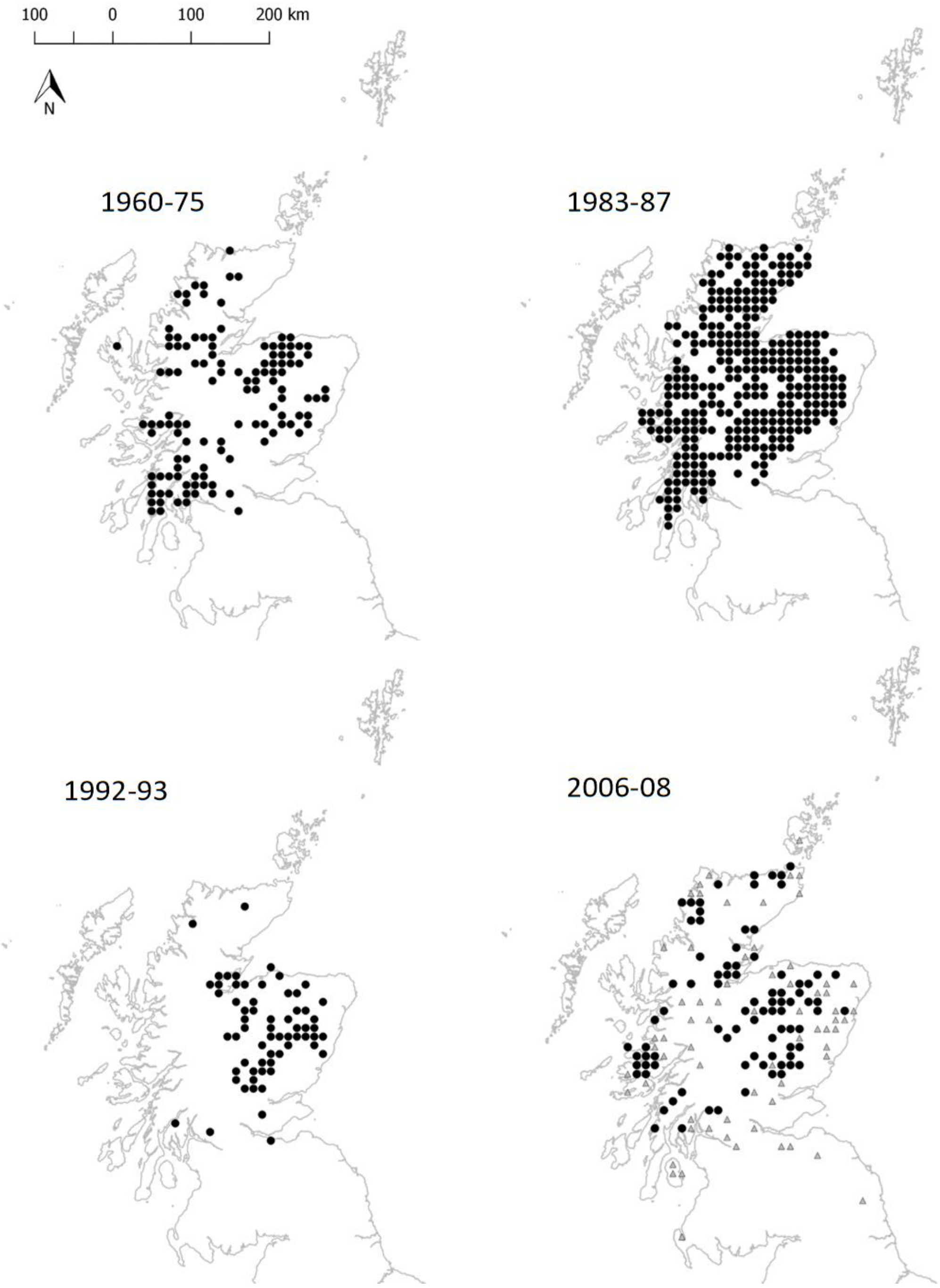


Figure 2.1. *Wildcat* Felis silvestris *distribution in Scotland from 1960 to 2008. Data are from Langley and Yalden (1977), Easterbee et al. (1991), Daniels et al. (1998), Davis and Gray (2010). Black circles indicate presence. All presence points were scaled to hectads. On the 2000s map, black circles indicate 'probable' wildcats, grey triangles indicate 'possible' wildcats (Davis & Gray 2010). 1992–1993 dates are the dates of Daniels et al.'s (1998) live trapping.*

In the 1980s, wildcats were distributed throughout northern and central Scotland and there was an increase in records in the east of the country and an expansion of range north-east into Caithness, compared to the 1970s (Easterbee et al. 1991). The two population groupings (Langley & Yalden 1977) were less evident. Davis and Gray (2010) divided records into ‘possible’ (44%) and ‘probable’ (56%) wildcat sightings, using pelage characteristics (Kitchener et al. 2005). ‘Probable’ wildcat records were more common north of the Highland boundary line than ‘possible’ wildcat records, which appeared more frequently in the south and east of Scotland. Wildcat distribution is currently assumed to be that of the ‘probable’ records (Scottish Natural Heritage 2013). Kilshaw et al. (2016) reported that the probability of wildcat occupancy is highest in the central and eastern Highlands, the edges of the Cairngorms, along the west coast and in a few areas in the far north. The Scottish Wildcat Action project has not received any records verified as wildcats from the northern Highlands since 2015 (R. Campbell, unpublished data). It is also believed that there are no wildcats south of central Scotland (Kilshaw et al. 2016). The latest population estimate for wildcats is 200 (95% confidence interval: 30–430; Mathews et al. 2018; Appendix 2.2). However, the reliability of this estimate is considered to be low and estimates vary, depending on how strict a definition of wildcat is used.

Red fox Vulpes vulpes

Red foxes are present throughout mainland Great Britain, Anglesey, Isle of Wight and Skye (Harris et al. 1995, Webbon et al. 2004). It is likely that the species’ value in sport hunting meant that foxes were protected to some degree from systematic control and this prevented the historic declines seen in other carnivores (Tapper 1992). Foxes feature in numerous surveys, including the Game and Wildlife Conservation Trust's (GWCT) National Gamebag Census (NGC; Aebischer et al. 2011) and the British Trust for Ornithology's (BTO) Breeding Birds Survey (BBS). The NGC provides a long-term index of individuals killed per unit area as part of game management. NGC records of foxes killed on game estates suggest a population increase in Britain from the 1960s, followed by stabilisation from the 1990s to 2009 (Fig. 2.2; Aebischer et al. 2011). Data from the BBS over a similar time period partly corroborate this; however, recent data indicate a 45% decline in the numbers of foxes seen on

BBS sites in England (−41% throughout the UK) from 1996 to 2016, particularly after *c*. 2008 (BTO 2018, Harris et al. 2018). There are no other data to corroborate this decline and causes are not understood, though timing is coincident with significant declines in BBS records of rabbits *Oryctolagus cuniculus* in England (−44%), Scotland (−82%), and Wales (−48%; Harris et al. 2018).

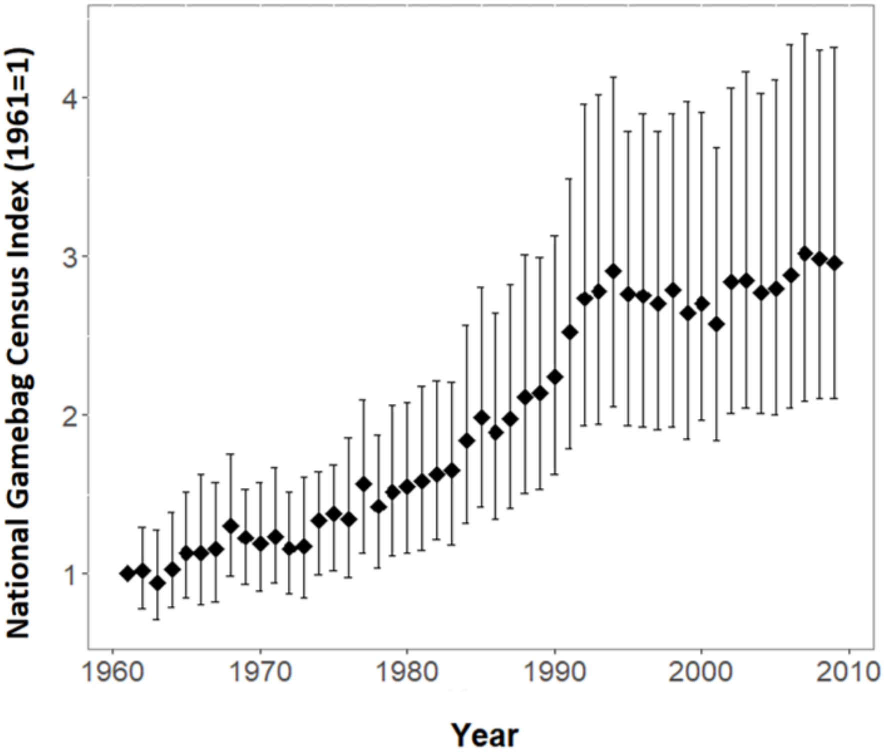


Figure 2.2. *National Gamebag Census index of red fox* Vulpes vulpes *bags in Great Britain from 1961 to 2009. Index values are relative to the start year, which has an arbitrary value of 1. Error bars represent 95% confidence intervals. Reproduced by kind permission of the Game and Wildlife Conservation Trust (Aebischer et al. 2011).*

Previous causes of fox declines include hunting pressure (Tapper 1992) and localised outbreaks of mange caused by *Sarcoptes scabiei* (Soulsbury et al. 2007). Some of these declines have been offset by spread into areas or habitats where foxes were previously scarce (Baker et al. 2006), such as Norfolk (Tapper 1992) and urban spaces (Scott et al. 2014). A survey of England and Wales found that in the 2010s foxes were recorded in ~90% of 65 cities where they had been scarce or absent in the 1980s (Scott et al. 2014).

Although urban foxes are increasing, they still comprise a small proportion of the total population. Webbon et al. (2004) estimated the total rural fox population in Britain to be 225000, whereas the estimate for urban foxes was 33000 in 1995 (Harris et al. 1995). The latest estimate of the total fox population is 357000 (95% confidence interval: 104000–646000; Mathews et al. 2018; Appendix 2.2).

European otter Lutra lutra

As an apparent competitor with humans for fish, the European otter has long been viewed as a pest. Otter hunting began in the Middle Ages (Lovegrove 2007). Historical records indicated a slow decline in numbers from the late eighteenth century onwards, caused by predator control, sport hunting with hounds, and pollution (Jefferies 1989). Otters rarely scavenge and have large territories, making them less likely than other carnivores to enter baited traps (Jefferies 1989). While local extinctions occurred in some catchments, regional extinctions were initially avoided (Harris et al. 1995).

By the late 1950s, hunt records indicated that otters were experiencing sudden and rapid decline, with the most severe reductions in southern England (Jefferies 1989). Various potential drivers were considered, including habitat destruction, disturbance, introduction of American mink, the associated spread of canine distemper virus, hunting pressure and the possibility of increased mortality arising from the severe winter weather of 1962–1963 (Chanin & Jefferies 1978). The timing and sudden onset of the decline, simultaneous to that observed in predatory birds, suggested that organochlorine pesticides, principally dieldrin, were likely to be responsible for increased mortality (Chanin & Jefferies 1978). Dieldrin, introduced in the 1950s as a sheep dip and seed dressing, was detected in 81% of otters examined between 1963 and 1973 (Mason et al. 1986). Voluntary restrictions were placed on dieldrin use in the 1960s and 1970s, followed by mandatory bans in the 1980s (Macdonald 1983).

National otter surveys began in the 1970s (Fig. 2.3, Appendix 2.3), when otters were recorded at only 6% of sites in England (Lenton et al. 1980), 20% in Wales (Crawford et al. 1979) and 57% in Scotland (Green & Green 1980). By the 1980s, European otters were present at 10% of sites in England (Strachan et al. 1990), 38% in Wales (Andrews & Crawford 1986) and 65% in Scotland (Green

& Green 1987). Reintroductions were carried out in East Anglia, Hertfordshire and the upper Thames in the 1980s and early 1990s (Jefferies et al. 1986, Harris et al. 1995, Roche et al. 1995). Surveys in the 1990s recorded otters present at 23% of sites in England (Strachan & Jefferies 1996), 53% in Wales (Andrews et al. 1993), and 88% in Scotland (Green & Green 1997). By the 2000s, European otters were recorded at 36% of sites in England (Crawford 2003), 72% in Wales (Jones & Jones 2004), and 92% in Scotland (Strachan 2007). The most recent surveys found European otters at 59% of the original sites surveyed in England (Crawford 2010) and, when accompanied by spot checks in areas not covered by the original surveys, these data show that only Kent and East Sussex are yet to be substantially recolonised (Fig. 2.3). Otters are considered to be at carrying capacity in south-west England and the Wye Valley, with evidence of otter presence at over 80% of sites (Crawford 2010). The 2009–2010 survey in Wales indicated otter presence at 90% of sites (Strachan 2015). The contemporaneous survey in Scotland indicated that there may have been a decline in occupancy since the previous decade, with detection at 78–80% of sites surveyed (Findlay et al. 2015). However, there was some uncertainty as to whether this was a real decline or a result of inclement weather during surveying and reduced detectability (Findlay et al. 2015). Otters are now widespread throughout both Wales and Scotland (Fig. 2.3). In England, Crawford (2010) estimated that otter distribution had expanded at approximately 3.6km per year, and this trend is expected to lead to complete recolonisation of England, and therefore Great Britain, by 2030 (Crawford 2010).

Dieldrin is still detectable in otters (Chadwick 2007) but is not considered likely to affect populations at the observed trace levels (Crawford 2010). The presence of invasive American mink, which became widespread during the otter's absence, has not impeded otter recolonisation, probably because otters cause shifts in mink behaviour (Harrington et al. 2009a). The latest population estimate for otters in Britain is 11000, although the reliability of this estimate is considered to be very low (Mathews et al. 2018; Appendix 2.2).

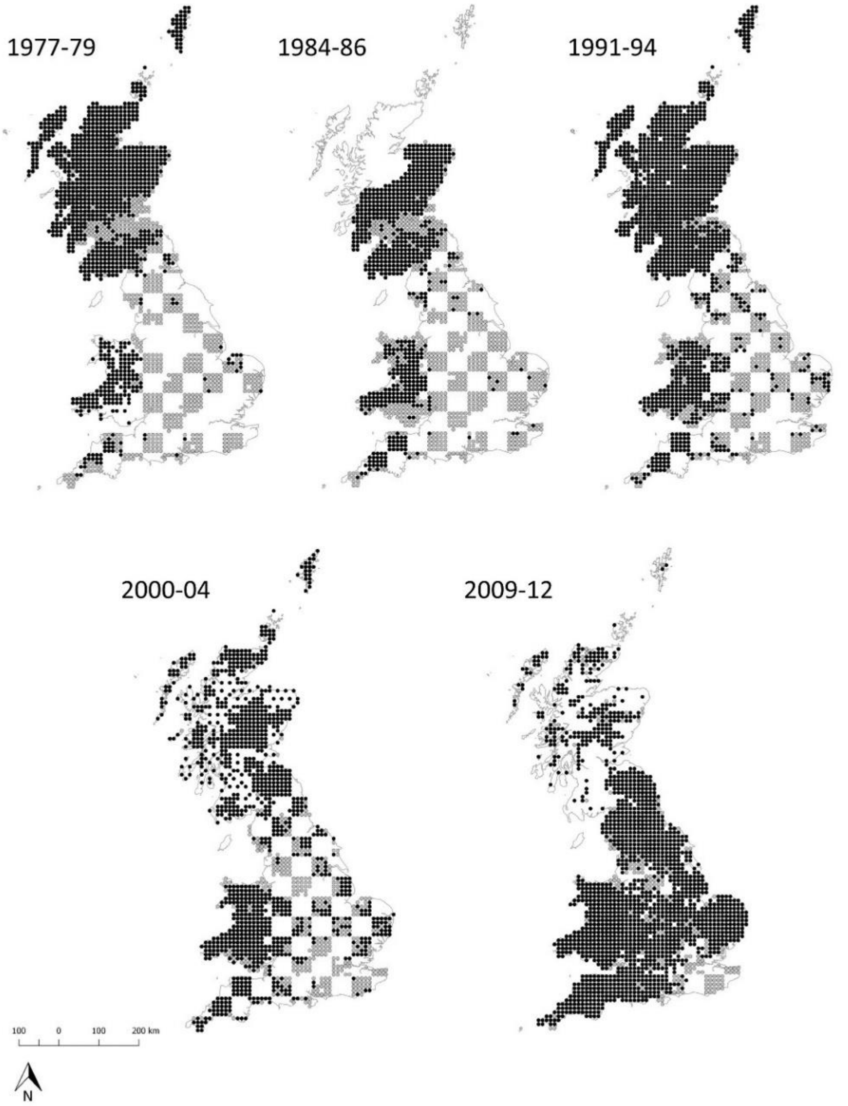


Figure 2.3. *European otter* Lutra lutra *distribution in Great Britain from 1977 to 2012. Maps recreated from National Otter Surveys of England (Lenton et al. 1980, Strachan et al. 1990, Strachan & Jefferies 1996, Crawford 2003, 2010), Scotland (Green & Green 1980, 1987, 1997, Strachan 2007, Findlay et al. 2015), and Wales (Crawford et al. 1979, Andrews & Crawford 1986, Andrews et al. 1993, Jones & Jones 2004, Strachan 2015) using data provided by Environment Agency (2018), Scottish Natural Heritage, Natural Resources Wales and Joint Nature Conservation Committee (2018). Black circles indicate presence. Grey circles indicate surveyed areas where otters were recorded as absent. Blank areas do not indicate absence. 1980s Scotland survey did not include the Western Isles, Northern Isles or the Scottish Highlands (Green & Green 1987). In England, surveys were carried out in alternate 50 × 50km squares until the most recent survey (Crawford 2010).*

European badger Meles meles

European badger populations declined during the nineteenth century to the extent that the species were considered uncommon (Cresswell et al. 1989). Declines were due to a combination of control by gamekeepers, sett disturbance and badger baiting (Wilson et al. 1997). The extent of pressure varied regionally. For example, in East Anglia, intensive activity by gamekeepers reduced numbers to a 10th of those in neighbouring counties (Harris 1993).

By the 1970s, badgers were more common in south-west and central England, and central and north Wales (Appendix 2.3), but remained unrecorded in parts of East Anglia and northern Scotland (Neal 1972). In the 1980s, badger distribution expanded and the population was estimated to be 250000 in Great Britain, although gaps remained in London, East Anglia, Lincolnshire, Lancashire, and northern Scotland (Cresswell et al. 1990). By 1994–1997, the number of badger social groups in Britain had increased by 24%, although colonisation of new areas was minimal (Wilson et al. 1997).

In 2006–2009, surveys of mainland Scotland indicated that badger main sett numbers had increased since the 1990s, though differences in methodology made direct comparisons difficult (Rainey et al. 2009). In England and Wales, numbers of badger social groups increased by 88% (equivalent to 2.6% per annum) between 1985–1988 and 2011–2013 (Judge et al. 2014). The magnitude of changes in sett density varied by region, due to a combination of landscape and local effects. England saw a 103% increase, whereas in Wales densities remained stable (Judge et al. 2014). Combining results from Scotland (Rainey et al. 2009), with Judge et al. (2014), leads to an estimate of 81000 (95% confidence interval: 75400–86600) badger social groups in Britain by 2013. Judge et al. (2017) combined their earlier sett survey with analysis of social group size variation, to derive a population estimate of 485000 individual badgers in England and Wales. Even allowing for methodological differences, evidence suggests that badger populations increased substantially in England and Wales between the 1980s and 2011–2013 (Cresswell et al. 1990, Judge et al. 2017).

European pine marten Martes martes

When the European pine marten population reached its nadir in *c*. 1915, its range was restricted to the north-west of the Scottish Highlands and small, isolated areas of northern England and north Wales (Langley & Yalden 1977). By 1975, there was some spread eastwards into the Scottish Grampians, while the Welsh population was not thought to have expanded and English records were limited to sporadic sightings in Yorkshire and the Lake District (Langley & Yalden 1977).

By the 1980s in Scotland, the main populations were still confined to north of the Great Glen, though pine marten occurrence was nearly continuous throughout the central and western Highlands (Velander 1983). As the prevailing view was that this northern population was too remote to recolonise southern Scotland, a reintroduction took place in Galloway Forest, southwest Scotland in 1980 and 1981 (Shaw & Livingstone 1992). In the 1990s, pine martens expanded south of the Highlands into Argyll and Bute, Stirling and Perth and Kinross. By 2013, they had been recorded throughout much of central and eastern Scotland, on Skye and Mull and beyond the release sites in Galloway (Fig. 2.4; Croose et al. 2013, 2014). Our model of range expansion estimates that between 1975 and 2015 the Scottish pine marten population expanded at a rate of 1.7km per year (95% confidence interval: 0.8–2.7km, Appendix 2.1b). Despite repeated surveys during the 1980s and 1990s (Appendix 2.3), evidence of pine marten presence in England and Wales remained limited, suggesting that at best only a few low-density populations remained. There is occasional evidence of pine martens from Shropshire and Hampshire, potentially the result of covert releases. Recent evidence in Northumberland indicates that European pine martens are expanding south through the Borders, recolonising parts of northern England (Vincent Wildlife Trust [VWT], unpublished data). Between 2015 and 2017, 51 pine martens were translocated from Scotland to Wales in order to reinforce populations there; this has proven successful with high survival and breeding in the wild (VWT, unpublished data). The latest population estimate for pine martens is 3700 (95% confidence interval: 1600–8900; Mathews et al. 2018; Appendix 2.2).

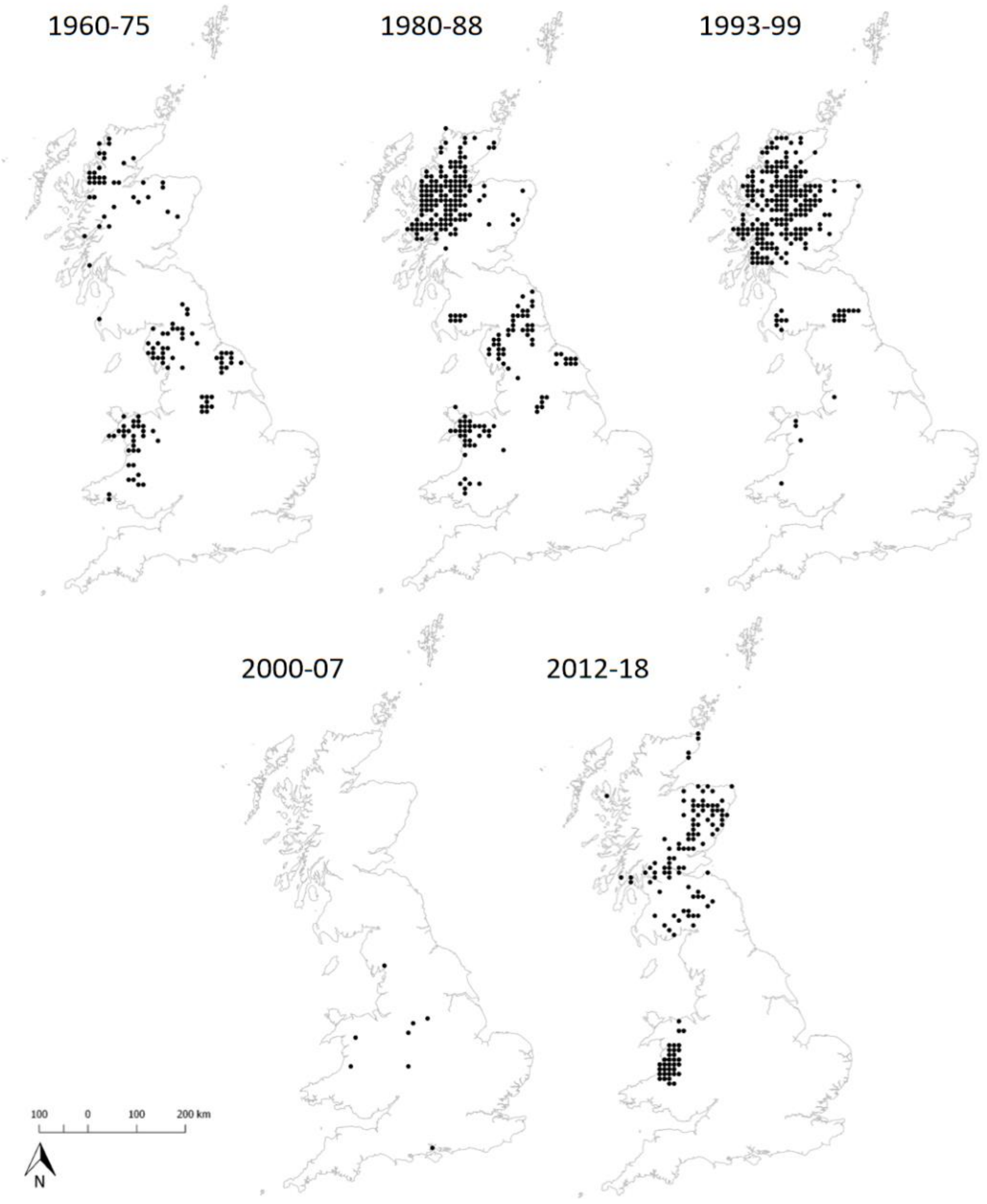


Figure 2.4. *European pine marten* Martes martes *distribution in Great Britain from 1960 to 2018. Data from Langley and Yalden (1977), Velander (1983), Bright and Harris (1994), McDonald et al. (1994), Balharry et al. (1996), Strachan et al. (1996), Birks and Messenger (2010), Croose et al. (2013, 2014), and VWT (unpublished data). Black circles indicate presence. All presence points were scaled to hectads. Only verified records in Birks and Messenger (2010) were included. No surveys were carried out in Scotland in the 2000s, and the 2010s Scotland surveys included only central and southern Scotland (Croose et al. 2013, 2014).*

Stoat (ermine) Mustela erminea

There are no national surveys for the stoat and so data are from the GWCT's NGC. Stoats are thought to be common and widespread throughout Great Britain, including on the Isle of Wight and the Scottish islands of Shetland, Islay, Jura, Mull, Skye, Raasay and Bute (McDonald & King 2008a). In 2010, stoats were sighted for the first time on Mainland, Orkney and an eradication programme is underway there in an attempt to protect ground-nesting birds, Orkney voles *Microtus arvalis orcadensis* and the predatory birds that eat them (Fraser et al. 2015). In spite of intensive predator control in the nineteenth century, stoat numbers did not exhibit the declines seen amongst the larger mustelids (Tapper 1992). This is likely to be due to the stoat's high productivity, reducing potential for culling to cause decline, and its mobility, facilitating immigration into areas where numbers are reduced (McDonald & Harris 2002).

Stoat numbers were severely reduced by myxomatosis in rabbits (Sumption & Flowerdew 1985). One game estate in Suffolk reported a tenfold reduction in the numbers of stoats killed in the years after the initial outbreak (Tapper 1992). Stoats were, and remain, extremely reliant on rabbits (McDonald et al. 2000) and the loss of this important food source was believed to have impaired productivity and survival (Sumption & Flowerdew 1985). The NGC shows that indices of the numbers of stoats killed per unit area on game estates increased steadily from the 1960s (Fig. 2.5; Aebischer et al. 2011), alongside rabbit recovery, though the NGC reported another dip in stoats killed in the 1980s (Aebischer et al. 2011). In a comparative study of stoat and weasel diets between the 1960s and 1990s, McDonald et al. (2000) concluded that there was little evidence that reductions in prey were causing this downturn, some of which may have been attributable instead to changes in trapping effort affecting the NGC (McDonald & Harris 1999). Since then, there has been a steady increase in stoats killed on game estates from the 1990s to 2009 (Fig. 2.5). The impact on stoats of the recent apparent reductions in rabbit numbers is unknown. The latest population estimate for stoats is 438000 (Mathews et al. 2018), unchanged from that of Harris et al. (1995), indicating the sparsity of data. Both of these estimates are considered to have low reliability (Appendix 2.2).

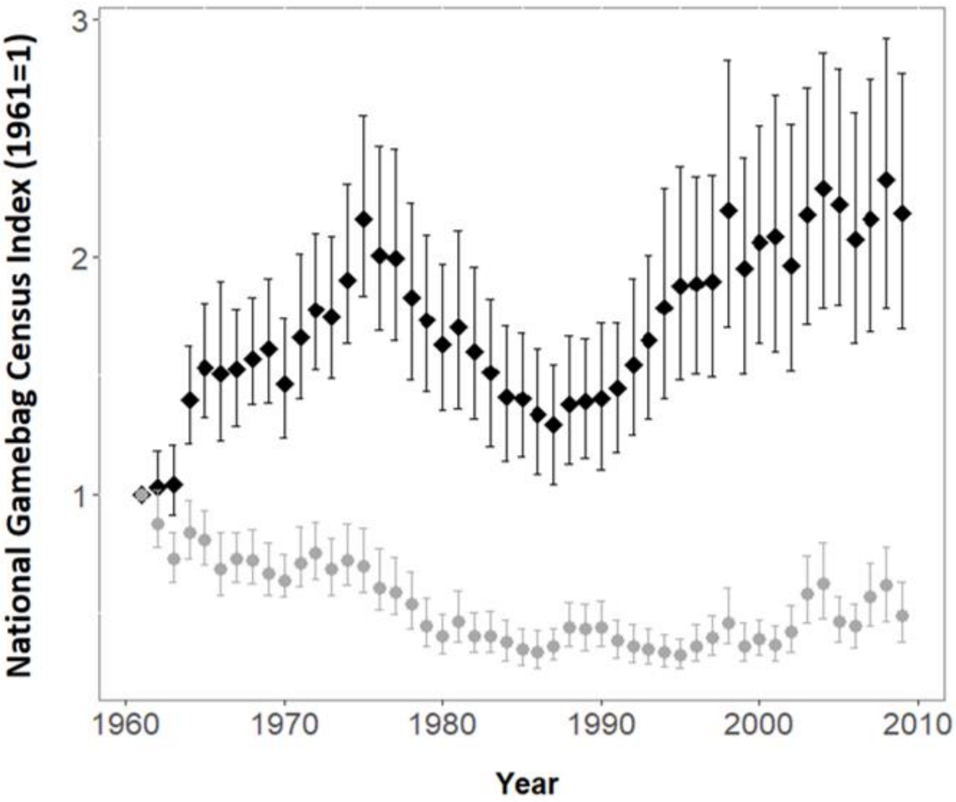


***Figure 2.5.** National Gamebag Census indices for stoats* Mustela erminea *and weasels* Mustela nivalis *in Great Britain from 1961 to 2009. Black diamonds are for stoats and grey circles are for weasels. Gamebags are indices of the numbers killed per unit area on game estates. All index values are relative to the start year, which has an arbitrary value of 1. Error bars represent 95% confidence intervals. Data reproduced by kind permission of the Game and Wildlife Conservation Trust (Aebischer et al. 2011).*

Weasel (common weasel, least weasel) Mustela nivalis

Weasel population trends are also from the GWCT's NGC. Weasels are relatively prolific breeders and, similar to stoats, did not appear to experience nineteenth century declines (Tapper 1992). They are also thought to be common and widespread throughout mainland Great Britain (McDonald & King 2008b). In contrast to stoats, weasel abundance increased during and after myxomatosis, likely a result of reduced rabbit grazing, increased rough grassland and increased abundance of field voles *Microtus agrestis* (Jefferies & Pendlebury 1968), which are frequent prey of weasels (McDonald et al. 2000).

The NGC reveals a decline in indices of weasels killed per unit area on game estates from the 1960s onwards (Fig. 2.5). Models of weasel populations suggest that this decline is unlikely to be the result of trapping by gamekeepers as, similar to the stoat, the weasel's high productivity and mobility buffer populations against intense culling (McDonald & Harris 2002). Weasel productivity is particularly sensitive to prey abundance (King 1980) and populations fluctuate with vole abundance (Tapper 1979). It is therefore possible that there has been a negative effect of rabbit recovery on field vole populations and, consequently, weasels (Sumption & Flowerdew 1985). Weasel indices from the NGC started to increase again from the 1990s but are still below those recorded in the 1960s (Fig. 2.5). The latest population estimate for weasels is 450000 (Mathews et al. 2018). In common with stoats, this estimate is the same as that of Harris et al. (1995), indicating the paucity of data for these species (Appendix 2.2).

European polecat Mustela putorius

Having reached their nadir in *c*. 1915, European polecat populations began to recover following the alleviation of predator control during the early twentieth century, the banning of gin traps in 1958, and the recovery of rabbit populations after the myxomatosis epizootic of the mid-twentieth century (Langley & Yalden 1977). Rabbits are also important prey for polecats (Birks & Kitchener 1999) and, although rabbits were previously abundant, they were catastrophically reduced as the disease swept across the country (Sumption & Flowerdew 1985). Rabbit numbers began to recover by the 1960s and by the 2000s were approaching pre-myxomatosis levels (Aebischer et al. 2011), although more recently rabbits have experienced significant declines (see the red fox section). Reports suggest that polecats were already expanding their range by the 1960s but rabbit and polecat recovery are likely to be closely linked (Sumption & Flowerdew 1985).

National polecat surveys have taken place between the 1980s and 2010s (Appendix 2.3). From the 1990s, surveys attempted to distinguish between polecats and hybrid polecat-ferrets, based on a pelage classification system (Birks & Kitchener 1999). Classifications of carcasses in this way and, more recently, using molecular genetic techniques, suggest that polecat-ferrets are more prevalent at the edge of the polecat's range (Costa et al. 2013).

In the 1980s, polecats occupied most of Wales and the border counties of Shropshire and Worcestershire (Tapper 1992). By the 1990s, polecats were present in all counties on the English side of the Welsh border (Birks & Kitchener 1999). The 2000s were characterised by increased density of records in Derbyshire, Buckinghamshire, Berkshire, Wiltshire, Dorset, and Hampshire (Birks 2008). Unofficial releases led to polecats becoming established in Cumbria, Argyll, and Perthshire, well outside of the core range, though the pelage characteristics of some of these animals suggested they were from captive stock (Birks 2008). By 2015, polecats had recolonised most of central and southern England (Fig. 2.6) and remained widespread in Wales and the West Midlands (Croose 2016). The most noticeable gaps in current distribution are in northern England and Scotland, potentially due to difficulties in dispersing around conurbations. Overall, the polecat's range expanded eastwards at 4.9km per year between 1975 and 2015 (95% confidence interval: 2.6–7.1km, Fig. 2.6, Appendix 2.1b). This is faster than the pine marten's expansion, which is not unexpected; polecats have faster reproductive ability and greater flexibility in habitat requirements than pine martens (Birks 2015, 2017). The latest population estimate for polecats is 83300 (95% confidence interval: 68000–99000; Mathews et al. 2018; Appendix 2.2).

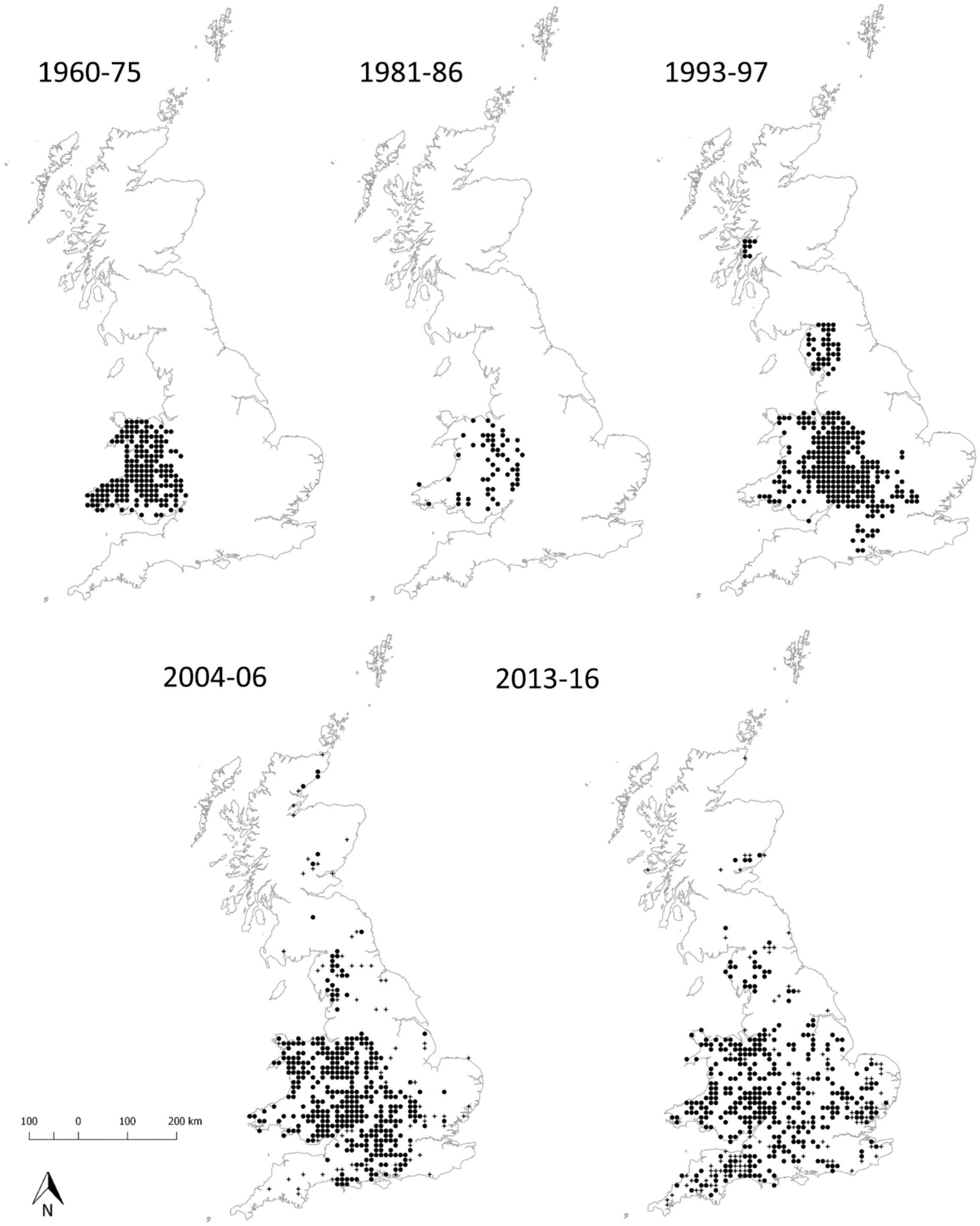


Figure 2.6. *European polecat* Mustela putorius *distribution in Great Britain from 1960 to 2016. Data are from Langley and Yalden (1977), Blandford (1987), Tapper (1992), Birks and Kitchener (1999), Birks (2008) and Croose (2016). Black circles indicate presence. Grey triangles indicate polecat-ferret hybrids. All presence points were scaled to hectads.*

Anthropogenic processes affecting carnivore status

Legislation

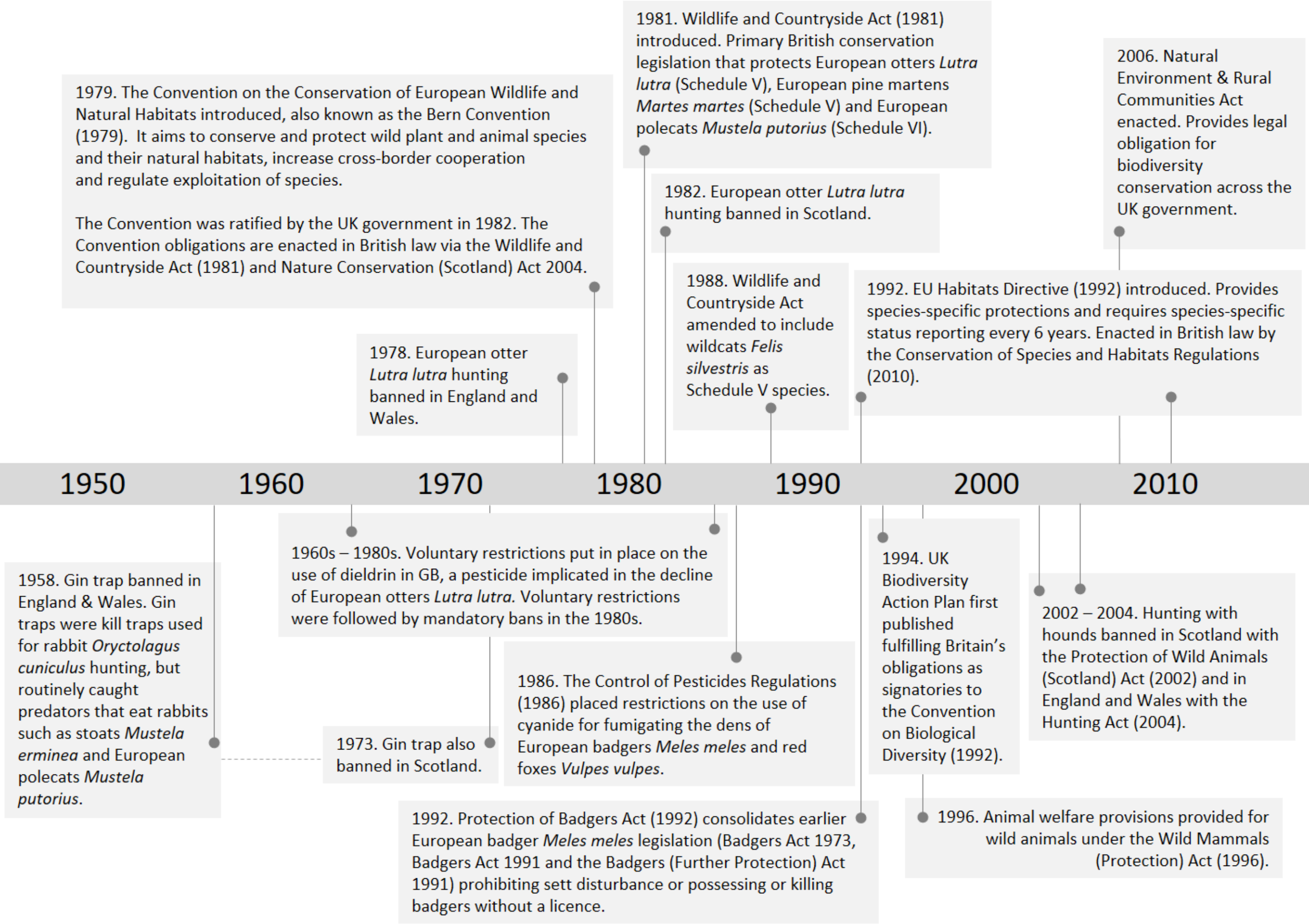
There are various legal protections for carnivores in Great Britain (Fig. 2.7, Appendix 2.4). Protections that ban direct control and disturbance are likely to aid species recovery where these pressures were a cause of population decline. Range expansions and population increases have occurred for some species (notably otters, badgers, pine martens and polecats) following the introduction of legal protection. However, legal protection is less effective where non-compliance is high, or where other factors beyond the legal mandate are limiting populations. Hybrid animals create a particular legal difficulty, as hybrids are not usually protected, even when sympatric 'pure' wild types are (Trouwborst 2014). 'Pure' animals may be confused with hybrids by hunters, leading to inadvertent killing. While badger recovery in Great Britain has been coincident with legislation, badger populations elsewhere have not increased following legal protection. For example, badger populations in Northern Ireland appear to be constrained by climate, habitat, farming practices, or food availability, rather than by persecution (Reid et al. 2012).

Habitat quantity, quality and connectivity

Habitat loss and fragmentation are major contributing factors to biodiversity loss and can be more significant for habitat specialists (otters and pine martens) than for generalists that are better able to exploit modified landscapes (foxes, stoats, and weasels; Bright 1993, Crawford 2010). Habitat fragmentation may increase intra-guild predation among carnivores, as has been observed between foxes and pine martens (Lindström et al. 1995). To counter habitat loss, a series of international and national regulations aimed at protecting habitat extent and quality have been implemented over the last six decades, including the European Union's Habitats Directive and Water Framework Directive. The result has been a wide-ranging protected area network that includes Special Areas of Conservation, Ramsar wetlands, national parks, and Sites or Areas of Special Scientific Interest. Existing habitats have been enriched via the creation and maintenance of den sites for otters and pine martens (Chanin 2003, Croose et al. 2016) and the promotion of wildcat-friendly forestry management in wildcat priority areas (Scottish Natural Heritage 2013).

More generally, afforestation since the 1950s, notably in Scotland, has provided additional, if not ideal, habitat for pine martens (e.g. Croose et al. 2013, 2014). Even with the protected area network, a lack of connectivity, through fragmentation or via natural or anthropogenic barriers, may prevent dispersal. Many monitoring tools rely on collecting road casualty carcasses, testament that these species are vulnerable to road mortality (Appendix 2.3). Roads, urban areas, and large continuous tracts of other unfavourable habitat may act as physical barriers to recolonisation. Genetic studies on badgers and wildcats suggest that while large roads can have a significant impact on gene flow, they are not impermeable, as animals can utilise crossing points (Frantz et al. 2010, Hartmann et al. 2013). Recolonisation of areas that require crossing of landscape barriers may therefore be possible, but the rate of expansion is likely to depend upon barrier size and landscape configuration.

Agricultural intensification and its consequences for biodiversity are well documented (e.g. Tattersall & Manley 2003). Agri-environment schemes aimed at mitigating the effects of agricultural intensification have been implemented since the 1980s, the most recent being the Environmental Stewardship scheme, which was introduced in 2005. Although Environmental Stewardship has been criticised for its limited benefits and high costs (Kleijn et al. 2011), studies show that it can lead to increases in small mammal abundance (Broughton et al. 2014), potentially benefitting their predators (Johnson & Baker 2003, Askew et al. 2007).



1958. Gin trap banned in England & Wales. Gin traps were kill traps used for rabbit *Oryctolagus cuniculus* hunting, but routinely caught predators that eat rabbits such as stoats *Mustela erminea* and European polecats *Mustela putorius*.

1960s – 1980s. Voluntary restrictions put in place on the use of dieldrin in GB, a pesticide implicated in the decline of European otters *Lutra lutra.* Voluntary restrictions were followed by mandatory bans in the 1980s.

1973. Gin trap also banned in Scotland.

1978. European otter *Lutra lutra* hunting banned in England and Wales.

1979. The Convention on the Conservation of European Wildlife and Natural Habitats introduced, also known as the Bern Convention (1979). It aims to conserve and protect wild plant and animal species and their natural habitats, increase cross-border cooperation and regulate exploitation of species.

The Convention was ratified by the UK government in 1982. The Convention obligations are enacted in British law via the Wildlife and Countryside Act (1981) and Nature Conservation (Scotland) Act 2004.

1981. Wildlife and Countryside Act (1981) introduced. Primary British conservation legislation that protects European otters *Lutra lutra* (Schedule V), European pine martens *Martes martes* (Schedule V) and European polecats *Mustela putorius* (Schedule VI).

1982. European otter *Lutra lutra* hunting banned in Scotland.

1986. The Control of Pesticides Regulations (1986) placed restrictions on the use of cyanide for fumigating the dens of European badgers *Meles meles* and red foxes *Vulpes vulpes*.

1988. Wildlife and Countryside Act amended to include wildcats *Felis silvestris* as Schedule V species.

1992. EU Habitats Directive (1992) introduced. Provides species-specific protections and requires species-specific status reporting every 6 years. Enacted in British law by the Conservation of Species and Habitats Regulations (2010).

1992. Protection of Badgers Act (1992) consolidates earlier European badger *Meles meles* legislation (Badgers Act 1973, Badgers Act 1991 and the Badgers (Further Protection) Act 1991) prohibiting sett disturbance or possessing or killing badgers without a licence.

1994. UK Biodiversity Action Plan first published fulfilling Britain's obligations as signatories to the Convention on Biological Diversity (1992).

1996. Animal welfare provisions provided for wild animals under the Wild Mammals (Protection) Act (1996).

2002 – 2004. Hunting with hounds banned in Scotland with the Protection of Wild Animals (Scotland) Act (2002) and in England and Wales with the Hunting Act (2004).

2006. Natural Environment & Rural Communities Act enacted. Provides legal obligation for biodiversity conservation across the UK government.

Figure 2.7. *Timeline of interventions providing legal protection for native mammalian carnivores in Great Britain.*

Translocations, releases and escapes

Range expansion and density increase have, in some carnivore species, been assisted by human intervention. Formal conservation translocations have been carried out for otters and pine martens. These may use captive-bred stock, such as for otters (Jefferies et al. 1986) and possible future wildcat releases (Scottish Natural Heritage 2013), or translocations from the wild, such as for pine martens (Shaw & Livingstone 1992, VWT unpublished data). Rehabilitated animals are also released from wildlife rescue centres (Kelly et al. 2010, Mullineaux 2014). Furthermore, unofficial or accidental releases have occurred; examples include polecat releases in Cumbria and Argyll (Birks & Kitchener 1999, Fig. 2.6) and the arrival of stoats on Orkney (Fraser et al. 2015). Other unofficial releases have been smaller in scale, e.g. there are sporadic records of pine martens in England, where presumably individuals have escaped or been released from fur farms or wildlife collections (Birks & Messenger 2010, Jordan et al. 2012). The extent of, and survival rates of animals from, unofficial releases are unknown, but releases of sufficient scale can sometimes aid expansion. Polecat populations derived from such releases are thriving in Cumbria but apparently dwindling in Argyll (Fig. 2.6, VWT unpublished data).

Direct control

Nineteenth century declines in carnivore populations are testimony to the impact of intensive control measures, as are the resurgences of some species once control diminished (Langley & Yalden 1977). While managing predators remains central to game management, the intensity of control (with localised exceptions) is unlikely ever to return to pre-1915 levels (Tapper 1992). While some British carnivores are protected from unlicensed predator control, the trapping or shooting of foxes, stoats and weasels is not regulated in practice, other than to prevent cruelty. Land managers applying control must comply with welfare regulations and ensure that control is sufficiently discriminatory to avoid taking legally protected species. Wildcats (Macdonald et al. 2010), otters (Crawford 2010), pine martens (Strachan et al. 1996) and polecats (Packer & Birks 1999) are legally protected from unlicensed control, but are sometimes caught in traps, nets or snares set for other species. The potential for unintentional capture may be greatest in areas that are newly recolonised, as practices that were previously unproblematic may need to be adapted. For species with low reproductive rates, such as pine martens, any additional mortality might impede recovery. The current extent of any intentional or unintentional killing of protected carnivores is unclear. Collaboration between carnivore conservationists, farmers and managers of game estates and fisheries is required to find workable solutions for reducing conflicts with expanding carnivore populations. Mitigation methods include electric fencing to prevent carnivores gaining access to pheasant pens (Balharry & Macdonald 1996), exclusion barriers for spring traps (Short & Reynolds 2001) and diversionary feeding and translocations. There is little evidence of the uptake or efficacy of such mitigation methods in practice (Balharry & Macdonald 1996, Thirgood et al. 2000, Graham et al. 2005).

Environmental pollutants

Predators are at particular risk from bioaccumulating and biomagnifying pollutants. Carnivores may be exposed to insecticides herbicides, fungicides and biocides used for agricultural purposes, a wide range of industrial organic contaminants, toxic metals, and human and veterinary pharmaceuticals (Shore & Rattner 2001, Harrington & Macdonald 2002, Shore et al. 2014). There are relatively few data on current exposure of British carnivores to most of these (Appendix 2.5).

Although dieldrin is most commonly cited as the cause of otter decline, polychlorinated biphenyls (PCBs) may also have contributed by impairing reproduction in individuals not poisoned by dieldrin (Mason & Wren 2001). The combined effect of dieldrin and PCBs on otters may have been analogous to how dieldrin (acute mortality) and dichlorodiphenyltrichloroethane (DDT; eggshell thinning leading to reproductive failure) caused catastrophic declines in predatory birds (Ratcliffe 1980, Newton 1986). Otters in Britain are also frequently exposed to polybrominated diphenyl ethers (PBDEs; Pountney et al. 2015), which are structurally similar to PCBs and may have a cumulative effect with PCBs (Hallgren & Darnerud 2002), though there is no evidence that exposure of otters in Britain to PCBs and PBDEs is impairing their reproductive output (Pountney et al. 2015).

Second generation anticoagulant rodenticides (SGARs) are widely used to manage rodent populations (Dawson et al. 2003). SGARs disrupt the blood-clotting mechanism (Watt et al. 2005) leading to fatal haemorrhaging. Evidence of sub-lethal effects caused by exposure is uncertain (Van den Brink et al. 2018). Predators are exposed secondarily by consuming contaminated target prey (rats *Rattus norvegicus,* mice *Mus domesticus*) and non-target prey (mice *Apodemus* spp., voles; Tosh et al. 2012, Van den Brink et al. 2018). SGAR residues have been detected in most British mammalian carnivores (Appendix 2.5) and rates of exposure in polecats have increased over the last 20 years (Sainsbury et al. 2018). While mortality caused by rodenticide does occur in mammalian carnivores in Britain (Appendix 2.5), the extent of this mortality and whether it affects populations, remains unknown.

Hybridisation

In Britain, hybridisation occurs between wildcats and domestic cats (Driscoll et al. 2007) and between polecats and feral ferrets (Costa et al. 2013). There is also evidence of limited historical hybridisation between European pine martens and American martens *Martes americana* that had presumably escaped from fur farms (Kyle et al. 2003). Hybridisation between wildcats and domestic cats occurs throughout the wildcat's range (Macdonald et al. 2010). Domestic cat DNA is commonly, if not universally, present in Scottish wildcats (Driscoll et al. 2007, Senn & Ogden 2015, Senn et al. 2018), which have experienced the highest levels of introgression among wildcats in Europe (Hertwig et al. 2009). Classifications of wild-living cats using combinations of skull morphology, pelage and genetic techniques suggest that, depending on the definition used, between 40% and 90% of wild-living cats in Scotland do not qualify as ‘true’ wildcats (Kitchener et al. 2005). Hybrids occupy similar habitat to wildcats, masking potential range expansion, impeding population estimation and perpetuating introgression (Kilshaw et al. 2016). Currently, a ‘trap, neuter, vaccinate and return’ programme for farm and feral cats is underway in five priority wildcat areas in the Scottish Highlands, with the aim of reducing hybridisation (Scottish Wildcat Action 2018). In comparison to the wildcat, polecat-ferret hybridisation appears less problematic. Analysis by Costa et al. (2013) of polecats collected during the 1990s and 2000s found that 31% of wild polecats were hybrids, with the highest frequency of hybrids at the eastern edges of the polecat's range. First-generation hybrids were not detected, suggesting that the incidence of hybridisation may have been greater in the past (Costa et al. 2013).

Disease and associated interventions

Disease, both naturally occurring and in association with human intervention, can reduce carnivore populations directly. For example, in 1994–1995, sarcoptic mange reduced fox numbers in Bristol by over 95% (Soulsbury et al. 2007). Carnivore populations may also be affected indirectly by disease if it alters the abundance of prey or other sympatric species, as evidenced by changes in stoat and weasel abundance associated with myxomatosis in rabbits (Aebischer et al. 2011). Recent and current effects of rabbit calicivirus on rabbit populations in Britain, and the potential impact on dependent carnivores, are unquantified, although it is possible that rabbit diseases and the associated declines may be contributing to coincident reductions in fox numbers (Harris et al. 2018).

Other indirect consequences may arise from human intervention to control the risk of transmission of zoonoses or diseases of livestock. Wild species may become persistent reservoirs for zoonotic disease (Hassell et al. 2017) and this can lead to control efforts, such as for managing bovine tuberculosis (bTB) in badgers (Wilson et al. 2011). Bovine tuberculosis is enzootic in a large part of the badger population in England and Wales and badgers are implicated in the spread of the infection to cattle (Delahay et al. 2013). Methods used to control bTB differ between the countries of Great Britain. Scotland, officially free of bTB since September 2009, has no proactive policy for managing the disease in wild animals, the Welsh government has pursued a badger vaccination strategy since 2012 (Welsh Government 2012) and in England proactive, large-scale badger culling is one of a range of policies aimed at eradicating bTB (DEFRA 2011). From 2013 to 2017 inclusive, 34103 badgers were killed as part of licensed culls in England (Giesler & Ares 2018) and 32601 badgers were killed in 2018 (DEFRA & Natural England 2018). Culling aims to reduce badger populations by around 70% in licensed areas and draws on evidence derived from the Randomised Badger Culling Trial (Bourne et al. 2007). This Trial showed that reduced badger numbers resulted in increased fox numbers in cull areas (Trewby et al. 2008), indicating that there may be broader implications for carnivore community structures emerging from badger culling.

Conclusions

Our aim was to compare and contrast the current status of Britain's mammalian carnivores and the anthropogenic processes that affect their populations. Overall, the outlook for British carnivores is more positive than in the account of decline drawn by Langley and Yalden (1977). Two of their three ‘rarer carnivores’ (pine marten and polecat) have staged remarkable recoveries, while the third (wildcat) continues to be threatened by hybridisation. Meanwhile, akin to pine martens and polecats, the formerly rare and restricted otter has recovered much of its former range and is increasing in density. Of the nationally distributed species, badgers have increased in population density but are subject to increasingly widespread, intensive culling; foxes have increased but appear to be in a current period of decline; and stoats and weasels remain data-deficient. The recent apparent declines in rabbit records are a cause for concern, given the number of native carnivores that depend on them as food. Since the 1970s there have been significant advances in our understanding of the anthropogenic processes that affect carnivore populations. If humans are to coexist with more abundant carnivores, in more places and in greater diversity, greater emphasis will need to be placed on the social aspects of these processes, whether concerning best-practice use of rodenticides, selective predator control practices, minimisation of hybridisation or management of disease risk.

Chapter 3

Recovery of European polecats (*Mustela putorius*) in Great Britain: stable isotopes indicate ecological changes over time

Chapter 3: Recovery of European polecats (*Mustela putorius*) in Great Britain: stable isotopes indicate ecological changes over time

This chapter is to be submitted to the Journal of Animal Ecology as:

Sainsbury KA, Drake L, Shore RFS, Schofield H, Croose E, Hantke G, Kitchener AC, Sykes N, McDonald RA (in prep) Recovery of European polecats (*Mustela putorius*) in Great Britain: stable isotopes indicate ecological changes over time.

Abstract

Following severe declines in the nineteenth century, the European polecat *Mustela putorius* has been returning to much of its former range in Great Britain. To examine spatial, temporal and ecological variation in resource use by polecats during their recovery, we analysed variation in stable isotope ratios and isotopic niche characteristics of polecats collected from 1960 to 2016. $\delta^{15}N$ in whiskers was lower at the frontline of their expansion compared to their core range and the size of this effect varied among decades. $\delta^{13}C$ was lower in all decades compared to the 1960s. $\delta^{13}C$ declined with distance from the polecat's historical refugium and this effect was greater in males than in females. Within individual variation in $\delta^{13}C$ was greater at the frontline of expansion than in the core. Male polecats exhibited significantly less within-individual variation in $\delta^{15}N$ than female polecats. There was a significant difference between male and female isotopic niche size at the core of the polecat range, but not at the frontline. The isotopic niche sizes of females were significantly smaller in the 1960s than all other decades, whereas niche sizes of male polecats remained relatively unchanged throughout the period of range expansion. This study highlights the interacting effects of sex, time and position in a dynamic range in this generalist predator. Our results indicate that, even in a generalist predator, the distinct ecological requirements of the two sexes may need to be considered separately during the process of population recovery.

Introduction

Contrary to global declines in populations of mammalian carnivores (Schipper et al. 2008), and in contrast to their fortunes elsewhere in Europe (Croose et al. 2018), the European polecat *Mustela putorius* is currently recovering its range in Great Britain (Sainsbury et al. 2019). In the 1970s the species' distribution was largely restricted to Wales and the Welsh border counties (Langley & Yalden 1977) and successive monitoring studies have since shown how polecats have recolonised much of central, southern and eastern England (Sainsbury et al. 2019). The manner of polecat recolonisation is consistent with simple diffusion models, in which increases in population density within settled areas lead to a 'wave-front' of expansion at the edge of the range, akin to colonisations of invasive species (Skellam 1951, Elton 1958, Andow et al. 1990, Hastings et al. 2005). Invasive species typically display flexibility in behaviour (Sol & Lefebre 2000, Sol et al. 2002, Bodey et al. 2010), diet and habitat selection (Ehrlich 1989, Jeschke & Trayer 2006, Ibarra et al. 2009) and while polecats are a native species in Britain, it is possible that the process of colonisation has involved similar plasticity in their patterns of resource use. Expanding populations of invasive species go through a staged process of colonisation and naturalization as they become established (Richardson et al. 2000). Overall habitat use and selection in low density populations is generally less well understood than in saturated habitats at carrying capacity (Greene & Stamps 2001). A variety of factors, including search costs (Stamps et al. 2005) and conspecific cues (Stamps & Krishnan 2005) may affect habitat selection in dispersing individuals, especially those at the leading edge of an expanding range. Polecat range expansion in Britain therefore provides a rare opportunity to study ecological variation associated with population recovery and range expansion in a native species.

Stable isotope analysis provides a quantitative means of examining the processes underpinning ecological change (English et al. 2018). Stable isotopes of consumer tissues reflect variation in what they consume over the period of tissue synthesis in a predictable way (Peterson & Fry 1987). This property has led to the now commonplace application of stable isotope approaches to provide insight into resource use (e.g. Peterson & Fry 1987, Hopkins & Kurle 2016), behaviour change (Bodey et al. 2010), as well as contemporary (Hobson 1999, Rubenstein & Hobson 2004) and historical movements of species (Hoppe et al. 1999, Pellegrini & Longinelli 2008, Sykes et al. 2016). Ratios of the heavier to lighter stable isotopes of ^{13}C to ^{12}C and ^{15}N to ^{14}N, denoted as $\delta^{13}C$ and $\delta^{15}N$ respectively, can provide powerful measures for exploring diversity in resource use (DeNiro & Epstein 1981). Progressive increases in $\delta^{15}N$ occur with trophic level of consumers as a result of the enrichment of ^{15}N that takes place through trophic transfer between prey and predator while variation in $\delta^{13}C$ tends to reflect diversity in resource production, e.g. between marine and terrestrial systems or between plants with C3, C4 or CAM photosynthetic pathways (Smith & Epstein 1971, DeNiro & Epstein 1978, 1981). Stable isotope ratios may be analysed individually or in combination to create “isospaces” that present quantitative indicators of variation in some dimensions of the ecological niche (Jackson et al. 2011). Metabolically inert keratinous tissues such as vibrissae (whiskers), claws or nails fix the consumer’s isotope ratios during their synthesis (Bearhop et al. 2003, Newsome et al. 2007, Robertson et al. 2013) and such keratinous tissues, along with bone collagen, have the dual advantages of preserving well and being frequently kept by museums. This makes stable isotope approaches a particularly useful investigative tool for species that are otherwise difficult to study for ecological reasons (Crawford et al. 2008) and when applied to temporal series of museum specimens, stable isotope analyses have the potential to reveal long-term ecological trends that would otherwise be unobservable (English et al. 2018).

In common with many other carnivorans (Karanth & Chellam 2009), polecats occur at relatively low population densities and are hard to observe directly (Blandford 1987, Birks & Kitchener 1999). As a result, the polecat is one of Britain’s least studied mammals and its ecology remains poorly characterised (Blandford 1987, Birks & Kitchener 1999). Indirect means of studying polecats are therefore important tools for understanding their ecology. Polecats have been described as generalists in terms of diet (Blandford 1987, Lodé 1997, Santos et al. 2009) and habitat selection (Lodé 1994, Birks & Kitchener 1999). In Britain, they specialise on rabbits *Oryctolagus cuniculus*, although brown rats *Rattus norvegicus*, other small mammals and amphibians are frequently eaten (Birks & Kitchener 1999). Dietary studies from the 1980s and 1990s, using gut contents and faecal samples, showed that while females may eat smaller-sized prey than males, there was no statistical difference in diet between the sexes (Blandford 1986, Birks & Kitchener 1999). Male home ranges usually encompass multiple female territories (Blandford 1987) and studies in mainland Europe have shown that home range sizes can vary with resource availability (Weber 1989a). Although males and females utilise similar proportions of habitat types, radio-tracked polecats in France have demonstrated between-sex temporal and spatial segregation, particularly when resources are less abundant (Lodé 1996a). In the 1950s, rabbit populations in Britain crashed following the myxomatosis epizootic (Sumption & Flowerdew 1985) and recovered between the 1970s and 1990s, but are currently experiencing a further period of decline (Harris et al. 2018). These marked changes in the availability of rabbits, as an important food resource for polecats, may have led to variations in resource use during polecat expansion.

As polecats have recolonised Britain from west to east, they have moved from landscapes largely comprising unimproved and semi-improved pasture and woodlands in Wales to more diverse mixed farming and improved grasslands in central England and onwards to the predominantly arable landscapes in the east of England (Cole et al. 2015, Rae 2017). To date, studies of polecat behaviour and ecology in Britain have focused initially on animals inhabiting their refugium in central Wales (Walton 1968, Blandford 1986) and latterly to the English counties that border Wales (Birks & Kitchener 1999). Now that the polecat’s range once again extends from the west coast to the east coast of Britain, there is an opportunity to explore any changes in resource use that may have accompanied the expansion process either on a west-east gradient, or between animals at the frontline of expansion compared to the centre of the range.

Therefore, our research objectives were to assess whether polecats displayed any between-sex differences in resource utilisation and how these differences may have varied through time and space, particularly as these relate to the species’ expanding range as it has recovered from near extirpation. To achieve this, we took whiskers from polecats collected between 1960 and 2016 and analysed variation in carbon and nitrogen stable isotope ratios. These specimens have been collected as part of recurring distribution surveys to monitor polecat range expansion (e.g. Walton 1968, Birks & Kitchener 1999, Birks 2008, Croose 2016) and their skins are preserved in the collections of National Museums Scotland. We compared variation in $\delta^{15}N$ and $\delta^{13}C$ and the isotopic niche sizes of polecats at the frontline of the species range as it expanded to that at the centre of the range over time, as we hypothesised polecats may demonstrate greater variation in resource use at the frontline of their expansion. We compared changes over time between the sexes as we hypothesised that behavioural differences between the sexes may be associated with different patterns of resource use during expansion. We did not aim to reconstruct the specifics of polecat diet but instead have explored broad trends and discuss our findings in the context of what is known about the availability of resources to polecats over the period of their recovery.

Methods

Sampling approach

All samples were from polecats in the collections of National Museums Scotland. We sampled whiskers from polecats that died in the 1960s, 1990s, 2000s, 2010s. These four decades were chosen as they contained sufficient numbers of polecats from across the whole of what was the species' range at the time of collection (Walton 1968, Birks & Kitchener 1999, Birks 2008, Croose 2016). Specimens classified as ferrets were excluded from the analysis. Most of the animals died as a result of road-traffic collisions, with a minority due to being killed by dogs, traps, shot or poisoned (Birks & Kitchener 1999, Birks 2008, Croose 2016). Museum records included the location and date of carcass collection. At least two whiskers were taken at random from each specimen and stored at room temperature.

Stable isotope analysis

Whiskers were cleaned in distilled water and freeze dried for 24 hours. One whisker per animal was selected at random. Starting at the base, whiskers were cut into ~1mm sections. Serial sections were put into a tin cup until the sample weight reached ~0.6mg (mean±SE: 0.615 ± 0.004 mg) when the cup was sealed for analysis. These steps were repeated until the whole whisker was used. Some whiskers only produced one or two samples of sufficient mass, whilst longer whiskers resulted in between three and five. All samples were placed under continuous-flow isotope ratio mass spectrometry with a Sercon Integra 2 Elemental Analyser at the University of Exeter (samples from the 1960s, 1990s and 2000s) or on a Thermoquest EA1110 elemental analyser linked a to a Europa Scientific 2020 isotope ratio mass spectrometer at Elemtex Ltd Cornwall UK (samples from the 2010s) for analysis of $\delta^{15}N$ and $\delta^{13}C$. $\delta^{15}N$ and $\delta^{13}C$ levels are expressed as δ-values as a per mil (‰) deviation from international reference standards (Vienna PeeDee Belemnite for carbon and air for nitrogen) (Mariotti 1983):

$$\boldsymbol{\partial^{15}X}‰ = \left[\frac{\boldsymbol{({}^{15}X/{}^{14}X)sample}}{\boldsymbol{({}^{15}X/{}^{14}X)standard - 1}]}\right] \times \mathbf{1,000}$$

Replicate analysis of standards on University of Exeter instrument (using Alanine) returned standard deviations of 0.149 for $\delta^{15}N$ and 0.151 for $\delta^{13}C$. Analysis of standards on Elemtex instrument (USGS 40, USGS 41, USGS 41A and an in-house bovine liver standard) returned standard deviations of 0.153 – 0.179 for $\delta^{15}N$ and 0.054 – 0.121 for $\delta^{13}C$. The mean difference between actual and measured values on the University of Exeter instrument was 0.027‰ (standard deviation 0.152) for $\delta^{15}N$ and -0.008‰ (standard deviation 0.055) for $\delta^{13}C$. The mean difference between the actual and measured values on the Elemtex equipment was -0.017‰ (standard deviation 0.167) for $\delta^{15}N$ and -0.014‰ (standard deviation 0.108) for $\delta^{13}C$. The variation due to instrument accuracy was <=5% of individual whisker variation and therefore the decision was made not to correct for any differences in estimates between instruments.

Data analysis

All data were analysed using R [version 3.5.1] and R Studio [version number 0.99.896] (R Core Team 2013). Separate generalised linear mixed models were built using $\delta^{13}C$ and $\delta^{15}N$ as the response variables. Sub-samples of whiskers were used as repeated measures of the individual polecat and so polecat identity was included as a random effect. Within-individual variation was also investigated, using the standard deviation of $\delta^{13}C$ or $\delta^{15}N$ as response variables. The standard deviations were based on three basal samples for each individual, thereby excluding any animals with fewer than three sections and excluding distal samples from any animals with more than three sections. Separate general linear models (GLM) with normal error structures were built for the standard deviations of $\delta^{13}C$ and $\delta^{15}N$. The response variables were log-transformed to conform with assumptions of normality.

Fixed variables included in all models were: decade of collection (1960s / 1990s / 2000s / 2010s), distance from the species' refugium (km), position in the range (core / edge), sex (male / female) and interactions between the effects of sex and each of decade, distance to refugium and position in the range. The species' refugium was taken as the centroid of the 1915 range (Langley & Yalden (1977) and the distance from this point to the collection location was included to represent changes in space as polecats expanded outwards from their refugium in Wales. Distances were calculated in Quantum GIS (QGIS Development Team 2009). Animals that were not considered part of the expansion from the 1915 stronghold, for example those from Scotland and from a discrete Cumbrian population that was reintroduced during the twentieth century, were excluded from these analyses. Position in the range was included to subdivide space between the established parts of the polecat range. This variable was established by creating a polygon of the known polecat distribution for each decade (1960s - Langley & Yalden 1977; 1990s – Birks & Kitchener 1999; 2000s – Birks 2008; 2010s – Croose 2016) and drawing a 20km perimeter around the inside of the range extent. Collection locations that were more than 20km inwards from the range edge were considered to be from an established part of the range ("core"), polecats less than 20km from the range edge were considered to represent the frontline of the range expansion ("edge"). The western side of the core range extended all the way to the Welsh coastline, i.e. no edge boundary was allocated to this side, as west Wales has been part of the polecat's established range since the 1960s. Other "edge" parts of the range became "core" in future decades as the species' range expanded.

Although we accounted for any effects of expansion into new areas with the distance from refugium variable within our GLMMs, we also carried out a separate comparison between a subset of samples from a single 100 x 100km area on the Welsh/English border (OSGB grid reference SO) and the rest of the dataset to check that temporal effects were consistent between areas with and without polecat expansion. This grid square was selected as polecats had been present there throughout the four decades and it maximised the number of points available for comparison across all four decades. It encompasses the eastern edge of the polecat range in the 1960s, but a central part of the polecat range in all later decades (Fig. 3.1). We created boxplots for $\delta^{13}C$ and $\delta^{15}N$ for both the whole dataset and the subset and compared the two in order to check whether the effects of time differed when range expansion was excluded.

Models were built using lme4, MuMIn and car packages. Models were checked for spatial autocorrelation and collinearity (none was evident). Collection locations were not strongly correlated and we concluded there was no spatial structure to the data. As models were found to be better (lower AIC) without including spatial correlation we excluded it. Explanatory variables were standardised in models (Gelman 2008). Standardised conditional average models were created from a top model set which included all models with an increase in Akaike's Information Criterion (ΔAIC) values of no more than two when compared to the best model. Model fit was assessed using QQ plots.

Samples from three decades (1960s, 1990s and 2000s) were taken from specimens that had undergone a museum preservation process. Although the whiskers were not subject to specific treatments, the whole pelts, of which the whiskers were part, had been treated in turn with solutions of salt and formic acid, aluminium triformate, sodium carbonate and were then oiled with Lipederm. To test for the potential effect of preservation on isotopic signatures, a subset of 23 animals from the 2010s from which both fresh and preserved whiskers were taken, were analysed to compare the values of preserved and fresh samples. Separate linear regression models (LMs) for $\delta^{13}C$ and $\delta^{15}N$ were created. The LMs showed that preservation had no significant effect for $\delta^{13}C$ (coefficient estimate: 0.17, 95% confidence intervals: -0.09 – 0.44) and were borderline for $\delta^{15}N$ (coefficient estimate: -0.29, 95% confidence intervals: -0.55 – -0.02). indicating that correction factors were not required to account for the preservation process for $\delta^{13}C$ but might be for $\delta^{15}N$. To this end, we checked the effect of preservation by adding correction factors derived from the effect sizes of preservation treatment from these models to the $\delta^{13}C$ and $\delta^{15}N$ values from fresh material from the 2010s and rerunning the main statistical analysis. As there was no significant difference evident in the model selection or the size of the effects in average models between models including the correction factors and those without, we did not include the correction factors in the final models reported here.

Analysis of isotopic niches

Polecat isotopic niches were represented by Bayesian variants of standard ellipse areas (SEAB) estimated using the statistical package “Stable isotope ellipses in R” (SIBER) (Jackson et al. 2011). SEABs were calculated using the per specimen mean value of all sections in each polecat whisker. Separate SEABs were created for each decade, sex, position in range, sex*decade and sex*position in range and decade*position in range. Significant differences among the SEABs were calculated by comparing the differences in SEAB within each category of polecats. Using the example of “decade”, the SEABs were estimated for 1960s, 1990s, 2000s and 2010s using 160000 SEAB replicates calculated as part of the Bayesian methodology. Then the replicate SEABs for the 1990s, 2000s and 2010s were each subtracted from the 1960s SEABs and then the replicate SEABs from the 1990s were subtracted from the 2000s and 2010s and so on until all combinations of categories had been compared. The mean difference in SEAB size between each category and associated credible intervals were then calculated for each category. Mean differences where credible intervals did not cross zero were considered to be significant. We checked for a three-way interaction effect between sex*decade*position in range, but as the direction of the effects of core and edge were the same for males and females in all decades with data available, we concluded there was none.

Results

Whiskers from 256 polecats (178 male and 78 female) were analysed, of which 34 were from the 1960s, 73 from the 1990s, 61 from the 2000s and 88 were from the 2010s (Fig. 3.1). At the time of collection, 188 were from the core of the species’ range and 73 from the edge. There were 117 polecats with three or more whisker segments (97 male and 20 female) of which 18 were from the 1960s, 38 from the 1990s, 43 from the 2000s and 18 from the 2010s. 78 animals were from the core, 39 from the edge.

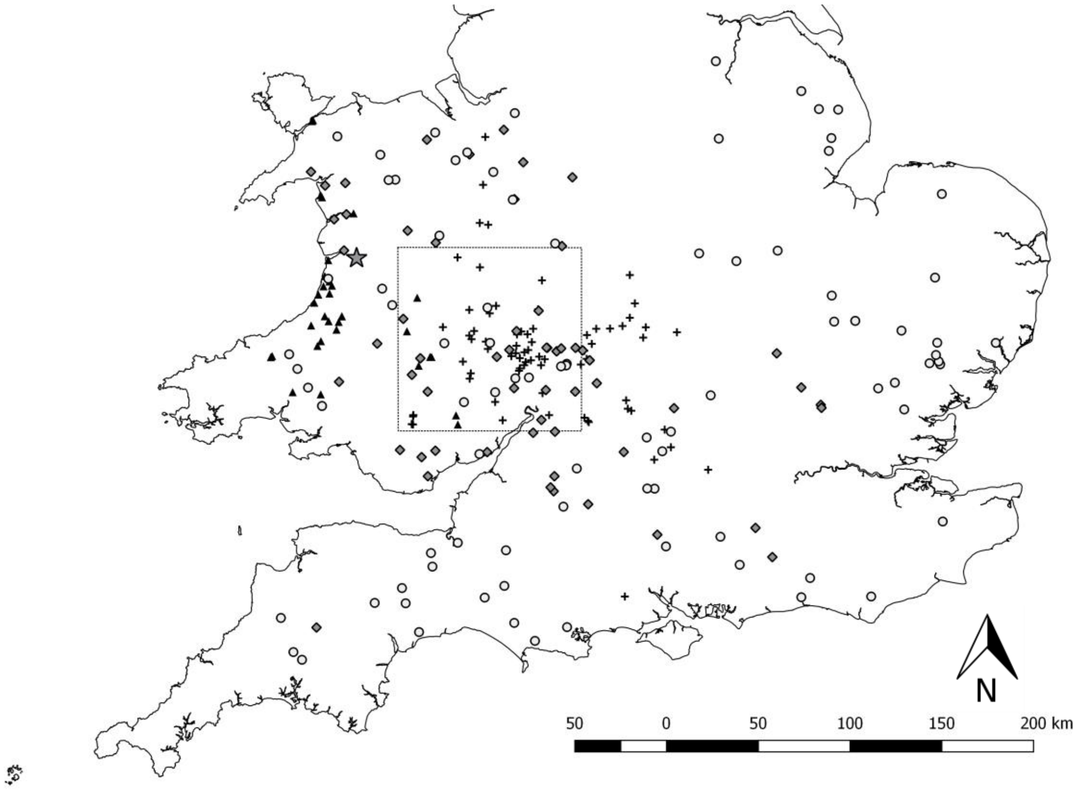
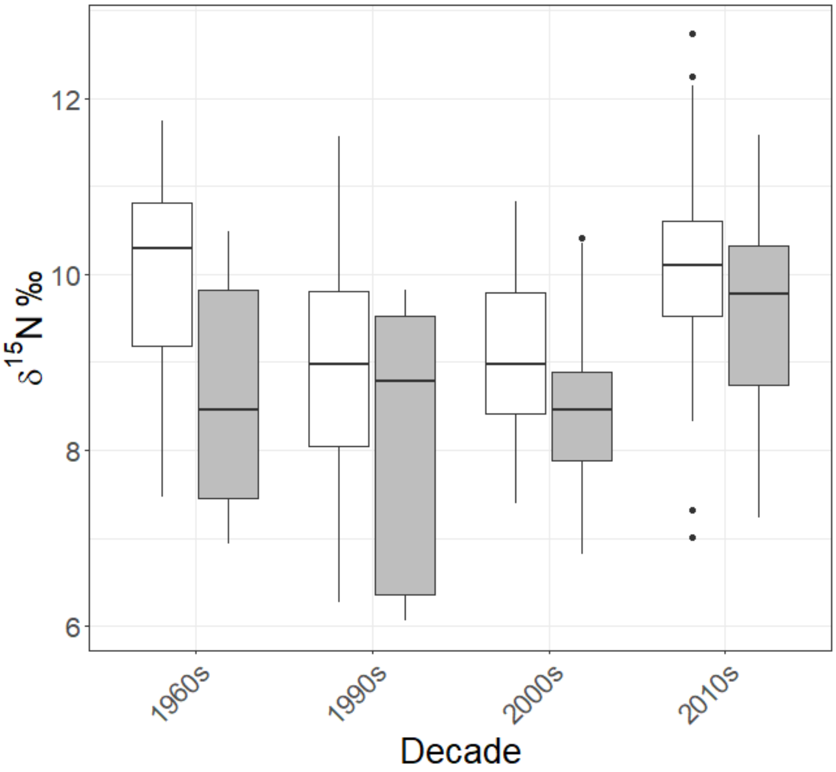


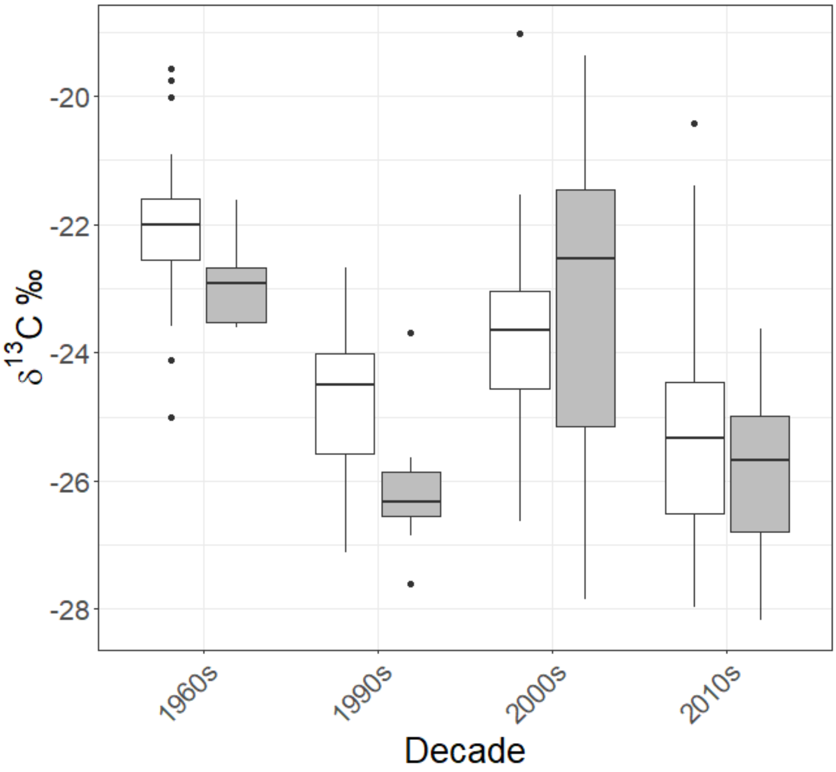
Figure 3.1. *Map of the collection locations of polecat specimens by decade. Specimens collected in the 1960s are indicated by triangles (n=34), in the 1990s by crosses (n=73), in the 2000s by diamonds (n=61) in the 2010s by circles (n=88). The square marks out the area (OSGB SO) of the subset of samples that were analysed to compare the temporal effects on isotopes without any effect of range expansion. The grey star in mid-Wales marks the central point of the polecat's range in 1915.*

Variation in $\delta^{13}C$ and $\delta^{15}N$

For analysis of variation in $\delta^{15}N$ (Table 3.1a), Decade and Position in range appeared in the two top models and the Decade*Position in range interaction in one. The average model showed that $\delta^{15}N$ values were lower (^{15}N was depleted) at the edge when compared to the core of the range and that the magnitude of this difference varied among decades (Table 3.1b, Fig. 3.2).



(A)



(B)

Figure 3.2. *Boxplots of (A) mean* δ^{15}*N and (B) mean* δ^{13}*C values for polecat whiskers. Plots show the median values and interquartile ranges for the combined effects of decade (1960s, 1990s, 2000s and 2010s) and position in range (white boxes = core and grey boxes = edge).*

Table 3.1. *Models of variation in stable isotope ratios of polecat whiskers in Great Britain, 1960-2016. a) Top models (ΔAIC <2) explaining variation in i) δ^{15}N, ii) δ^{13}C, iii) standard deviation of δ^{15}N and iv) standard deviation of δ^{13}C and b) Average model coefficients and importance of variables included in the top models. Top model sets are based on ΔAIC <2. i) and ii) are generalised linear mixed models with individual polecat as a random effect. iii) and iv) are generalised linear models with log transformed response variables. Conditional average results of standardised models are presented. Base model is decade: 1960s, position: core, sex: female. Bold indicates parameters where CI do not cross zero. Importance is the number of models in which each variable features.*

Table 3.1a

Model	**Covariates**	***df***	**Log likelihood**	**AIC**	**ΔAIC**	**Weight**
δ^{15}N	Decade + position in range	7	-829.7	1673.7	0.0	0.7
	Decade + position in range + decade*position in range	10	-827.5	1675.5	1.7	0.3
δ^{13}C	Decade + sex + position in range + distance + decade*position in range + sex*distance	13	-1018.9	2064.3	0.0	0.3
	Decade + sex + position in range + distance + decade*position in range + sex*position in range + sex*distance	14	-1018.1	2064.9	0.5	0.3
	Decade + sex + position in range + distance + decade*position in range + decade + position in range + sex*distance	16	-1016.4	2065.7	1.3	0.2
	Decade + sex + position in range + decade*position in range + decade + position in range	14	-1018.61	2065.9	1.5	0.1
	Decade + sex + position in range + decade*position in range	11	-1022.0	2066.3	1.9	0.1
SD δ^{15}N	Sex	3	13.5	-21.0	0.0	1.0
SD δ^{13}C	Position in range	3	-8.1	22.5	0.0	0.4
	Null	2	-9.5	23.1	0.6	0.3
	Decade + position in range	6	-5.7	24.1	1.7	0.2
	Decade	5	-6.9	24.3	1.8	0.2

Table 3.1b

Model	Parameter	Coefficient estimate	SE	2.5% CI	97.5% CI	Importance
δ^{15}N	(intercept)	9.83	0.22	9.40	10.27	-
	Decade (1990s)	**-0.91**	**0.26**	**-1.42**	**-0.41**	**1.0 (2)**
	Decade (2000s)	**-0.81**	**0.27**	**-1.33**	**-0.28**	**1.0 (2)**
	Decade (2010s)	0.33	0.27	-0.19	0.86	1.0 (2)
	Position in range (edge)	-0.84	0.45	-1.72	0.04	1.0 (2)
	Decade(1990s)*position(edge)	0.93	0.52	-0.10	1.96	0.3 (1)
	Decade(2000s)*position(edge)	0.86	0.50	-0.11	1.84	0.3 (1)
	Decade(2010s)*position(edge)	**0.98**	**0.48**	**0.04**	**1.92**	**0.3 (1)**
δ^{13}C	(intercept)	-21.73	0.46	-22.63	-20.83	-
	Decade (1990s)	**-2.70**	**0.50**	**-3.69**	**-1.71**	**1.0(5)**
	Decade (2000s)	**-1.82**	**0.51**	**-2.82**	**-0.83**	**1.0(5)**
	Decade (2010s)	**-3.32**	**0.54**	**-4.38**	**-2.27**	**1.0(5)**
	Sex (male)	-0.26	0.46	-1.17	0.64	1.0(5)
	Position in range (edge)	-1.01	0.63	-2.24	0.23	1.0(5)
	Distance to refugium	**0.93**	**0.39**	**0.17**	**1.68**	**0.7(3)**
	Decade(1990s)*position(edge)	0.17	0.69	-1.19	1.54	1.0(5)
	Decade(2000s)*position(edge)	**1.31**	**0.65**	**0.04**	**2.58**	**1.0(5)**
	Decade(2010s)*position(edge)	0.22	0.63	-1.02	1.46	1.0(5)
	Sex (male)*distance to refugium	**-1.04**	**0.42**	**-1.87**	**-0.21**	**0.7(3)**
	Sex(male)*position(edge)	0.55	0.55	-0.53	1.64	0.3(1)
	Decade (1990s)*sex(male)	-0.77	0.71	-2.15	0.61	0.3(2)
	Decade (2000s)*sex(male)	0.15	0.79	-1.40	1.71	0.3(2)
	Decade (2010s)*sex(male)	-0.60	0.83	-2.22	1.02	0.3(2)
SD δ^{15}N	(intercept)	0.53	0.05	0.43	0.62	-
	Sex (male)	**-0.15**	**0.05**	**-0.26**	**-0.05**	**1.0(2)**
SD δ^{13}C	(intercept)	0.43	0.06	0.30	0.57	-
	Position in range (edge)	**0.08**	**0.05**	**-0.02**	**0.19**	**0.6(2)**
	Decade (1990s)	0.09	0.08	-0.06	0.24	0.3(2)
	Decade (2000s)	**0.16**	**0.07**	**0.01**	**0.31**	**0.3(2)**
	Decade (2010s)	0.12	0.09	-0.05	0.29	0.3(2)

The degree of ^{15}N depletion at the edge versus the core was greatest in the 1960s and lowest in the 2010s. For analysis of variation in δ^{13}C, there were five evenly weighted top models (Table 3.1a). Of the variables that appeared in the top models (Decade, Sex, Position in range and all two-way interaction terms), Decade was in all six models (Table 3.1b), the Position in range*Sex interaction appeared in only one model and was of low importance, while all the other variables featured in at least four of the top models. In the average model, there was a significant effect of Decade, in which δ^{13}C was significantly lower (^{13}C was depleted) in all decades compared to the 1960s (Table 3.1b). This effect was greatest in the 2010s compared to the 1960s and least in the 2000s compared to the 1960s. There was also a significant effect of Distance from refugium*Sex, in which male δ^{13}C declined more (became more depleted) than female δ^{13}C the further away from the 1915 refugium that the polecats were collected (Table 3.1b, Fig. 3.3). The confidence intervals for all of the other variables crossed zero and were not considered significant.

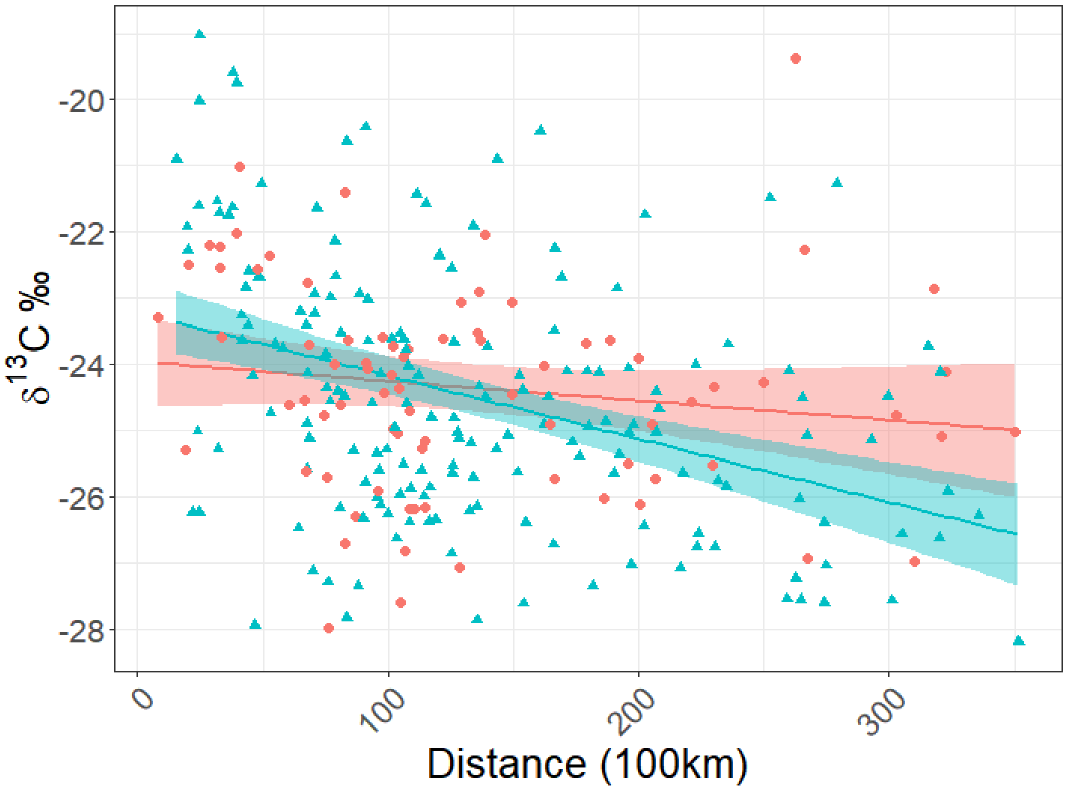


Figure 3.3. *Relationship between mean δ^{13}C values for polecat whiskers and distance from 1915 refugium (in 100kms) for male (blue) and female (red) polecats. Bands show 95% confidence intervals.*

We did not find any consistent patterns of isotopic difference for either δ^{13}C and δ^{15}N between the subset of data that included polecats from the area (OSGB SO) where they had been present for four decades and the rest of the data which included polecat expansion (Appendix 3.1). The boxplots indicated there was a difference in the mean δ^{13}C and δ^{15}N values between the subset and whole dataset in the 1960s, when this square largely constituted the edge of the species' range, that was not present in subsequent decades. In later decades the subset area is in the core of the range and the rest of the data comprises a mixture of core and edge polecats.

Individual whisker variation

For analysis of variation in the standard deviation (SD) of $\delta^{15}N$, there was one top model, which included Sex as the only variable (Table 3.1a). Males had lower SD (less within-individual variation) in $\delta^{15}N$ than females (Table 3.1b). For analysis of the standard deviation of $\delta^{13}C$, there were four top models (Table 3.1a) and in the average model, polecats collected at the edge of the range exhibited greater SD in $\delta^{13}C$ than those collected in the core (Table 3.1b). Polecats from the 1990s, 2000s and 2010s had greater SD in $\delta^{13}C$ than those collected in the 1960s, although the difference was only significant between the 2000s and 1960s.

Analysis of isotopic niche size

Analysis of variation in isotopic niche size by sex and decade showed there was no significant variation in male standard Bayesian ellipse areas (SEABs) among decades but that female SEABs varied among the decades (Fig. 3.4). There was a significant increase in female SEABs between the 1960s and 1990s (mean difference = 1.74‰^{2}, 95% credible intervals: 0.05 to 3.50‰^{2}), between the 1960s and 2000s (mean difference = 4.12‰^{2}, 95% credible intervals: 1.34 to 8.47‰^{2}) and between the 1960s and 2010s (mean difference = 3.47‰^{2}, 95% credible intervals: 1.55 to 5.63‰^{2}). Male SEABs were significantly greater than those of females in the 1960s (mean difference = 3.39‰^{2}, 95% credible intervals: 1.32 to 5.85‰^{2}) but not in other decades.

SEABs differed between the sexes at the edge of the range compared to the core: SEABs were significantly larger for males than females at the core (Fig. 3.4 mean difference = 2.07‰^{2}, 95% credible intervals: 0.19 to 3.91‰^{2}). There was a similar between-sex difference at the edge, although the difference was not statistically significant (Fig. 3.4, mean difference = 3.51‰^{2}, 95% credible intervals: -0.12 to 6.91‰^{2}). Male edge SEAB was also significantly larger than the female core SEAB (mean difference = 3.61‰^{2}, 95% credible intervals: 1.05 to 6.57‰^{2}). There was no significant difference in SEAB sizes between polecats at different positions in range either for males (Fig. 3.4, mean difference = -1.53‰^{2}, 95% credible intervals: -4.46 to 0.98‰^{2}), or for females (Fig. 3.4, mean difference = -0.10‰^{2}, 95% credible intervals: -3.30 to 2.36‰^{2}).

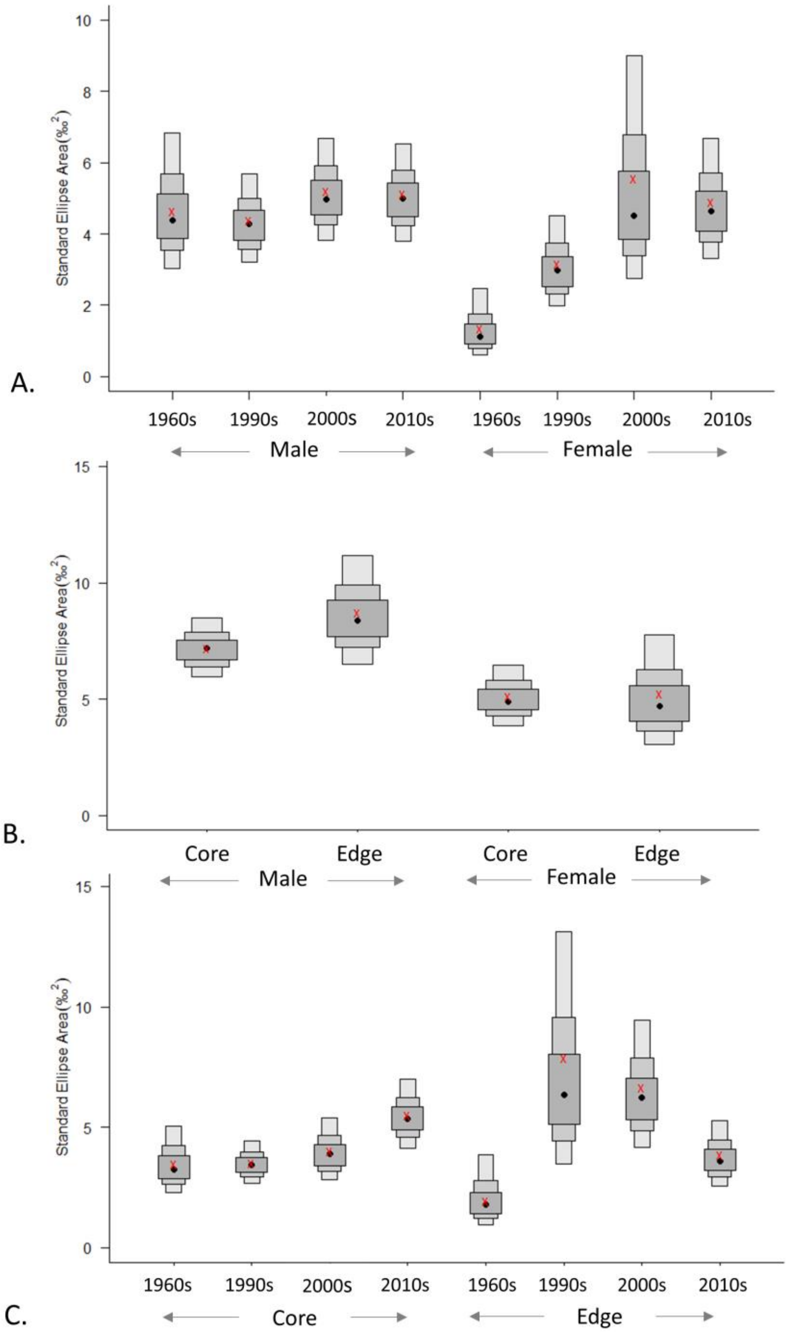


Figure 3.4. *Isotopic niche space, measured by Bayesian Standard Ellipse Areas (SEABs), occupied by polecats in Great Britain, categorised by decade, sex and position in range. SEABs were calculated from* $\delta^{13}C$ *and* $\delta^{15}N$ *values from polecat whiskers collected from the 1960s to 2010s. The core range = >20 km from the edge of the range, edge = <20 km of the range edge. A) SEABs for male and female polecats by decade, B) SEABs for male and female polecats by position in range and C) SEABs for polecats at the core and edge of the range by decade. Black dots indicate the mode SEAB and grey bars are credible intervals (50%, 95% and 99%). Red crosses indicate the size of the standard ellipse areas estimated using the raw data.*

Comparisons of SEABs between the edge and the core of the range through the decades showed SEABs of polecats in the edge exhibited greater variation in size over time (1.79‰^{2} to 6.38‰^{2}) than SEABs of polecats in the core (3.27‰^{2} to 5.33‰^{2}; Fig. 3.4). SEABs in the core were significantly smaller in the 1990s than in the 2010s (mean difference = -1.98‰^{2}, 95% credible intervals: -3.83 to -0.36‰$^{2)}$. Analysis of SEABs of polecats at the edge showed that isotopic niche size was significantly smaller in the 1960s than in 1990s (mean difference = -5.54‰^{2}, 95% credible intervals: -12.50 to -1.34‰^{2}) and the 2000s (mean difference = -4.42‰^{2}, 95% credible intervals: -7.94 to -1.39‰^{2}) and that in the 2000s SEABs were significantly larger than in the 2010s (mean difference = 2.80‰^{2}, 95% credible intervals: 0.03 to 6.29‰^{2}). SEABs at the edge were significantly larger than the core in the 1990s, (mean difference = 4.24‰^{2}, 95% credible intervals: 0.41 to 11.10‰^{2}) but not in any other decade.

Discussion

As polecat populations and ranges have expanded in England and Wales from the 1960s to the 2010s, we have identified that location, sex and time interact to affect isotopic measures of variation in polecat ecology.

Collectively, our models of δ^{15}N, δ^{13}C, within-individual variation in δ^{13}C and of isotopic niche size suggest that position in range influenced resource use by polecats during their range expansion. Several of the models (SEAB and within-individual variation in δ^{13}C) indicated that resource use was more variable at the edge of the polecat range than at the core. δ^{15}N values were lower at the edge than the core and this difference was greatest in the 1960s. The fact that we did not observe any significant effects of distance from the 1915 stronghold in our models of δ^{15}N or individual variation in δ^{15}N suggests that the exact geographical location of the animal’s collection contributed less to variation in these metrics than whether the polecat was located at the front line of expansion or in a more core part of the range.

Foraging theory dictates that generalist predators, such as polecats, should consume abundant and high-quality resources to maximise net energy intake (Pyke et al. 1977). This behaviour has been observed in dietary studies of other mustelids such as American martens *Martes americana* during seasonal resource fluctuations (Ben-David et al. 1997) and American mink *Neovison*

vison switching to eat the most abundant prey during the process of invasion (Ibarra et al. 2009). There is no reason to think that food availability would be consistently different at the (moving) edge of the polecat's range compared to the core over time, particularly given that the edge becomes core in subsequent decades. However, population densities are typically lower towards the periphery of species' ranges (Lomolino & Channell 1995) and we expect that this principle would apply to polecats as, through the process of recolonisation, polecats were expanding into areas without other conspecifics. Reduced population densities at the edge may have permitted easier access to some resources than was later available as the edge became core and intraspecific competition increased with polecat abundance. Changes to relative trophic position associated with varying population densities has been observed in invasive carnivorous Argentine ants *Linepithema humile*, Tillberg et al. (2007) observed that the relative trophic position of the ants was higher at the frontline of an invasion, but declined after population establishment, due to resource depletion.

Dietary and habitat niche breadth and behavioural flexibility are important attributes of successful colonisers (Ehrlich 1989, Sol & Lefebre 2000). In a study of brown rats *Rattus norvegicus* released on rat-free islands in New Zealand, Russell et al. (2008) found some rats dispersed far further than would be expected of normal ranging behaviour in higher density, established populations. It is possible that the greater isotopic variation evident in polecats at the edge of their range is a result of exploratory behaviours that are manifest at low population densities. Overall our results suggest that resource utilisation varies markedly depending on position within a dynamic, expanding species range.

We predicted that polecat isotopic niche sizes would increase over time as polecats expanded into more intensely managed habitats from the pastures and woodlands of Wales and that male polecats would have greater isotopic niche sizes over time, due to their larger territories and exposure to a greater variety of basal resources than females. Contrary to this, we observed significant variation in the isotopic niche size of female polecats over time, whereas males had relatively consistent SEABs (Fig. 3.3). Our models of within-individual variation of $\delta^{15}N$ indicate that isotopic variation was greater for females than males, and there was no evidence that this effect varied over time. It is possible that this is a result of variations in territory sizes of females, which may have altered depending on the availability of resources in different habitat types. Female polecats had smaller isotopic niches in the 1960s than in any other decade (Fig. 3.3) but isotopic niche size increased subsequently, suggesting that female polecats diversified their resource utilisation after expanding out of the species' refugium in Wales. Increases in dietary niche breadth have been observed in American mink, during a period of colonisation (Sidorovich et al. 2010), although these increases were not observed to be different between the sexes.

Intraspecific resource partitioning by prey size is common between the sexes in mustelids (McDonald 2002), although it does not always occur; stoat diet differs between the sexes, but weasel diet does not (McDonald et al. 2000). The relative scarcity of rabbits in the 1960s may have resulted in partitioning of resources between male and female polecats that subsequently diminished as rabbit numbers recovered. Anecdotal reports suggest that rabbit populations in Wales were particularly severely affected by myxomatosis compared to the rest of Britain (Blandford 1986). The loss of rabbits in Wales was not considered to have had a devastating effect on the relict polecat population there as polecats were able to exploit alternative prey (Blandford 1986). Dietary studies of polecat stomach contents and scats have demonstrated an increase in the proportion of lagomorphs occurring in polecat diet over time (Blandford 1986, Birks & Kitchener 1999), consistent with increases in rabbit populations over the same time period (Aebischer et al. 2011). It is notable that there was also an increase between the 1960s and 1990s in the proportion of rabbit in the gut contents of stoats, which in Britain have a more similar dietary niche to polecats than other mustelids (McDonald et al. 2000). In Britain, stoat records appear to be positively correlated with rabbit numbers (Sumption & Flowerdew 1985, Sainsbury et al. 2019). It is possible that rabbit recovery in Wales also fuelled polecat expansion by increasing the abundance of prey, leading to increased polecat numbers locally and enabling colonisation of new areas at the periphery of the species' range (e.g. Brown 1984).

Our findings are inconsistent with previous point-in-time estimates of polecat diets in Britain, where no significant differences between the sexes were observed (e.g. Birks & Kitchener 1999). This may be due to the limitations of dietary analyses using gut contents and faecal samples, which can only reveal items consumed during a brief window of time and may be biased by the digestibility of items consumed. Overall the variations in size of female SEABs indicate plasticity of resource use through a period of change. It is unclear why, given the reported scarcity of rabbits, males do not exhibit the same variation in isotopic niche size, even in the 1960s when compared to other decades. This may be a function of intraspecific competition whereby males have preferential access to resources (compared to females) when resources are less abundant – for example Lodé (1996) found that intraspecific tolerance between male and female polecats increased with resource abundance.

We have revealed differences in polecat resource use between the sexes and in different parts of their range through time. The coincident expansion of polecats, changes in $\delta^{15}N$ and recovery and decline of rabbit populations suggest that rabbits may have been a major driver of polecat expansion. Our results also suggest that the current declines in rabbit populations in Britain (Harris et al. 2018) have the potential to affect polecat resource use, particularly in females. Our study highlights the utility of forensic analysis of long-term historical datasets in understanding the ecology underpinning changes in species abundance and distribution. In particular that, even for a generalist predator like the polecat, it should not be assumed that males and females use resources in the same way, as resource utilisation may vary between the sexes in time and space throughout the process of recovery.

Chapter 4

The diets of European polecats *Mustela putorius* in Great Britain during 50 years of population recovery

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Abstract

Polecats *Mustela putorius* are recolonising their former range in Great Britain, following severe historical declines. Two potential risks to their continuing recovery relate to their diet: i) population fluctuations of rabbits *Oryctolagus cuniculus,* which are particularly important prey for polecats in Great Britain, and ii) secondary exposure to second generation anticoagulant rodenticides, via consumption of contaminated rodents. We analysed stomach contents from 99 polecats collected from 2013 to 2015 and compared our results with earlier studies of polecat diet in Great Britain, carried out since the 1960s. Lagomorphs were the most abundant prey in the polecats we examined (66% frequency of occurrence (FO), followed by amphibians/fishes (13% FO), other mammals (12% FO) and birds (7% FO). Diet varied seasonally, with lagomorph occurrence highest in the spring and summer and lowest in the autumn. Dietary niche breadth was greatest in the 1960s, when rabbits were most scarce. Niche breadth did not differ between the 1990s and the 2010s, indicating that polecat diets have not diversified during current declines in rabbit populations. Rodents did not increase as a proportion of diet between the 1990s and 2010s and remain at <10% of diet. This indicates that rodents need not constitute a high proportion of polecat diet for these carnivores to be exposed to rodenticides, potentially limiting the effectiveness of management actions designed to minimise polecat exposure to contaminated rodent prey.

Introduction

Successfully colonising species often demonstrate ecological flexibility during the process of population establishment and expansion (Rosecchi et al. 2001, Lee & Gelembiuk 2008). Some species have flexible foraging strategies that allow them to exploit variation in resource availability across temporal and spatial scales (Zhou et al. 2011). The European polecat *Mustela putorius* is a medium-sized generalist carnivoran that is currently recolonising its former range in Great Britain following severe declines, mostly in the nineteenth century (Langley & Yalden 1977, Sainsbury et al. 2019). A significant period of this range expansion has coincided with extreme population fluctuations of rabbits *Oryctolagus cuniculus* (Sumption & Flowerdew 1985, Aebischer et al. 2011, Harris et al. 2018), which are a major source of food for polecats in Great Britain. It is unknown whether polecats in Britain may have altered their feeding strategy in response to recent rabbit declines and whether these declines may have impacted upon their continued recolonisation.

Foraging theory predicts that animals will maximise their net energy intake (MacArthur & Pianka 1966, Pyke et al. 1977, Perry & Pianka 1997), which may be maximised via different foraging strategies. For instance, specialist predators have narrow dietary niches and will forage for specific prey species, independent of their availability, whereas generalists have comparatively large dietary niches and will adapt their feeding strategy based on what prey are available (Futuyma & Moreno 1988, Amundsen 1995). Polecats exhibit dietary flexibility across their European range and are usually described as generalist predators (Erlinge 1986, Lodé 1995, Baghli et al. 2002, Santos et al. 2009, Malecha & Antczak 2013). Rodents and amphibians are common food items in all regions (Lodé 1997), although polecats appear to specialise on lagomorphs in Britain and the Mediterranean (Birks & Kitchener 1999, Santos et al. 2009) and on amphibians in Switzerland (Weber 1989b). However, it may be that any impression of specialisation simply reflects the relative abundance of a given prey item in a local place or time (Lodé 1995). This foraging strategy is thought to allow polecats to occupy and exploit diverse habitats, such as lowland, grassland, farmland and riparian habitats (Blandford 1987) and may play an important role in enabling population persistence (Lodé 1997).

In Great Britain, studies since the 1960s have found that mammals, primarily lagomorphs, comprise the majority of polecat dietary items (Walton 1968, Blandford 1986, Birks & Kitchener 1999), though there is some evidence of seasonal preferences for rodents (including brown rats *Rattus norvegicus,* and field voles *Microtus agrestis*) particularly in the winter months (Birks 1998, Birks & Kitchener 1999). Consumption of rodents is thought to be the major route by which polecats are exposed to second generation anticoagulant rodenticides (SGARs) in Britain (Shore et al. 2003). Exposure of polecats to SGARs increased 1.7 fold between 1993 and 2016 and currently some 78% of polecats appear to be exposed (Sainsbury et al. 2018) and it may be that this increase has been a result of an increase in the proportion of rodents in polecat diet.

In the 1950s, rabbit populations crashed by up to 95% across Great Britain as a result of a myxomatosis epizootic (Sumption & Flowerdew 1985), and this is known to have affected the diet composition and population dynamics of other small carnivorans, such as stoats *Mustela erminea* and weasels *M. nivalis* (McDonald et al. 2000). Rabbit populations recovered to their pre-myxomatosis levels by the 1990s (Aebischer et al. 2011) but since then, rabbit numbers have declined across Britain (England: -44%; Scotland: -82%; and Wales: -48%; Harris et al. 2018), possibly as the result of rabbit haemorrhagic disease (RHD), which has devastated rabbit populations across mainland Europe (Lees & Bell 2008). In Spain, carnivorans have shown reduced consumption of rabbits, in response to declines in rabbit populations following RHD outbreaks (Ferreras et al. 2011). While between-sex dietary differences have been observed in some mustelids (McDonald 2002), there is no evidence of this occurring in polecats (e.g. Blandford 1986, Birks & Kitchener 1999). However, it is possible that as rabbits have again declined in numbers, there may be evidence of more pronounced dietary differences between male and female polecat diet.

To explore dietary variation and niche breadth in polecats through the process of polecat population recovery and rabbit population variation, we analysed gut contents from polecats collected from 2013 to 2016 and compared our findings with historical analyses of polecat diet in Britain in the 1960s (Walton 1968), 1980s (Blandford 1986) and 1990s (Birks & Kitchener 1999). We hypothesised that i) rabbits will be reduced in importance in polecat diet compared to the 1990s, in response to reduced rabbit abundance; ii) rodent prey may have increased as a proportion of diet over the same period; iii) polecat dietary niche breadth will have fluctuated over time in line with known long-term variations in rabbit abundance but this may not be equally reflected in males and females. We discuss our findings in the context of prospects for polecat recovery.

Methods

Polecat carcasses, predominantly of animals killed on the road, were collected across Great Britain during the Vincent Wildlife Trust's national polecat survey 2012 – 2016 (Croose 2016). Date of death and location were recorded on collection. Animals were stored frozen until necropsy, which was carried out at National Museums Scotland. Stomach contents were collected from 99 polecats (Fig. 4.1) and refrozen prior to dietary analysis. Stomach contents were soaked in biological detergent for 24 hours, rinsed through a 53µm sieve, then stored in 70% ethanol. Identifiable animal remains (undigested body parts, fragments of bone, feathers, fur, individual hair and insect remains) were separated from unidentifiable tissues. The first ten processed samples were analysed for earthworm (Lumbricidae) chaetae and other microscopic remains (after Reynolds & Aebischer 1991). As no identifiable microscopic remains were found, the rest of the analyses only considered macroscopic remains. Plant debris was considered to be ingested when catching prey (Walton 1968) and was not included in diet composition quantification.

Fur remains were identified using guard hair cuticle patterns after Teerink (1991). All loose hairs were collected. Cuticle patterns were examined under a microscope at x40 magnification. Mammal remains were identified to species level, except for rabbits and brown hares *Lepus europaeus*, which were not separated and were classified as lagomorphs. Most bones were fragmented and unidentifiable but those that were intact, together with teeth, were identified as insectivore, rodent, larger mammal or amphibian. Bird remains were identified to order using Day (1966). Amphibians were determined by skin texture and, where possible, by webbing on feet. Fishes were identified by their bones and scales but not identified to species. Previous studies have indicated that polecat guts mostly only contain one item (Weber 1989b, Birks & Kitchener 1999). This was true in the current study, with only three stomachs (4%) containing remains of more than one identifiable item.

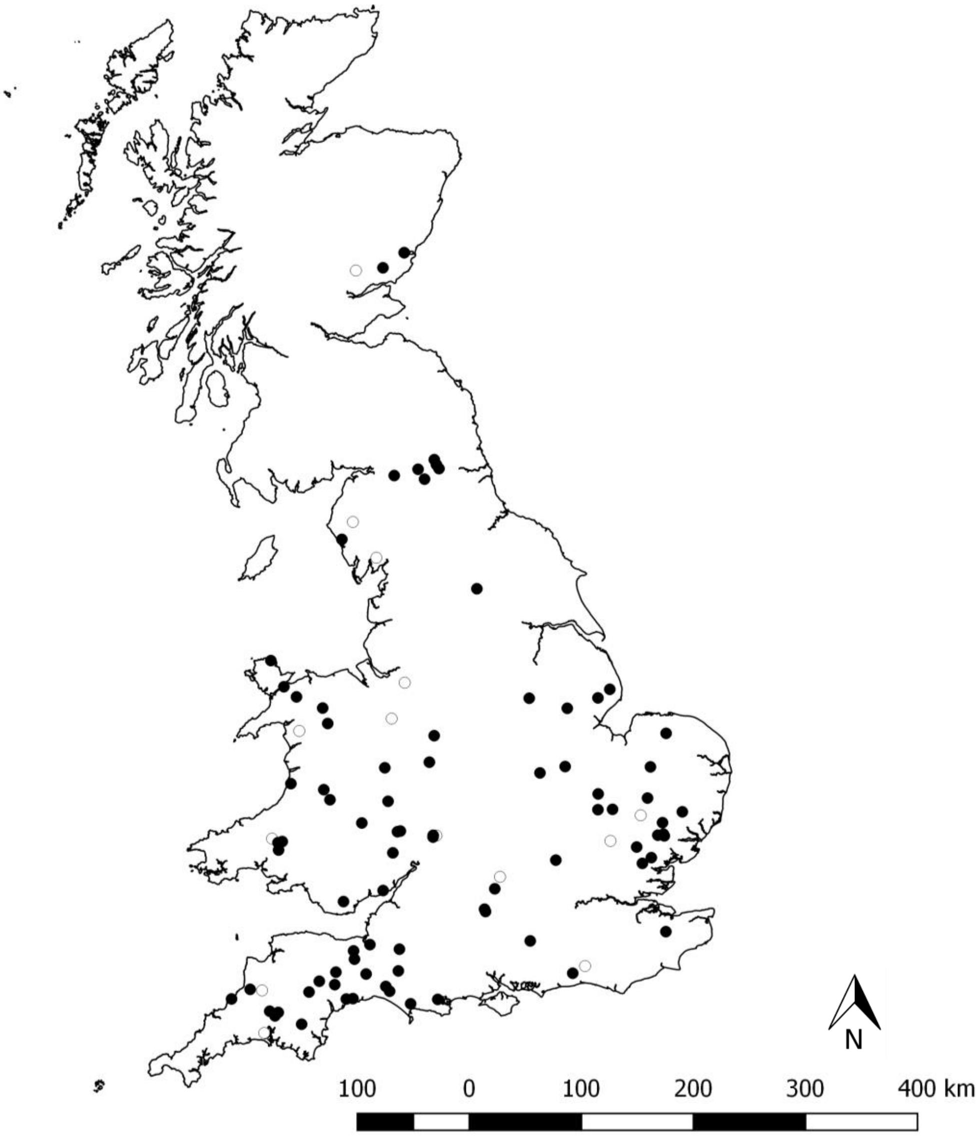

Figure 4.1. *Map showing the origin of polecat carcasses collected between 2013 and 2016. Sample size = 97, as two polecats came from unverified locations. Shaded circles indicate polecats with items in their stomach, white circles indicate empty stomachs.*

Two methods were used to assess accuracy when identifying guard hair cuticle pattern. First, 10% of samples were randomly selected for a second blind analysis by the same analyst; the correspondence in the results was 100%. A third analysis, again blind, was carried out by a second researcher, this time on 10% of samples that contained hard parts and 20% of the samples that relied on hair identification. There was a 100% match between analysts for samples containing hard parts, an 86% correspondence for hair samples and a calculated Cohen's Kappa test of interrater agreement of 0.7, which is "substantial" according to Landis & Koch (1977). The level of overlap in identification indicated that identification of guard hair was sufficiently robust for inclusion in our data analysis.

All analyses were carried out in R (R Core Team 2013). Diet was summarised as the percentage frequency of occurrence (%FO), calculated as the number of each type of dietary item as a percentage of the total number of identifiable prey items (e.g. Lodé 1994; McDonald et al. 2000). Frequency of occurrence values were bootstrapped with replacement 1000 times to generate 95% confidence intervals following Reynolds and Aebischer (1991). Levins' (1968) niche breadth was calculated following the formula:

$$N_b = 1/\sum p_i^2$$

Where p_i is the proportion of records for each species in each group. Results were again bootstrapped with replacement 1000 times to generate 95% confidence intervals (Reynolds & Aebischer 1991).

To analyse variation in the occurrence of lagomorphs in polecat diets, a logistic regression model of presence/absence was fitted to sex, season (where spring is March to May, summer is June to August, autumn is September to November and winter is December to February) and region (north, south, east and west based on British government regions) as explanatory variables. Stepwise model selection was carried out to find the most parsimonious model. The baseline levels in the model were set to the lowest effect sizes to aid interpretation.

Our results were compared with earlier large scale studies of polecat diets by Walton (1968), Blandford (1986) and Birks and Kitchener (1999). Levins' niche breadth was calculated using four categories (all mammals, birds, amphibians/fishes and invertebrates) for comparisons between 1960s, 1980s, 1990s and 2010s, as the available data from the 1960s did not distinguish between polecat sex or identify mammal species. For analyses of variation by polecat sex and decade between the 1980s and 2010s, Levins' niche breadth was calculated based on five categories (lagomorphs, other mammals, birds, amphibians/fishes and invertebrates). Analysis of niche breadth changes over time involved comparing the differences in the confidence intervals of the bootstrapped values.

Results

The stomachs from 99 polecats collected in the 2010s were examined (65 male, 32 female, 2 sex unknown), of which 14 were empty and six contained unidentifiable remains, such as undigested tissue. This left 79 stomachs containing identifiable prey items (54 male, 24 female, 1 unknown). Sixteen stomachs contained polecat hair, but this was excluded from the dietary analysis as it was assumed to be the result of grooming (Rysava-Novakova & Koubek 2009). Ten stomachs contained plant matter.

Mammals were the most frequently identified prey group (78%FO) and lagomorphs comprised two-thirds (66%FO) of prey items (Table 4.1). Eight of the 54 lagomorph samples (15%FO) were neonates or juveniles, identified on the basis of intact ears, tails or feet (Fig. 4.2). Amphibians/fishes were the second most frequently identified prey group (13%FO) and mostly comprised frogs. "Other mammals" constituted 12%FO of items, although brown rat remains were identified in only one polecat stomach. Birds and invertebrates comprised approximately 7% and 1%FO of all items, respectively. Only one instance of carrion was found, based on the presence of maggots in the tissue, which was classified as lagomorph.

The %FO of all prey items in male and female polecat stomachs was similar across the board and there was no significant difference in niche breadth between male (Levins' index = 2.2, 95% CI: 1.6- 2.3) and female polecats (2.2, 95% CI: 1.4-3.2).

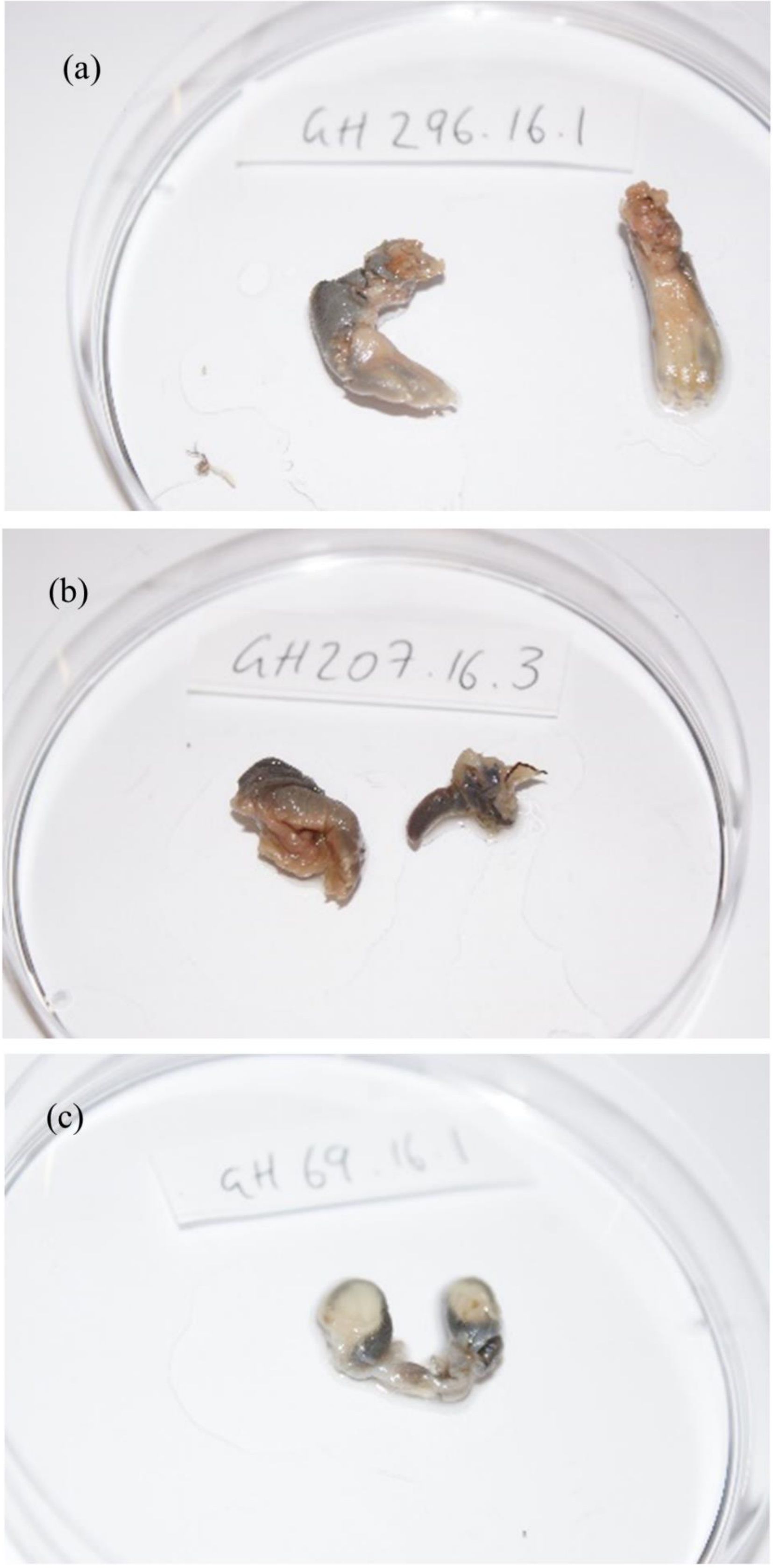

Figure 4.2. *Example of juvenile rabbit remains found in polecat stomachs. Photo a) shows two hind feet, b) front leg plus tail, and c) a pair of ears. Samples were collected from three different polecat specimens.*

Table 4.1. *Summary of composition of polecat Mustela putorius stomach contents in Great Britain between 2013 and 2016. Main prey groups are highlighted in bold. 95% percentile range confidence intervals are a bootstrapped estimate of the variability associated with sampling errors. There were 2 animals whose sex was unidentifiable (1 gut contained lagomorph, the other was empty).*

	Total		Males		Females	
Prey	FO	% FO (95% CI)	FO	% FO (95% CI)	FO	% FO (95% CI)
Lagomorph	**54**	**65.9 (53.7-74.0)**	**36**	**65.5 (50.8-76.5)**	**17**	**65.4 (44.4-81.5**
Other mammals	**10**	**12.2(4.2-17.5)**	**7**	**7.3 (22.3-19.5)**	**3**	**11.5 (0.0-23.0)**
Microtus agrestis	1	1.2 (0.0-3.5)	1	1.8 (0.0-5.4)		
Myodes glareolus	1	1.2 (0.0-3.6)			1	3.8 (0.0-10.8)
Sciurus spp.	3	3.7 (0.0-7.7)	3	5.5 (0.0-11.3)		
Rattus norvegicus	1	1.2 (0.0-3.6)			1	3.8 (0.0-11.2)
Sorex spp.	1	1.2 (0.0-3.7)			1	3.8 (0.0-11.0)
Unidentified small mammals	3	3.7 (0.0-5.8)	3	5.5 (0.0-8.7)		
Birds	**6**	**7.3 (1.2-12.9)**	**4**	**7.3 (0.4-14.2)**	**2**	**7.7 (0.0-17.2)**
Galliformes	1	1.2 (0.0-3.6)	1	1.8 (0.0-5.4)		
Columbiformes	1	1.2 (0.0-3.6)			1	3.8 (0.0-11.2)
Passeriformes	2	2.4 (0.0-5.9)	1	1.8 (0.0-5.4)	1	3.8 (0.0-11.0)
Unidentified bird	2	2.4 (0.0-5.5)	2	3.6 (0.0-8.7)		
Amphibians/fishes	**11**	**13.4 (5.8-20.7)**	**7**	**12.7 (4.0-21.4)**	**4**	**15.4 (0.5-29.1)**
Rana temporaria	7	8.5 (2.2-14.7)	3	5.5 (0.0-11.5)	4	15.4 (1.0-28.6)
Bufo bufo	1	1.2 (0.0-3.7)	1	1.8 (0.0-5.4)		
Fish	3	3.7 (0.0-20.7)	3	5.5 (0.0-11.5)		
Other						
Invertebrate	**1**	**1.2 (0.0-3.6)**	**1**	**1.8 (0.0-5.3)**		
Non-prey items						
Mustela putorius	16		10		5	
Vegetation	10		8		2	
Stomachs examined	99		65		32	
Empty stomachs (excluding polecat guard hairs)	14		8		5	
Stomachs containing remains	85		57		27	
Stomachs containing identifiable remains	79		54		24	
Stomachs with 2 items	3		1		2	
Total number of prey items	82	100	55	100	26	100

Our model analysing the factors influencing polecat diet found that Season was the only factor that significantly affected the occurrence of lagomorphs (Fig. 4.3). The occurrence of lagomorph remains identified in the diet was higher in the spring (odds: 8.9, 95% CI: 2.5-38.8), summer (odds: 3.4, 95% CI: 1.0-12.8) and winter (odds: 1.8, 95% CI: 0.5-7.4) than in the autumn. Niche breadth was greater in autumn (Levins' index, 95% CI. Spring: 1.1, 1.0-1.3) than in all other seasons (Summer: 1.9, 1.2-3.1; Autumn: 4.1, 2.5-5.0; Winter: 2.6, 1.4-4.3; Fig 4.3).

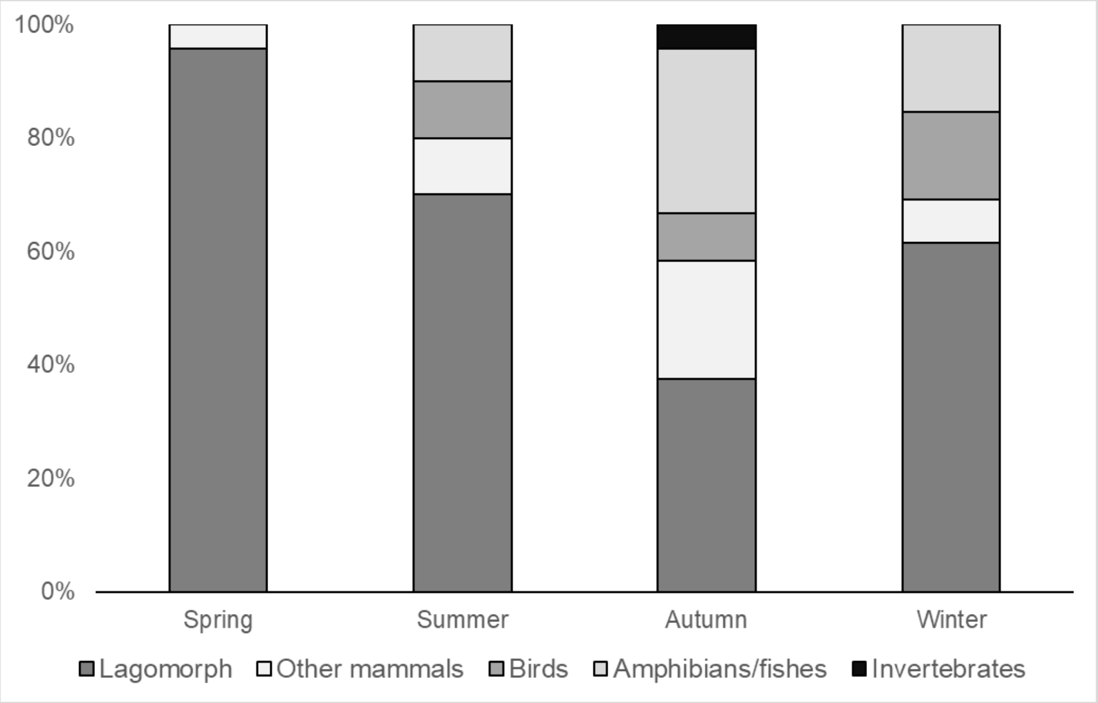

Figure 4.3. *Percentage frequency of occurrence of five categories of prey groups identified in polecat stomachs from animals collected between 2013 and 2016. Presented by season and as a percentage of prey items collected. Seasons are divided so that Spring: March – May (n = 24), Summer: June – August (n = 20), Autumn: September – November (n = 24), Winter; December – February (n = 13). The collection season of 1 animal was unknown.*

Analysis of changes in polecat diets over time indicated that the occurrence of all mammals more than doubled between the 1960s (35%) and the 2010s (78%), while birds, amphibians/fishes and invertebrates decreased (Table 4.2). Lagomorph occurrence increased between the 1980s (25%) and 1990s (69%) but did not differ between samples collected in the 1990s and the 2010s (66%). There was no difference in the occurrence of all mammals between male and female polecats in the1980s, 1990s or 2010s (Table 4.2). However, the occurrence of lagomorphs did differ between males and females between decades and was similar for males and females in the 1980s and 2010s but greater in males (75%) than in females (58%) in the 1990s. Polecat dietary niche breadth was greatest in the 1960s and least in the 1990s and 2010s (Table 4.2).

Table 4.2. *Summary of percentage frequency of occurrence (FO) of items found in polecat diets from the 1960s to the 2010s. Sources are Walton (1968), Blandford (1986), Birks and Kitchener (1999) and the current study. 1960s data are calculated using FOC in stomachs (n=38). 1980s data are calculated based on FO in scats (n=754, males = 411, females = 343). 1990s data (n=87, males = 56, females = 31) and 2010s data (n = 82, males = 55, females = 26, 1 animal of unknown sex) are calculated based on the total prey items identified. Levins' niche breadth was calculated using four categories (all mammals, birds, amphibians/fishes and invertebrates) for the 1960s, 1980s, 1990s and 2010s. For the male and female calculations by decade, Levins' niche breadth was calculated based on five categories (lagomorphs, other mammals, birds, amphibians/fishes and invertebrates). 95% percentile range confidence intervals are a bootstrapped estimate of the variability associated with sampling errors. Dietary information by sex was not available for the 1960s.*

	1960s	1980s	1990s	2010s
	% FO (95% CI)	% FO (95% CI)	% FO (95% CI)	% FO (95% CI)
All mammals	35.1 (19.6-48.8)	73.7 (70.6-76.9)	79.3 (71.8-89.0)	78.0 (64.4-85.0)
Lagomorph	NA	25.1 (21.8-28.1)	69.0 (59.0-78.9)	65.9 (53.7-74.0)
Birds	14.0 (2.2-24.1)	16.0 (13.4-18.7)	9.2 (2.9-15.5)	7.3 (1.2-12.9)
Amphibians/fishes	26.3 (11.7-40.9)	8.2 (6.2-10.2)	9.2 (2.7-15.6)	13.4 (5.8-20.7)
Invertebrates	24.6(9.8-37.5)	2.0 (0.9-3.1)	1.1 (0.0-3.3)	1.2 (0.0-3.6)
Levins' niche breadth (95% CI)	*3.9 (1.9-4.3)*	*1.7 (1.6-1.9)*	*1.6 (1.3-1.9)*	*1.6 (1.3-1.9)*
n=	38	754	87	82
Males				
All mammals		73.2 (69.0-77.5)	82.1(71.9-92.4)	78.2 (63.1-85.9)
Lagomorph		26.3 (21.9-30.7)	75.0 (63.1-86.9)	65.5 (50.8-76.5)
Birds		14.4 (10.9-17.8)	7.1 (0.5-13.8)	7.3 (22.3-19.5)
Amphibians/fishes		8.8 (6.1-11.5)	8.9 (1.3-16.5)	12.7 (4.0-21.4)
Invertebrates		3.6 (1.8-5.5)	1.8 (0.0-5.3)	1.8 (0.0-5.3)
Levins' niche breadth (95% CI)		*3.1 (2.9-3.4)*	*1.7 (1.4-2.3)*	*2.2 (1.6-2.3)*
n=		411	56	55
Females				
All mammals		74.3 (69.6-79.0)	74.2 (58.3-90.1)	76.9 (54.4-93.7)
Lagomorph		23.6 (19.0-28.2)	58.1 (40.5-75.6)	65.4 (44.4-81.5)
Birds		18.1 (13.9-22.3)	12.9 (0.8-25.0)	7.7 (0.0-17.2)
Amphibians/fishes		7.6 (4.8-10.4)	9.7 (0.0-20.1)	15.4 (1.0-28.6)
Invertebrates			3.2 (0.0-9.6)	
Levins' niche breadth (95% CI)		*2.9 (2.6-3.1)*	*2.7 (1.8-3.8)*	*2.2 (1.4-3.2)*
n=		343	31	26

Discussion

Polecat diet composition in Great Britain was dominated by lagomorphs in all the samples analysed between the 1960s and 2010s, although there was seasonal variation which reflects the opportunistic foraging of this species. Contrary to our expectations, there was no evidence of a reduction in rabbit consumption by polecats since the 1990s, despite declines in rabbit records over this period (Harris et al. 2018). We did find an increase in the frequency of occurrence of lagomorphs in polecat diet since the 1960s, consistent with similar variation in the importance of lagomorphs in the diet of stoats over the same time period (McDonald et al. 2000). We also found that lagomorphs were equally important as prey for both male and female polecats in the 1990s and 2010s (Table 4.1) and so there was no evidence of resource partitioning between the sexes, consistent with McDonald (2002). We found frequent evidence of polecat predation on young rabbits, which was also found in the 1990s study (A. Kitchener, unpublished data).

There are several possible explanations for this lack of dietary shift in response to declining resources. One is that the more recent rabbit declines have been patchy across the landscape, unlike the 1950s myxomatosis epizootic (Sumption & Flowerdew 1985), and so polecats have still been able to find and take rabbits as their major prey item. Walton's (1968) study, for which samples were collected when rabbit populations were at their nadir, suggested that when rabbit availability was very restricted, polecats did increase the size of their dietary niche (Table 4.2). Similarly, when rabbit numbers were still low in Wales in the 1980s (Aebischer et al. 2011) and polecats were predominantly found only in Wales (Sainsbury et al. 2019), lagomorphs comprised a lower proportion of polecat diet than in the 2010s and niche breadth was correspondingly greater than in the 1990s or 2010s (Table 4.2, Blandford 1986). There was also some evidence of differences in resource use between males and females in the 1980s (lower lagomorph consumption by females) when rabbits were reduced in availability (Table 4.2, Blandford 1986); this resource partitioning was not evident in the 2010s.

The continued high prevalence of rabbits in polecat diets means that other prey items, notably rodents, were detected less frequently than might have been expected. The relatively high occurrence of amphibians is in line with polecat diet studies in France (Lodé 2000), Switzerland (Weber 1989b) and Denmark (Hammershøj et al. 2004). While some dietary studies have correlated amphibian consumption to periods of abundance (Lodé 2000), others have found that polecats eat them preferentially (Weber 1989c). In our study, where amphibians were consumed, more than just the hind limbs were found in the stomach. Weber (1989b) demonstrated that polecats usually only consume muscle meat when amphibians are very abundant, and as we only found whole hind limbs, it is possible that the amphibians found in this study were not necessarily eaten in a period of especially high abundance. Unlike in France, where amphibians are more commonly eaten in spring when amphibians are more active at the beginning of their breeding season (Lodé 2000), amphibians were most commonly caught in autumn in this study. The skin of the common toad *Bufo bufo* was consumed intact, irrespective of its apparently distasteful dermal secretions (Sidorovich & Pikilik 1997).

Given recent increases in the rates of exposure of polecats to SGARs (Sainsbury et al. 2018), it is perhaps surprising that we did not observe an increase in the proportion of rodents, especially brown rats, consumed by polecats over this same time period. Furthermore, our data indicate that the current high proportion of polecats exposed to SGARs is associated with an intake of rodents that comprises less than 10% of total diet. This suggests that even relatively low rates of rodent consumption can result in high rates of secondary exposure to rodenticides, especially when such exposure is likely cumulative over time. This means that our ability to minimise exposure of polecats to SGARs may be limited, as rodents comprise only a small component of their diet.

The recent occurrence of birds in the diet of polecats was consistent with that observed in previous decades. However, the importance of bird remains is often underestimated in analysing stomach contents (Reynolds & Aebischer 1991). Furthermore, polecats eat eggs but we did not detect any evidence of this, possibly because polecats tend to break them open and lick out the contents (Weber 1989b). In the 1980s, Blandford (1986) found that Galliformes (the order of birds that includes the locally abundant ring-necked pheasant *Phasianus colchicus* and red-legged partridge *Alectoris rufa*) comprised 5%FO of polecat diet. This study was carried out before polecats had expanded beyond the Welsh border counties, an area where game management is less widespread (Tapper 1992). Birks and Kitchener (1999), who collected roadkill carcasses from across Wales and the English Midlands, did not identify any Galliformes in polecat stomachs and our results are broadly consistent with this. Polecats spend time on game estates in Britain (Packer & Birks 1999) and, in other countries, polecats are known to consume wounded or dead gamebirds (Rysava-Novakova & Koubek 2009). Given this and the difficulties associated with detecting birds in stomach contents, it is possible that birds might be eaten more frequently than our results suggest.

Conclusion

We have highlighted long-term increases in the proportion of lagomorphs in polecat diet in Britain during a period of polecat population recovery. When rabbits were almost extirpated from Britain in the 1950s and 1960s, polecat diet was significantly more diverse. Polecat niche breadth has since declined as rabbit populations have recovered. Our results, which show how niche breadth and diet composition has varied over time, demonstrate the importance of long-term studies for determining whether species are generalist or specialists. Overall, polecats in Great Britain appear to be generalist feeders. Although rabbit populations are once again in decline, there is no evidence of a concomitant reduction in rabbit consumption but it is possible that such effects may only be apparent from studies conducted at a finer spatial scale. Finally, our study shows that rodents do not have to constitute a high proportion of polecat diet, to lead to the frequent secondary exposure to rodenticides seen in polecats in Great Britain.

Chapter 5

Long-term increase in secondary exposure to anticoagulant rodenticides in European polecats *Mustela putorius* in Great Britain

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Abstract

As a result of legal protection and population recovery, European polecats *Mustela putorius* in Great Britain are expanding into areas associated with greater usage of second-generation anticoagulant rodenticides (SGARs). We analysed polecat livers collected from road casualties from 2013 to 2016 for residues of five SGARs. We related variation in residues to polecat traits and potential exposure pathways, by analysing stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in their whiskers. 54 of 68 (79%) polecats had detectable residues of at least one SGAR. Bromadiolone (71%) was the most frequently detected compound, followed by difenacoum (53%) and brodifacoum (35%). Applying historical limits of detection to allow comparison between these new data and previous assessments, we show that in the 25 years from 1992 to 2016 inclusive, the rate of detection of SGARs in polecats in Britain has increased by a factor of 1.7. The probability of SGAR detection was positively related to increasing values of $\delta^{15}N$, suggesting that polecats feeding at a higher trophic level were more likely to be exposed. Total concentrations of SGARs in polecats with detectable residues were higher in polecats collected in arable compared to pastoral habitats, and in the west compared to the east of Britain. The number of compounds detected and total concentrations of SGARs increased with polecat age. There was no evidence of regional or seasonal variation in the probability of detecting SGARs, suggesting that the current risk

of exposure to SGARs does not vary seasonally and has increased (from that in the 1990s) throughout the polecat's range. We recommend quantification of current practices in rodenticide usage, particularly in the light of recent regulatory changes, to enable assessment and mitigation of the risks of secondary exposure to rodenticides in non-target wildlife.

Introduction

Rodents, primarily brown rats *Rattus norvegicus,* are estimated to cost the UK economy between £60 and £200 million a year, arising primarily from spoiling of food and from disease transmission (Battersby 2004). Anticoagulant rodenticides dispensed in baits are the primary means of reducing this damage. They function by interrupting the blood clotting mechanism by inhibiting the action of Vitamin K epoxide reductase (Watt et al. 2005) and lethal exposure leads to death by internal haemorrhaging (Watt et al. 2005, Rattner et al. 2014). In response to the emergence of resistance in rats to warfarin and other first generation rodenticides, second-generation anticoagulant rodenticides (SGARs) with higher acute toxicity were developed (Buckle et al. 1994, World Health Organization 1995) and are now used routinely worldwide to control rodent infestations (Stone et al. 2003, Buckle & Smith 2015).

The extensive use of SGARs has led to secondary exposure in a range of mustelids including stoats *Mustela erminea* and weasels *Mustela nivalis* (McDonald et al. 1998, Elmeros et al. 2011), European polecats *Mustela putorius* (Shore et al. 2003, Elmeros et al. 2018), American mink *Neovison vison* (Ruiz-Suárez et al. 2016), stone martens *Martes foina* (Elmeros et al. 2018) and fishers *Pekania pennanti* (Gabriel et al. 2012, Thompson et al. 2014). There is also evidence of widespread exposure in other predators such as red foxes *Vulpes vulpes* (Tosh et al. 2011, Geduhn et al. 2015), San Joaquin kit foxes *Vulpes macrotis mutica* (Cypher et al. 2014), mountain lions *Puma concolor* and bobcats *Lynx rufus* (Riley et al. 2007, Serieys et al. 2015), barn owls *Tyto alba* (Geduhn et al. 2016, Shore et al. 2016, Shore et al. 2017), sparrowhawks *Accipiter nisus* (Hughes et al. 2013, Walker et al. 2015) tawny owls *Strix aluco* (Walker et al. 2008) and red kites *Milvus milvus* (Walker et al. 2017). Secondary exposure occurs via the consumption of exposed prey (Smith et al. 1990, Smith et al. 2007, Rattner et al. 2014). These may be target species that are the subject of control measures, such as the brown rat and house mouse *Mus domesticus*, or non-target species that feed on bait and are inadvertently contaminated during control campaigns targeted at commensal rodents (Tosh et al. 2012, Elliott et al. 2014). The scale of secondary exposure in predators can vary with habitat (Geduhn et al. 2014, Nogeire et al. 2015), sex (McDonald et al. 1998) and time of year (Shore et al. 2003). In some species the magnitude of residues is greater in older animals (Ruiz-Suárez et al. 2016), arising from the cumulative effect of multiple sub-lethal exposures and the relatively long tissue half-lives of these compounds (Vandenbroucke et al. 2008, Environmental Protection Agency (EPA) 2008).

There is concern that secondary exposure may lead to significant impacts on predators, many of which are species of conservation interest. The extent of any mortality is likely to be species-dependent as tolerance varies by several orders of magnitude (World Health Organization 1995, Erickson & Urban 2004, Thomas et al. 2011, Berny et al. 2010). Relatively few poisoned animals are reported in national surveillance schemes, when compared to the numbers known to be exposed (e.g. Barnett et al. 2004, Barnett et al. 2005). The likelihood that exposed individuals die out of sight (Newton et al. 1999), combined with limited external signs of toxicosis (Murray 2011) and difficulties with using liver residues as a diagnostic of mortality (Thomas et al. 2011), mean that the true extent of secondary poisoning may be underestimated. There may also be sub-lethal effects such as increased susceptibility to natural and anthropogenic stressors (Albert et al. 2010), reduced body condition (Elmeros et al. 2011) and less resistance to pathogens mediated through impairment of the immune system (Riley et al. 2007, Serieys et al. 2015). However, the mechanisms by which any sub-lethal effects occur and their possible impacts on long-term survival and reproductive output remain unclear.

Species that consume rats and other target species may be at particular risk of secondary exposure and poisoning by SGARs (Eason & Spurr 1995, Brakes & Smith 2005). The European polecat, a medium-sized carnivore that occurs across Europe, is one such species. It is protected in England and Wales under the Wildlife and Countryside Act (1981) and is currently expanding its distribution, having been extirpated (through predator control) from most of its range in Great Britain during the nineteenth century (Birks 2015, Croose 2016).

Although the polecat is a generalist feeder with a diverse diet that varies across its European range (Blandford 1987, Lodé 1996b, Lodé 1997, Birks & Kitchener 1999, Baghli et al. 2002, Hammershøj et al. 2004, Rysava-Novakova & Koubek 2009, Santos et al. 2009, Malecha & Antczak 2013), in England and Wales rabbits *Oryctolagus cuniculus* and rats are the primary prey (Birks & Kitchener 1999).

A study of rodenticide residues in polecats in Great Britain that died between 1992 and 1999 established that 31 out of a sample of 100 animals had detectable residues of at least one SGAR (Shore et al. 2003). Detection rates were slightly higher (40%) in animals that died in the first half of the year. It was speculated that this may have been a result of the predominance of rats in the diet during the winter, since rats may comprise up to 65% of polecat diet in the winter months (Birks 1998). However, SGAR exposure in polecats has not specifically been linked to any contemporary dietary analysis. Stable isotope analysis offers the opportunity to explore such links. $\delta^{15}N$ and $\delta^{13}C$ are measures of the ratio of heavier to lighter stable isotopes of nitrogen (^{15}N–^{14}N) and carbon (^{13}C–^{12}C) relative to a standard (DeNiro & Epstein 1981). As the lighter ^{14}N is preferentially excreted during metabolic processes, ^{15}N enrichment from prey item to predator occurs (DeNiro & Epstein 1981). Variation in $\delta^{13}C$ reflects diversity in basal resources consumed, e.g. between marine and terrestrial, and plants with C3 or C4 photosynthetic pathways (Smith & Epstein 1971, DeNiro & Epstein 1978). Analysis of $\delta^{15}N$ has been widely used for developing understanding of biomagnification of contaminants with increasing trophic level in fresh-water and marine environments (Spies et al. 1989, Cabana & Rasmussen 1994, Kidd et al. 1995, Jarman et al. 1996, Bearhop et al. 2000, Hobson et al. 2002), and can be applied to examine secondary exposure to rodenticides. Rats are omnivorous opportunistic feeders and their diets vary with location (Major et al. 2007, Dammhahn et al. 2017), so polecats feeding on rats might be expected to have enriched $\delta^{15}N$ signatures compared to those eating a greater proportion of rabbits, which are herbivorous (Southern 1940). If rats are the main trophic pathway through which polecats are secondarily exposed to SGARs, it would be expected that there might be a positive association between liver SGARs and enriched $\delta^{15}N$ signatures.

In the 20–25 years since the last quantification of the exposure of polecats in Great Britain to SGARs (Shore et al. 2003), populations of this species have undergone a substantial recovery and have expanded their range into areas of the country associated with higher usage of SGARs (Packer & Birks 1999, Birks 2000, Dawson et al. 2003, Dawson & Garthwaite 2004). It might therefore be predicted that overall exposure in the polecat population is likely to have increased, if animals in newly recolonised areas subject to greater SGAR usage also feed on rats. Furthermore, the methods of chemical analysis for rodenticides have become more sensitive (lower limits of detection) and so earlier studies in any case are likely to have underestimated levels of exposure (Dowding et al. 2010). The current extent of exposure of polecats to SGARs, and how and why this varies between individuals, is therefore unknown. Using polecat carcasses collected from across their range in Great Britain between 2013 and 2016, our aims in the present study were to: (i) determine the current extent of SGAR exposure in polecats (via measurement of liver residues) and whether this has changed over the last 20–25 years; (ii) identify any spatial and temporal patterns in exposure; (iii) elucidate trophic correlates of exposure through stable isotope analysis of whiskers, and (iv) explore the effect of age on rodenticide accumulation in polecats, a factor not examined by Shore et al. (2003), but recently found to be important in other mustelids (Ruiz-Suárez et al. 2016).

Methods

Carcass collection and sample preparation

Polecat carcasses were collected as part of a national monitoring survey carried out by the Vincent Wildlife Trust between December 2013 and March 2016 (Croose 2016). Sixty-eight carcasses were selected for rodenticide analysis, based on stratification by sex, location and collection date. Of the animals selected, 82% (n = 56) were road traffic casualties; the remainder were found dead in fields, killed by dogs, trapped or the cause of death was unknown.

Collection date and location were recorded for all carcasses, which were stored frozen until necropsy examination at the National Museums Scotland. The poor condition of the majority of the carcasses precluded assessment of clinical signs of exposure to rodenticides. Where carcass condition allowed, gross necropsy examination included recording of sex, head and body length (nose to tip of tail), mass and internal fat, scored on a five-point scale (McDonald et al. 1998). A body condition score (e.g. Schulte-Hostedde et al. 2005) was not calculated because many carcasses were damaged or incomplete. Teeth (for ageing), whiskers (for stable isotope analysis) and liver tissue (for rodenticide analysis) were collected. Liver samples were frozen and transferred to the Centre for Ecology & Hydrology (CEH) for rodenticide analysis. Whiskers were prepared for analysis at the University of Exeter and analysed at Elemtex, UK and teeth were sent to Matson's Lab LLC, USA for aging by analysis of cementum layers.

Determination of rodenticides in liver using liquid chromatography tandem mass spectrometry

Concentrations of the five SGARs licensed for use in Great Britain (bromadiolone, difenacoum, brodifacoum, flocoumafen and difethialone) were determined in the polecat livers. The analytical method is summarised here. A detailed description is available in Walker et al. (2017). A 0.25 g sub-sample of each liver was thawed, weighed accurately, ground and dried with anhydrous sodium sulphate. Labelled standard (d^5- Bromadiolone, QMx) was added to each sample for quality control purposes and determination of analyte recovery. Each liver sub-sample was solvent-extracted and then cleaned-up using size exclusion chromatography followed by elution through solid-phase cartridges. Extraction was carried out twice with clean solvent. Each extraction involved vortex mixing of the sample with 1:1 v/v chloroform:acetone, mechanical shaking and centrifugation. The resultant supernatants from the two extraction runs were combined, solvent-exchanged into (1:1; v/v) chloroform:acetone, filtered (0.2 mm PTFE filter), subjected to a further solvent exchange into (1:23; v/v) acetone:DCM, filtered again, and cleaned-up by size-exclusion chromatography (Agilent 1200 HPLC). The cleaned extract was solvent-exchanged into 1:1:8; v/v. chloroform:acetone:acetonitrile and underwent a second clean-up using solid phase, methanol-washed, acetonitrile-activated extraction cartridges (ISOLUTE® SI 500 mg, 6 ml). The cartridges were eluted with the same solvent and the eluate exchanged for the mobile phase.

Liver SGAR residues were quantified by HPLC linked to a triple quadrupole mass spectrometer interfaced with an ion max source in Atmospheric Pressure

Chemical Ionisation mode (APCI) with negative polarity. Full details of the operational parameters used are as given by Walker et al. (2017). All rodenticide standards (Dr Ehrenstorfer) were matrix matched and linear calibration curves were defined such that $R^2 > 0.99$. A blank was run with each batch of unknowns. The mean method limit of detection (LOD) across batches for each compound was 0.0014 µg/g, except for difethialone which was 0.0022 µg/g. The mean (±SE) recovery for the total procedure was calculated from the labelled bromadiolone standard applied to each sample and was 68.0 ± 2.1%. Liver SGAR concentrations were not recovery corrected and are expressed on a wet weight basis. Summed (Σ) SGAR liver concentrations in individual animals were calculated by summing the concentrations of the five different SGARs, a zero concentration being assigned to individual compounds that were not detected.

Stable isotope analysis

Whiskers were gently rinsed in distilled water and then freeze dried for 24 h. One whisker per animal was cut into ~1 mm segments using a scalpel, starting at the proximal end of the whisker. Consecutive segments were pooled until the summed sample weight was ~0.7 mg (mean ± SE sample weight 0.68 ± 0.01 mg). The sample was enclosed in a tin cup and put into a tray for analysis. The next segment was prepared in the same way and the process was further repeated until either the whole whisker was used, or less than 0.2 mg was remaining. Samples were analysed on a Thermoquest EA1110 elemental analyser linked to a Europa Scientific 2020 isotope ratio mass spectrometer at Elemtex Ltd (Cornwall, UK) for $\delta^{15}N$ and $\delta^{13}C$. $\delta^{15}N$ and $\delta^{13}C$ abundance are reported as δ-values and expressed as a per mil (‰) deviation from the international reference standards (VPDB for carbon and AIR for nitrogen) (Mariotti 1983). Replicate analysis of standards (USGS 40, USGS 41 and an in-house bovine liver standard) yielded standard deviations of 0.05–0.29 for $\delta^{15}N$ and 0.05–0.22 for $\delta^{13}C$.

Cementum aging

Cementum ageing was undertaken by Matson's Lab LLC (Manhattan, MT, USA) following a standard protocol (Matson et al. 1993). In brief, after decalcification in a weak hydrochloric acid solution, teeth were sectioned sagittally and mounted on glass slides. The sections were stained to allow visual differentiation of annual cementum growth layers. These layers (annuli) were examined microscopically for age estimation at time of death. Birth date was set to 1 May for the purpose of estimating age in months.

Data analysis

All data were analysed using R [version 3.4.1] and R Studio [version number 0.99.896]. Generalised linear models were built using a) the 2013-16 data (henceforth "new data") and b) a combination of new data and the historical polecat rodenticides data from Shore et al. (2003) ("combined data"). Combination of new and historical data involved applying the limits of detection (LOD) for each compound from Shore et al. (2003), which were higher than those in the present study, to eliminate biases caused by changes in analytical sensitivity.

We modelled exposure in three ways: i) probability of detecting at least one SGAR; ii) number of SGARs detected; and iii) of those polecats with detectable residues, total concentration levels of all SGARs detected. Total SGAR concentration data were log-transformed before building models so that they were normally distributed. Polecats with no SGARs detected were excluded from the total SGAR concentration models to allow us to explore the variables related to differences in concentration levels.

Explanatory variables included in the three "new data" models were: age (months), sex (male/female), half of year in which the carcass was collected (first/second), region (North/South/East/West), land class (arable/pastoral), fat score, $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰). Carcasses collected between January–June were categorised as "first" half of the year, those collected between July–December were categorised as "second". Regions were defined using U.K. Government Office Regions. North comprised North East, North West, Yorkshire and the Humber; South comprised London, South East and South West; East comprised Eastern and East Midlands and West comprised Wales and West Midlands. No animals were analysed from Scotland. Quantum GIS [version 2.12.3] was used to generate land class classifications. Carcass collection locations were overlaid onto the CEH Land Cover map (2007 https://www.ceh.ac.uk/services/land-cover-map-2007), 1 km buffers were applied around each carcass coordinate and the majority land class calculated for each point, for whichever was largest between “arable” or “pastoral”, i.e. improved grasslands. Models included the mean $\delta^{15}N$ and $\delta^{13}C$ for each whisker. We also modelled the maximum $\delta^{15}N$ value for each whisker in place of the mean $\delta^{15}N$, as it was considered that it may only take one contaminated meal to cause secondary exposure and maximum $\delta^{15}N$ might better reflect such episodic incidents than the mean value for the whole whisker. However, models with the maximum $\delta^{15}N$ did not differ markedly from the models with the mean $\delta^{15}N$ and hence analysis of maximum values is not reported.

The “combined data” models, adjusted for limits of detection, included two categorical explanatory variables: collection period (1992–1995, 1996–1999, 2013–2016) and location (inside or outside of the 1990s polecat range, as determined by Birks & Kitchener (1999)). The first two carcass collection periods were 1992–1995 and 1996–1999 and represent an approximately even split (in calendar years and numbers) of the 100 polecats analysed by Shore et al. (2003). The third collection period related to the “new data” carcasses collected in 2013–2016. Location was included with the aim of assessing whether polecat expansion into new areas, where SGAR use may have been greater, might affect the frequency of SGAR exposure.

Models were built using lme4, MuMIn and car packages in R. Models were checked for collinearity (none was evident). Model fit was assessed using QQ plots. Models were mean centred and standardised using two standard deviations to facilitate comparisons between effect sizes (Gelman 2008). Top models were then selected using Akaike's Information Criterion (AIC), where values differed by less than two from the best model. Averaged models were created using the top models as none of the top models was weighted >0.9 (Grueber et al., 2011). Interaction effects between parameters were not significant and did not appear in any of the top models when added, and so were removed for simplicity. Standardised conditional averaged model outputs were summarised. Model predictions were drawn using the ggplot2 package in R.

Results

The 68 polecats analysed for SGARs came from throughout England and Wales (Fig. 5.1); 29 were female, 38 male and the sex of one could not be determined.

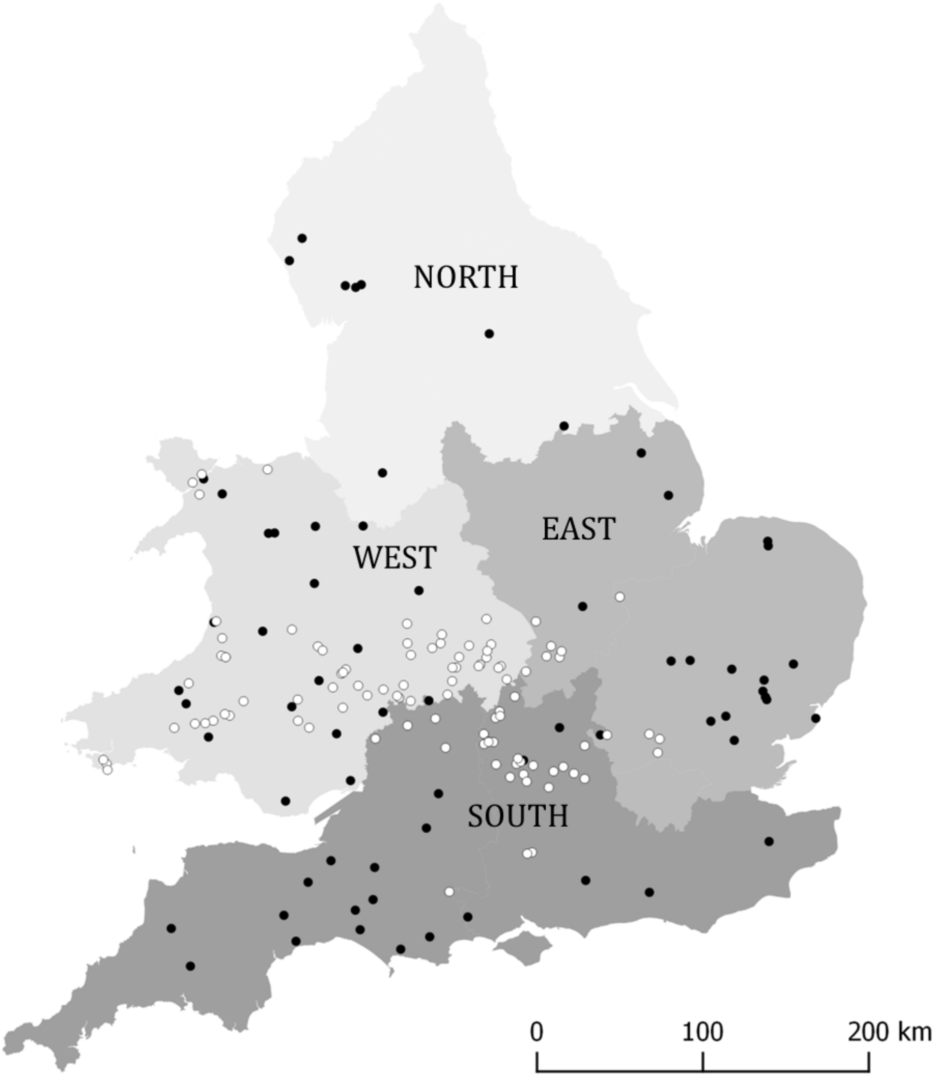

Figure 5.1. *Collection locations of polecat carcasses used for analysis of second generation anticoagulant rodenticides. Black points are carcasses collected and analysed in this survey while white points are carcasses collected and analysed in Shore et al. (2003).*

The age of the polecats in our sample ranged from one month to six years. The youngest polecats with detectable residues of SGARs were two months old while the oldest polecat without detectable SGARs was three years old. Mean $\delta^{15}N$ values for polecat whiskers ranged between 7.2 and 13.2‰. Mean $\delta^{13}C$

values ranged from −27.98 to −21.41‰. In all, 54 of 68 (79%) polecats had detectable liver residues of at least one SGAR compound (Table 5.1). The number of polecats with one, two, three or four compounds in the liver were 19 (27.9%), 16 (23.5%), 16 (23.5%) and 3 (4.4%) respectively. The median number of compounds detected in polecat livers was 2.

Table 5.1. *Prevalence and concentrations of residues of second generation anticoagulant rodenticides (SGARs) in the livers of 68 polecats collected in England and Wales, 2013–2016. Totals are the prevalence of residues of any SGAR and the median of the summed SGAR concentrations.*

Compound	Number (% of total sample) of polecats with detected residues	Median (range) concentration (µg/g wet weight)
Bromadiolone	48 (71%)	0.0581 (0.0014 – 3.0833)
Difenacoum	36 (53%)	0.0587 (0.0021 – 0.5125)
Brodifacoum	24 (35%)	0.0080 (0.0016 – 0.7298)
Difethialone	3 (4%)	0.0193 (0.0035 – 0.0505)
Flocoumafen	0 (0%)	N/A
Total	54 (79%)	0.1204 (0.0014 – 3.1628)

The rate of detection of liver SGARs differed significantly between compounds ($\chi^2 = 77.5$, df = 4, $p < 0.0001$), with bromadiolone most frequently detected, followed by difenacoum and brodifacoum (Table 5.1). Difethialone was only detected in livers that contained residues of all three commonly detected SGARs. Flocoumafen was never detected. There was no significant difference between compounds in the median concentrations of residues in those animals with detected residues (KW = 2, df = 2, p = 0.37). Appendix 5.1 provides a histogram of the distribution of total SGAR concentrations contained in Table 5.1.

Probability of detecting at least one SGAR in the liver

The probability of detecting liver SGAR residues could be explained by a set of top models that included age, $\delta^{15}N$, $\delta^{13}C$, fat score and land class; age and $\delta^{15}N$ appeared in all the top models (Table 5.2a). In the resultant averaged model (Table 5.2b), there was a positive effect of enriched $\delta^{15}N$ signatures on the likelihood of SGAR detection in livers. The model predicted that at the mean level of δ^{15}N (9.9‰), the probability of detecting SGARs was 89% (95% confidence limits: 68%–97%, Fig. 5.2). Although age, δ^{13}C, fat score and land class also featured in the averaged model, the confidence intervals for the effects of these parameters overlapped 0, indicating that they had no significant effect on the probability of detecting liver SGAR residues.

Table 5.2a. *Summary of statistical models of variation in second generation anticoagulant rodenticide (SGAR) residues in polecat livers collected from 2013 to 2016. Top models are from analyses of i) probability of detecting residues ii) number of compounds for which residues were detected and iii) total concentrations. AIC is Akaike's Information Criterion and ΔAIC is the difference in AIC from the best model. Only models with ΔAIC <2 are included in the top model set. Weight is the weighting given to that model when the averaged model is calculated. Sample sizes vary because of missing variables and the exclusion of animals with no residues detected in models of total concentrations.*

Model	Covariates	df	Log likelihood	AIC	Δ AIC	Weight
i) Probability of detecting ≥ 1 liver SGAR residue (n = 59)						
1	Age + δ^{15}N	3	-24.72	55.8	0.00	0.24
2	Age + δ^{15}N + land class	4	-23.76	56.2	0.39	0.20
3	Age + δ^{15}N + δ^{13}C + land class	5	-22.70	56.5	0.66	0.17
4	Age + δ^{15}N + δ^{13}C	4	-24.04	56.8	0.96	0.15
5	Age + δ^{15}N + fat score + land class	5	-23.04	57.2	1.34	0.12
6	Age + δ^{15}N + fat score	4	-24.34	57.4	1.54	0.11
ii) Number of SGARs detected (n = 59)						
1	Age + δ^{13}C + δ^{15}N	4	-85.54	179.	0.00	0.27
2	Age	2	-88.31	180.	1.01	0.16
3	Age + δ^{13}C	3	-87.24	180.	1.10	0.15
4	Age + δ^{15}N	3	-87.33	181.	1.28	0.14
5	Age + half of year + δ^{13}C	4	-86.20	181.	1.33	0.14
6	Age + half of year + δ^{13}C + δ^{15}N	5	-85.04	181.	1.40	0.13
iii) Total SGAR concentration (n = 46)						
1	Age + land class + region	7	-87.51	191.	0.00	0.33
2	Age + land class	4	-92.11	193.	1.22	0.18
3	Age + land class + δ^{13}C	5	-90.86	193.	1.25	0.18
4	Age + land class + δ^{13}C + region	8	-86.71	193.	1.34	0.17
5	Age + land class + region + fat score	8	-86.92	193.	1.75	0.14

Table 5.2b. *Standardised conditional averaged model coefficients and relative importance of variables included in top model sets (ΔAIC < 2) of variation in second generation anticoagulant rodenticide residues in polecat livers. Three measures were assessed: i) probability of detecting residues; ii) number of compounds for which rodenticides were detected; and iii) total concentrations. Parameter names with brackets show the effect of that parameter category against the reference category (half of year = first, land class = arable, region = east). Parameters highlighted in bold are those where the confidence intervals do not span zero on the model scale, indicating a consistent directional effect. Coefficient estimates, standard errors and confidence limits are presented on the model scales. Importance reflects the number of models that the parameter appears in and its importance to the averaged model.*

Parameter	Coefficient estimate	SE	2.5% CI	97.5% CI	Importance
i) Probability of detecting ≥ 1 liver SGAR residue (binomial regression, logistic scale)					
(intercept)	1.54	0.55	0.44	2.65	-
Age	2.20	1.18	-0.17	4.57	1.00 (6)
δ^{15}N	**2.53**	**0.92**	**0.68**	**4.37**	**1.00 (6)**
Land class (pastoral)	1.16	0.80	-0.43	2.76	0.50 (3)
δ^{13}C	1.10	0.88	-0.66	2.86	0.32 (2)
Fat score	-0.78	0.78	-2.34	0.78	0.24 (2)
ii) Number of SGARs detected (Poisson regression, log scale)					
(intercept)	0.46	0.13	0.20	0.73	-
Age	**0.47**	**0.17**	**0.13**	**0.81**	**1.00 (6)**
δ^{13}C	0.40	0.22	-0.05	0.84	0.70 (4)
δ^{15}N	0.36	0.22	-0.09	0.81	0.54 (3)
Half of year (second)	-0.28	0.24	-0.76	0.19	0.27 (2)
iii) Total SGAR concentration (linear regression, log scale)					
(intercept)	-1.97	0.52	-3.03	-0.92	-
Age	**1.44**	**0.56**	**0.30**	**2.57**	**1.00 (5)**
Land class (pastoral)	**-1.98**	**0.67**	**-3.33**	**-0.62**	**1.00 (5)**
Region (north)	0.29	0.97	-1.67	2.25	0.64 (3)
Region (south)	0.37	0.79	-1.22	1.97	0.64 (3)
Region (west)	**1.97**	**0.82**	**0.32**	**3.63**	**0.64 (3)**
δ^{13}C	0.74	0.55	-0.38	1.85	0.35 (2)
Fat score	0.56	0.56	-0.56	1.69	0.14 (1)

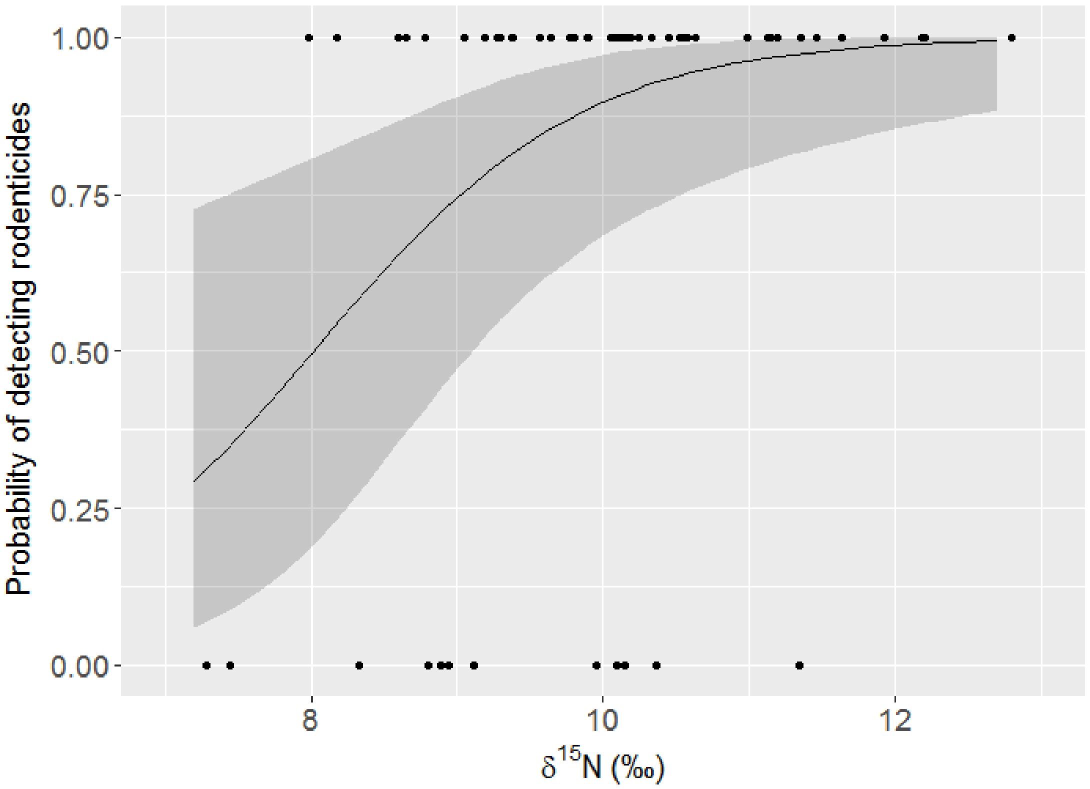

Figure 5.2. *Predictions based on output of the averaged model for the probability of detecting second generation anticoagulant rodenticide residues in polecat livers at different levels of δ^{15}N in pastoral landscapes. Polecat age, δ^{13}C and fat score are kept constant at their mean values (16.2 months, −25.54‰ and 2.6, respectively).*

Number of SGARs detected in the liver

Age, δ^{13}C, δ^{15}N and half of year were included in the top models of the number of liver SGARs detected in individuals (Table 5.2a). Age appeared in all of the top models and, in the averaged model (Table 5.2b), was positively associated with the number of compounds detected. The effects of δ^{15}N, δ^{13}C and time of year were also included in the averaged model but had no clear effect on the number of SGARs detected. Overall, the model predicted that by thirty-six months old, polecats will on average have accumulated detectable concentrations of 2.1 SGARs (95% confidence limits: 1.5–2.7) in their livers, assuming mean δ^{15}N, mean δ^{13}C and first half of year values.

Total SGAR concentrations

There were five top models for total SGAR concentrations and these contained age, land class, region, $\delta^{13}C$ and fat score as variables (Table 5.2a). Age was positively associated with total SGAR concentrations in the averaged model. Total SGAR concentrations were also significantly higher in polecats collected from arable compared with pastoral landscapes and in animals in the west compared with those in the east (Table 5.2b). There was no clear effect of $\delta^{13}C$ or fat score on total SGAR concentrations.

Comparison of exposure in polecats from 1992–9 and 2013–16

When historical limits of detection (0.027, 0.010 and 0.005 µg/g for bromadiolone, difenacoum, and brodifacoum respectively) from less sensitive analytical techniques as used in the earlier study by Shore et al. (2003) were applied to our "new data" for animals that died in 2013–16, the rates of detection in the "new data" were reduced to 40% (bromadiolone), 35% (difenacoum), 21% (brodifacoum) and 54% (any SGAR). As flocoumafen was not detected in any animals in either study and difethialone was not tested for in the 1990s, these compounds were excluded from this part of the analysis. These compare to detection rates of 12%, 22%, 3% and 31% respectively in Shore et al. (2003). The change in prevalence from 31% to 54% of polecats with one or more SGAR detected equates to an increase in the rate of detection by a factor of 1.7 between the two studies. A greater proportion of animals in the "new data" had two (24%) and three compounds (9%) than those recorded by Shore et al. (2003), who found that only 2% of polecats had liver residues of two compounds and a further 2% had detectable liver residues of three compounds.

Survey period and location appeared in all top model sets (Table 5.3a). In the averaged models of the probability of detecting SGARs residues and the number of SGARs detected, the period 2013–2016 was associated with higher rates of detection of rodenticides than the period 1992–1995 (Table 5.3b). There was also an increase in the rate of detection between the period 2013–2016 when compared to polecats collected in the period 1996–1999, but this was a smaller effect. The number of compounds detected was higher in the most recent survey period than both of the previous collection periods. Survey period did not have a consistent effect on the total concentrations of SGARs detected. Location (animals in 1990s range vs animals in areas colonised post 1990s) did not have a consistent effect in any of the averaged models.

Table 5.3a. *Summary of statistical models of variations in second generation anticoagulant rodenticide (SGAR) residues in polecat livers. Top models from analysis of i) probability of detecting residues; ii) number of rodenticides detected and iii) total concentrations using "combined" Shore et al. (2003) and new rodenticide data. AIC is Akaike's Information Criterion and ΔAIC is the difference in AIC from the best model. Only models with ΔAIC <2 are included in the top model set. Weight is the weighting given to that model when the averaged model is calculated. Sample sizes vary because of the exclusion of animals with no residues detected in models of total concentrations.*

Model rank	**Covariates**	**df**	**Log likelihood**	**AIC**	**ΔAIC**	**Weight**
i) Probability of detecting ≥ 1 liver SGAR residue (n = 168)						
1	Survey	3	-107.70	221.55	0.00	0.72
2	Survey + location	4	-107.59	223.43	1.88	0.28
ii) Number of SGARs detected (n = 168)						
1	Survey	3	-168.05	342.26	0.00	0.52
2	Survey + location	4	-167.10	342.45	0.19	0.48
iii) Total SGAR concentrations (n = 68)						
1	Null	2	-104.13	212.44	0.00	0.43
2	Location	3	-103.26	212.90	0.46	0.34
3	Survey	4	-102.53	213.69	1.25	0.23

Table 5.3b. *Standardised conditional averaged model coefficients and relative importance of variables include in top model sets (ΔAIC < 2) of variation in second generation anticoagulant rodenticide (SGAR) residues in polecat livers. Three metrics were modelled: i) probability of detecting residues; ii) number of compounds for which rodenticides were detected; and iii) total concentrations using "combined data" incorporating Shore et al. (2003). Parameter names with brackets show the effect of that parameter category against the reference category (survey = "2013–2016", location = "inside 1990s range"). Parameters highlighted in bold are those where the confidence intervals do not span zero on the model scale, indicating a consistent directional effect. Coefficient estimates, standard errors and confidence limits are presented on the model scales. Importance reflects the number of models that the parameter appears in and its importance to the averaged model.*

Parameter	Coefficient estimate	SE	2.5% CI	97.5% CI	Importance
i) Probability of detecting ≥ 1 liver SGAR residue (binomial regression, logistic scale)					
(intercept)	0.21	0.28	-0.34	0.76	-
Survey (1992 - 1995)	-1.40	0.46	-2.30	-0.50	1.00 (2)
Survey (1996 - 1999)	-0.75	0.39	-1.52	0.03	1.00 (2)
Location (outside 1990s range)	-0.23	0.49	-1.19	0.74	0.28 (1)
ii) Number of SGARs detected (Poisson regression, log scale)					
(intercept)	0.03	0.16	-0.29	0.35	-
Survey (1992 - 1995)	-1.22	0.32	-1.86	-0.59	1.00 (2)
Survey (1996 - 1999)	-0.89	0.26	-1.41	-0.38	1.00 (2)
Location (outside 1990s range)	-0.35	0.25	-0.85	0.15	0.48 (1)
iii) Total SGAR concentrations (linear regression, log scale)					
(intercept)	-1.93	0.20	-2.32	-1.54	-
Survey (1992 - 1995)	-0.49	0.40	-1.28	0.31	0.23 (1)
Survey (1996 - 1999)	-0.48	0.31	-1.09	0.13	0.23 (1)
Location (outside 1990s range)	0.41	0.31	-0.22	1.04	0.34 (1)

Discussion

The detection of SGARs in 79% of the polecats collected in the period 2013–16 was comparable with the findings of recent studies of other mustelids from elsewhere. Detection rates of ~79% were reported for American mink in Scotland (Ruiz-Suárez et al. 2016), 78% for fishers in California (Gabriel et al. 2012) and 95% for stoats and weasels in Denmark (Elmeros et al. 2011). A recent study of the exposure of polecats and stone martens *(Martes foina)* in Denmark detected SGARs in 94% and 99% of animals respectively (Elmeros et al. 2018). Similarly high prevalence of residues has been found in birds of prey in Britain, with 94% of barn owls (a generalist small mammal predator) with detectable residues of one or more SGARs (Shore et al. 2016) and 100% of a sample of 18 red kites, a scavenger that often feeds on rats, with detectable liver SGAR residues (Walker et al. 2017).

Overall, the prevalence of residues in the present study is greater than that reported for polecats that were collected in the 1990s in Britain (Shore et al. 2003). This is in part due to improvements in analytical sensitivity, but even when this methodological difference is accounted for (by applying common limits of detection), we identified an increase by a factor of 1.7 in the prevalence of SGAR residues over the 25 years from 1992 to 2016 inclusive. We found no evidence of differences in rates of detection between polecats within and beyond the limits of their 1990s range, suggesting that the increase in exposure over time has occurred throughout the polecat's current range in Britain, and has not been caused simply by expansion into areas where SGAR usage has traditionally been considered to be higher (Dawson et al. 2003, Dawson & Garthwaite 2004).

SGAR detection in polecats may have increased owing to more widespread use of SGARs and/or changes in polecat diet. There is some evidence of an increase over time in SGAR usage. In a nationwide survey of rodenticide usage, Dawson et al. (2003) found that between 1992 and 2000 the proportion of farms in Britain using SGARs changed from 74% to 89%. Furthermore, rabbit populations have declined since 1995 (Aebischer et al. 2011, Battersby 2005), which may have increased the reliance of polecats on rats and other rodents as prey. In our study, the increased prevalence of brodifacoum from 3% in Shore et al. (2003) to 35% in our most recent survey (21% using historical LODs) was particularly notable and may reflect growing resistance in rats to bromadiolone and difenacoum in England and Wales (Buckle 2013) and a consequent attempt to control resistant populations through use of brodifacoum. The proportion of American mink in Scotland recently found with liver residues of brodifacoum and flocoumafen was only 10% (Ruiz-Suárez et al, 2016) but resistance to bromadiolone and difenacoum is not widely documented in Scotland (Buckle & Prescott 2012) and so there may be less pressure to use compounds, such as brodifacoum, when there is little or no known resistance in rats.

The positive relationship between higher values of $\delta^{15}N$ and the presence of rodenticide residues (Fig. 5.2) was consistent with our hypothesis that polecats would be more likely to be exposed to SGARs due to their consumption of contaminated target prey, primarily rats, which are likely to have higher $\delta^{15}N$ signatures than herbivorous rabbits. Other studies have found that detection of SGAR residues in predators varies with available food sources (Hegdal & Blaskiewicz 1984, Tosh et al. 2011, Geduhn et al. 2016) and while it seems most likely that the elevated $\delta^{15}N$ signatures reflect polecats feeding at higher trophic level, we cannot be certain whether the sources of contamination are rats as the target species, or other non-target omnivorous rodents. Alternatively, enriched $\delta^{15}N$ signatures might distinguish polecats that had been living and feeding in landscapes exposed to anthropogenic enrichment of soil ^{15}N, perhaps associated with practices associated with agricultural intensification (Rubenstein & Hobson 2004, Crawford et al. 2008). It was notable that there was no significant relationship between $\delta^{15}N$ and total SGAR concentrations and this suggests that dietary preferences may have the greatest effect on whether exposure takes place at all, rather than influencing the magnitude of exposure. The frequency of exposure and resultant residue accumulation is likely to be driven more by patterns that influence the extent of exposure in the prey and the numbers of those prey that are eaten over time.

Age was positively related to number of SGARs detected in the liver and to total SGAR concentrations in polecats that died between 2013 and 2016. This reflects the greater time period over which older polecats can encounter and eat contaminated prey, together with the persistence of SGAR residues in liver tissues. Similar positive associations between age and exposure have been found in birds (Christensen et al. 2012, Walker et al. 2015) and mustelids (Gabriel et al. 2012, Ruiz-Suárez et al. 2016).

We found that total SGAR concentrations in the 2013–16 polecats varied with the predominant land-use in the area in which they died. Geduhn et al. (2015) found a significant difference in contamination between urban areas and areas with high livestock density. Total SGAR concentrations were higher in polecats from arable than pastoral areas, which may indicate heavier SGAR usage on arable farms. This is in line with findings from previous national rodenticide usage surveys on arable farms compared to farms growing grass and fodder (De'Ath et al. 1999, Garthwaite et al. 1999). The higher total SGAR concentrations in polecats collected in the west compared to the east was surprising, as we might have expected rodenticide usage to be higher in the east of England, where there is a greater density of arable farms (Dawson et al. 2003). However, this finding is consistent with those of Shore et al. (2003), in which bromadiolone residues were higher in polecats in Wales, Midlands and West England than in animals in the East and the South-East of England, and difenacoum residues were higher in Wales than in the East and South-East of England. We did not detect significant variation between exposure at different times of year in the polecats that died in 2013–16, contrary to the earlier polecat surveys (Shore et al. 1999, Shore et al. 2003). Thus we have no evidence that current exposure in polecats is greatest in the autumn and winter, as previously thought, and may indicate that exposure is now similar year-round.

In conclusion, we have determined that SGAR contamination in polecats in Britain is likely to be greatest in older animals that eat rodents, live in the west of the country and inhabit arable areas; these individuals may therefore be at greater risk of adverse effects. We have also demonstrated that exposure has increased in scale (proportion of animals exposed, number of residues accumulated) since the 1990s and that this increase appears to have occurred throughout the polecat's range. The implications for polecats arising from this widespread exposure to SGARs is a key question arising from this study. Diagnosis of mortality caused by rodenticides would ideally draw upon ante-mortem observations, post-mortem detection of non-trauma related haemorrhaging and quantification of liver residues (Murray 2018). Although liver concentrations >0.2 µg/g wet weight have elsewhere been considered to be potentially lethal (in barn owls; Newton et al. 1999), liver residues alone cannot be used as clear indicators of lethal poisoning, as the relationship between residue magnitude and likelihood of mortality is variable (Thomas et al. 2011). We have identified high liver SGAR residues in some polecats but most of these animals were killed on the road and the resultant trauma precluded clinical detection of any rodenticide-related haemorrhaging. It is conceivable that SGAR exposure may have contributed to their mortality, if such exposure affected the likelihood of animals being run over and/or if it exacerbated trauma. It is also possible that these animals may ultimately have succumbed to SGAR poisoning, had they not been run over. We did not find any evidence of sub-lethal effects, such as reduced kidney fat levels, in animals with detectable liver residues, which might have been expected, given that reduced body condition has been observed in other studies of secondary exposure in mustelids (Elmeros et al. 2011). Overall, whilst we have shown that the rate of detection of SGARs and the number of compounds detected per animal have both increased over time, polecats have continued to recolonise Great Britain over the same period (Birks & Kitchener 1999, Birks 2008, Croose 2016). They are now widespread in central, eastern and southern England, but are yet to re-establish themselves in parts of northern England and Scotland. Research exploring polecat survival and productivity in relation to varying degrees of exposure to SGARs would help inform our understanding of the impacts that SGARs may have on polecat populations and rates of recolonisation.

The regulatory framework concerning SGAR deployment in Britain changed in July 2016, with a relaxation of restrictions on the use of brodifacoum, flocoumafen and difethialone, but there has been a concomitant introduction of a stewardship scheme designed to promote best practice in use and thereby reduce non-target primary and secondary exposure (http://www.thinkwildlife.org/stewardship-regime/Stewardship). The effect of these regulatory changes for primary consumers of SGAR target species, such as polecats, is uncertain. The outcome could be less prolonged use of difenacoum and bromadiolone in areas where resistance in rats to these two compounds is a problem, while at the same time there may be an increase in the use of more acutely toxic, “resistance-busting” SGARs, such as brodifacoum and flocoumafen.

One of the biggest gaps in our understanding of the risk posed by SGARs to polecats and other non-target wildlife, concerns usage patterns and rodent control practices. There is a need to determine how much and how frequently SGARs are used and how usage varies between different types of landowners in different parts of the country. Contemporary research into predator diets, including fine-scale application of stable isotope approaches to predators and their prey, will also improve understanding of pathways of exposure. Exploring user practices and how these may change following the introduction of stewardship is critical to inform our understanding of the current and likely future scale of the risks presented to non-target wildlife by anticoagulant rodenticides.

Chapter 6

Keeping The Balance: gamekeeping perspectives on wildlife management in Britain

‘The Gamekeeper forms, indeed, so prominent a figure in rural life as almost to demand some biographical record of his work and ways. From the man to the territories overwhich he bears sway—the meadows, woods, and streams—and to his subjects, their furred and feathered inhabitants, is a natural transition.’

Richard Jefferies (1878) The gamekeeper at home: sketches of natural history and rural life.

Chapter 6: Keeping The Balance: gamekeeper perspectives on wildlife management in Britain

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Sainsbury KA, DeSilvey C, Crowley SL, Shore RFS, Schofield H, McDonald RA (in prep.) Keeping The Balance: gamekeeper perspectives on wildlife management in Britain.

Abstract

Gamekeepers play an influential and widespread role in countryside management in Great Britain by managing landscapes to produce game for sport shooting. As individuals and collectively as a profession, gamekeepers often frame their management approach through notions of 'keeping the balance'. The balance-of-nature is a term used in popular science and culture. In order to understand gamekeepers' conceptions of 'The Balance', we carried out 23 'go-along' interviews with gamekeepers working in a variety of landscapes across Great Britain. We found that the gamekeepers' Balance is articulated as a concept unifying habitat management, animal husbandry and predator control to mitigate pressures from predators and disease. For gamekeepers, keeping The Balance is a collection of ritualised processes and responses, with the primary goal of creating local, shootable surpluses of game, but also fulfilling wider stewardship objectives, including correction of anthropogenic perturbations, which may also stem from their own actions, in their system of nature. Their explanations of keeping The Balance uncover a complex social-ecological system of interacting anthropogenic and ecological processes, to which gamekeepers see themselves as integral and connected via the interdependencies of humans, gamebirds and predators. Ambiguity around potential multiple interpretations of The Balance and the intensity of management required to achieve it, opens up potential lines of misunderstanding between gamekeepers and other users of the term.

Introduction

In his nineteenth century account *The Gamekeeper at Home*, Jefferies (1878) describes in some detail the position held by the gamekeeper (keeper) in the workings of a rural estate, including how the keeper is connected to 'meadows, woods, and streams—and to his subjects, their furred and feathered inhabitants.' Today, keepers continue to play an influential, if sometimes controversial, role in countryside management in Great Britain. Some 60% of rural land area is managed for gamebirds that will be shot for sport in some form (Piddington 1981). This management is undertaken by 3-5000 keepers (Tapper 1992), a relatively small number compared to the 120000 keepers employed in the heyday of sport shooting in the nineteenth century (Tapper 1992).

The National Gamekeepers Organisation (NGO) was established in 1997 by gamekeepers who felt that the profession was 'threatened by public misunderstanding and poor representation' (NGO n.d., Mitchell & Manning 2014) and, according to their website, "gamekeeping helps to ensure a balanced environment with plentiful wildlife". The NGO's byline is 'Keeping the Balance', which is also the title of their magazine (Fig. 6.1), issued quarterly to some 16000 members. The Game and Wildlife Conservation Trust's[1] first published 'comprehensive' policy document is entitled 'A Question of Balance' and it emphasises the role of game preservation in conserving the countryside and all of the wildlife within it (Tapper 1999). In this context, it seems that 'the balance' is employed to mean improving the balance of opinion towards keepers and game management given public misunderstanding. A study of the motivations behind predator controls in 2016 by Swan et al. (in prep) found that keepers talked about 'balance' in terms of reducing predator numbers to what was perceived to be more natural levels of abundance. An online media search for the term 'balance' in relation to keepers uncovers a variety of interpretations:

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[1] Formerly the Game Conservancy Trust. The Game and Wildlife Conservation Trust (GWCT) is a 'UK charity conducting conservation science to enhance the British countryside for public benefit.' GWCT researches and develops game and wildlife management techniques and uses its findings to provide training and advice on 'on how best to improve the biodiversity of the countryside. www.gwct.org.uk.

balancing the needs of humans and wildlife, providing ‘a conservation balance’, restoring nature, considered decision making, providing a public service and rearranging the ‘wildlife equilibrium’ (Table 6.1). Unpacking notions of ‘balance’ therefore seem an appropriate starting point for exploring the gamekeepers’ worldview.

Figure 6.1. *The National Gamekeepers Organisation issues a quarterly members magazine called ‘Keeping the Balance’. (Source: NGO website)*

***Table 6.1**. Summary of views about gamekeepers and ‘balance’. Results from an internet search using the terms ‘gamekeeper’ and ‘balance’ on 26 June 2019. Bold is added for emphasis.*

Reference to ‘balance’	**Source**
‘**The skilled management of predators and habitat helps to maintain a balance in the countryside,** providing food for species such as golden eagles and over-winter sustenance for many species. Gamekeepers and stalkers also manage deer, using their knowledge to provide a sporting cull but also **to keep deer numbers at a level which balances sport with animal welfare** and the need to reduce grazing impacts on land and forestry.’	Scottish Gamekeepers Association (n.d.). Webpage about gamekeeping.
‘Achieving the balance between environmental stewardship and cover crop requirements needs knowledge and know-how, but when you’ve cracked the formula, you have achieved something very worthwhile.’	NGO (2014). Article about game crop management.
‘There is no doubt in my mind that if we lose our keepers our wildlife will suffer, and we will lose that broad biodiversity that our public may take for granted … **Governments and their agencies need the gamekeepers to hold the balance in our fragile communities although this is rarely acknowledged.** They have now spent millions of public money trying to eradicate mink, stoats, badgers and hedgehogs. Gamekeepers offer this service to the nation for nothing.’	Financial Times (n.d.) Letter from Alex Hogg, Chairman of Scottish Gamekeepers’ Association.
‘Always feisty and forthright in his opinions, Balharry came to realise that **the key to success in managing wild land lay in restoring the balance between grazing animals and the natural vegetation**.’	Marren (2015) Obituary about a gamekeeper in The Independent.
‘The thing is, in order to keep conditions just right for shooting game and admiring songbirds, Garrod finds that quite a lot of other animals living on the estate require shooting too … **It sounds like a delicate - not to mention messy - rearrangement of the wildlife equilibrium.** “It is," he agrees. "By controlling foxes we've now got a nice population of hares. That brings trouble because then you've got poachers and hare coursers coming in." He shrugs. "But that's the price you pay.”’	Snowdon (2008) Article about gamekeeping as a career in The Guardian.
‘Like any other use of woodland, whether recreational or economic, **the underlying objective in creating or managing woods for game is to provide an overall conservation balance which is positive**, i.e. where the wider benefits of woodland management for game to wildlife and their habitats are maximised and not outweighed by any potentially negative impacts.’	GWCT and Woodland Trust (n.d.) Publication on best practice in woodland management.
‘**Many animal populations are stable over time and have reproduction and death rates that exactly balance each other.** This happens because natural resources (e.g. food supply, nesting habitat) are limited and as these resources are used up and	Tapper (2005) Report on the benefits of gamekeeping.

Reference to ‘balance’	Source
competition for them intensifies, the mortality rate increases (density dependent mortality) and fecundity reduces (density dependent natality). **This density dependence maintains the population around a stable equilibrium level**… Game managers (gamekeepers and others) try both to enhance the productivity by providing better breeding habitat and more food, and reduce the natural mortality due to predators and disease.’	
‘If gamekeepers and others could legally control excess badgers as local circumstances required, just as they do now with foxes, badger numbers nationally would slowly return to a lower, sustainable level, **in balance with the needs of man and wildlife**.’	NGO (n.d.b) Position statement on badger management.
In this 17-minute DVD, ‘Adam - who is lost on the moors after becoming separated from his school party - meets Fred, the gamekeeper. On the way back to the minibus Fred teaches Adam about the moorland - the landscape, the wildlife it supports, the bird species which need protecting, the importance of sustainable management and **the need to maintain a natural balance**.’	National Gamekeepers Organisation (2013). Video about moorland gamekeeping.

The keepers’ ‘balance’ is evocative of the longstanding heuristic of the balance-of-nature (Egerton 1973). Ideas of an inherent natural ‘balance’ date back to antiquity (see Egerton (1973) for a full account) and have profoundly influenced Western perspectives of human relationships with nature, with the natural world seen variously as something to be exploited (White 1967), perfected (Thomas 1983), mastered (Leiss 1974) and, more recently, protected (McKibben 2010). From ancient Greece until the Reformation, discussions were primarily Christian-centric and it was believed that Providence had determined species traits to ensure a harmonious co-existence of the whole of Creation[2] (Egerton 1973). Since then, although the concept of balance has been implicit in theoretical and applied conceptions of nature for centuries, its exact meaning, and therefore the role of humans in perturbing and redirecting it, has been much debated (see Simberloff (2014) for a detailed review). By the eighteenth century, scholarly debate had moved to exploring interactions between species, rather than pre-determined traits that would keep nature in balance (Simberloff 2014). In the early twentieth century, the idea of balance became synonymous

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[2] For example, lower reproductive rates in carnivores compared to herbivores was interpreted as Divine punishment for their carnal desires (Egerton 1973).

with ideas of equilibria in natural processes as part of a whole supraorganism (e.g. Clements 1936). Nicholson (1933), one of the few scholars to attempt to precisely define the concept as opposed to exploring the processes that may enable it (Egerton 1973), described nature as a system moving around an equilibrium but never settling at it:

> ‘The balance of animal populations is similar to that of a balloon acted upon by the changing temperatures of night and day. Such a balloon rises and falls in relation to the change in temperature, for this varies the volume of the balloon and the density of the surrounding air. The balloon is continually in a state of tending towards a position of stationary balance, but continues to rise and fall because the position of stationary balance is changing all the time.’ (1933: 133)

Early animal ecologist Charles Elton (1930) rejected the balance-of-nature concept on the basis that it was precluded by irregular variabilities in population cycles among communities of species. At the same time, while developing the science of wildlife management, Aldo Leopold (1933) thought that while there may be a balance in nature, human intervention could have unforeseen consequences. Centuries of human disturbance had come to be seen as having destroyed any natural biological equilibrium that may have existed and instead a new ‘human ecological equilibrium’ would need to be sought (De La Tour 1956). Since then, whether or not such a balance exists has continued to be questioned (e.g. Ehrlich & Birch 1967) and it has been dubbed a ‘panchreston’: a broad term that oversimplifies a complex idea with the result that it means many different things to many people, and in doing so becomes redundant (Simberloff 2014). In the second half of the twentieth century ecological research turned away from equilibria to focus more on community dynamics and interactions (Wu & Loucks 1995). Ecological debates notwithstanding, concepts of balance continue to be part of popular framings of nature and of language, particularly among environmentalists and wildlife managers, where the usual application of the term implies a nature that is fragile and requires human intervention, or alternatively human abstention, to be protected (Simberloff 2014).

In this paper our objective is to explore the ‘balance’ as it is understood and realised by modern gamekeepers through their specific land and wildlife management practices. To this end, we interviewed gamekeepers from across Britain to ask them about the what and the why of how gamekeeping is done. It is not our aim to review the efficacy of their approach or assess the viability of specific game management practices, rather to arrive at an understanding of keepers’ worldviews through the general lens of keeping ‘the balance’.

Background to gamekeeping in Great Britain

In Britain, gamekeeping is a venerable profession that is steeped in tradition (Munsche 1981). Since its earliest days, when the job of the keeper was to provide game for the Royal table during Norman times (Munsche 1981, Lovegrove 2007), keepers have held a unique position in rural society. Acting as a gateway to game—a valued recreational resource and an important source of protein—from the Middle Ages onwards, the keeper was caught between the landed gentry for whom they worked and the rural classes, with whom they lived but were sometimes unpopular, due to their key responsibility of protecting game from poachers[3] (Munsche 1981, Lovegrove 2007).

By the eighteenth century, developments in artificial brood rearing[4] and the growing popularity of sport shooting lead to increases in predator controls, to maximise game returns (Munsche 1981). Today, the role of the gamekeeper broadly entails fostering young game, whether these are wild birds or are reared and released for shooting, providing food and enhancing their habitat, protecting birds, eggs, and chicks from being eaten by predators and overseeing the successful shooting of the produced game on shoot days (Bell 2015). Keepers follow an annual cycle of management, although exact timings and details vary by shoot. Predator controls are most important during the spring egg laying, incubation and hatching of wild broods and in the early lives of juvenile birds (called ‘poults’) that are released on reared game shoots. Once wild birds are able to fly, smaller ground predators like stoats *Mustela erminea* and weasels

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[3] Taking of game was not permitted without a licence by Game Laws (Munsche 1981).

[4] In which birds were fenced into enclosures, thereby creating pockets of high densities of birds that would attract predators.

M. nivalis become less of a risk, although larger predators like foxes *Vulpes Vulpes* and goshawks[5] *Accipter gentilis* continue to be a problem all year round. For reared birds, pens[6] are erected in which to release the birds and it is important that the released birds see these pens and their vicinity as a 'home' or relaxed haven where they can return each evening to roost or 'jug'[7], depending on the species. During the day, reared birds are encouraged, by regular feeding and provision of game crops[8], to make regular trips to the areas from which they will eventually be driven[9] during the shoot. In wild game shoots, there is less direct intervention with the birds and habitat management and predator controls are fundamental to a successful season (Appendix 6.3 summarises the different habitat management efforts carried out on different shoot types).

Management by gamekeepers is generally limited to areas within the boundaries of their shoot, though within larger shooting estates multiple beat keepers can be responsible for their discrete patches, or beats[10]. Underkeepers working on the same estate may assist with activities as necessary. Keepers often have permission from owners of land adjacent to the shoot to control pest species on their land, while some keepers will travel to help colleagues and friends on other shoots.

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[5] Predator controls of birds of prey are only permitted for some species under specific licenses.

[6] Pheasant pens are built in woodland, or woodland edge and may be several acres in size, including a mixture of woodland and open features (ideally 1/3 woodland, 1/3 game crop, 1/3 open. They may contain cover crops, or the crops may be adjacent to pens. The pens are in place from just before the poults are introduced to wood until the end of the shooting season and may be dismantled over the shooting hiatus and reinstated again in spring. Partridge pens are smaller, temporary structures and typically placed in arable fields. They are dismantled once the birds are mature enough to live outside of them. Pheasants are usually released at 6-8 weeks old, partridges may be 12 weeks depending on the field management system in place as they cannot be released into fields until crops have been harvested.

[7] When birds sit on the ground at night to rest.

[8] Game crops are used to provide food and cover. Typically include mixes of one or more of: maize, kale, triticale, buckwheat, fodder radish, sorghum, chicory, quinoa, red millet, millet, asparagus, elephant grass, as well as small bird, bee and wildflower mixes. Some game crop is part of HLS stewardship schemes, others are not. Used by lowland keepers (wild and reared game).

[9] The majority of gamebird shooting in Britain is 'driven'. Birds are flushed from over the line of Guns by beaters following instructions of someone, usually the head or beatkeeper, to ensure that the birds fly over the Guns at the optimum speed, height and direction. Beaters and pickers up are people who help the gamekeeper on shoot day by assisting with flushing birds (walking in a line with flags and dogs) and collecting dead and pricked (wounded) birds respectively.

[10] Game estates are divided up into areas of responsibility called 'beats' which each keeper is assigned too. Smaller shoots may just comprise one beat, others will have multiple beats with different keepers responsible for each one.

The vast majority of birds produced for shooting in Great Britain are reared pheasant *Phasianus colchicus* and red-legged partridge *Alectoris rufa*, of which 20 to 40 million birds are released[11] each year for commercial and private shoots (Madden et al. 2018)[12]. Wild red grouse *Lagopus lagopus scotica* and grey partridge *Perdix perdix*, are fostered in the wild by enhancing the productivity of wild stock. Red grouse live in upland heath and moorland and comprise approximately 12% of game shot per annum (PACEC 2006). Grey partridge, which declined dramatically in population numbers and distribution due to agricultural intensification in the twentieth century, have been subject to major conservation efforts from game shooting interests (Potts 1980, Potts & Aebischer 1995, Aebischer & Ewald 2004) and are gaining in popularity as a quarry on lowland shoots. Ducks are also shot from reared and wild stock, but are not our primary focus here. In this paper we refer to red grouse and grey partridge as 'wild' game, while pheasant and red-legged partridge are 'reared' game.

The gamekeeping profession has been associated with a number of controversies over its long history. Eighteenth and nineteenth century predator controls made a significant contribution to the catastrophic population declines in many native mammalian and avian predators, some of which (pine marten *Martes martes*, wildcat *Felis silvestris* and polecat *Mustela putorius*) were almost eliminated from Britain (Langley & Yalden 1977, Reynolds & Tapper 1996, Lovegrove 2007). At the time, predator controls by keepers were a continuation of state-sponsored culls of pest species, or 'vermin', that had been in place since the sixteenth century[13] (Lovegrove 2007). Predators were seen as inimical to game management (Reynolds & Tapper 1996) and in this historical context, keepers were considered to be doing their job (Lovegrove 2007) to keep population numbers low. The societal shift towards valuing the conservation of predators is a relatively recent phenomenon, when compared to

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[11] In lowland shoots, improvements in husbandry techniques of game birds have made rearing and releasing birds preferable to fostering wild game (Reynolds & Tapper 1996).

[12] The shift away from managing wild game towards to fostering reared game continued apace in the twentieth century. Approximately nine times as many pheasants were released in 2011 compared to 1961 (Robertson et al. 2017).

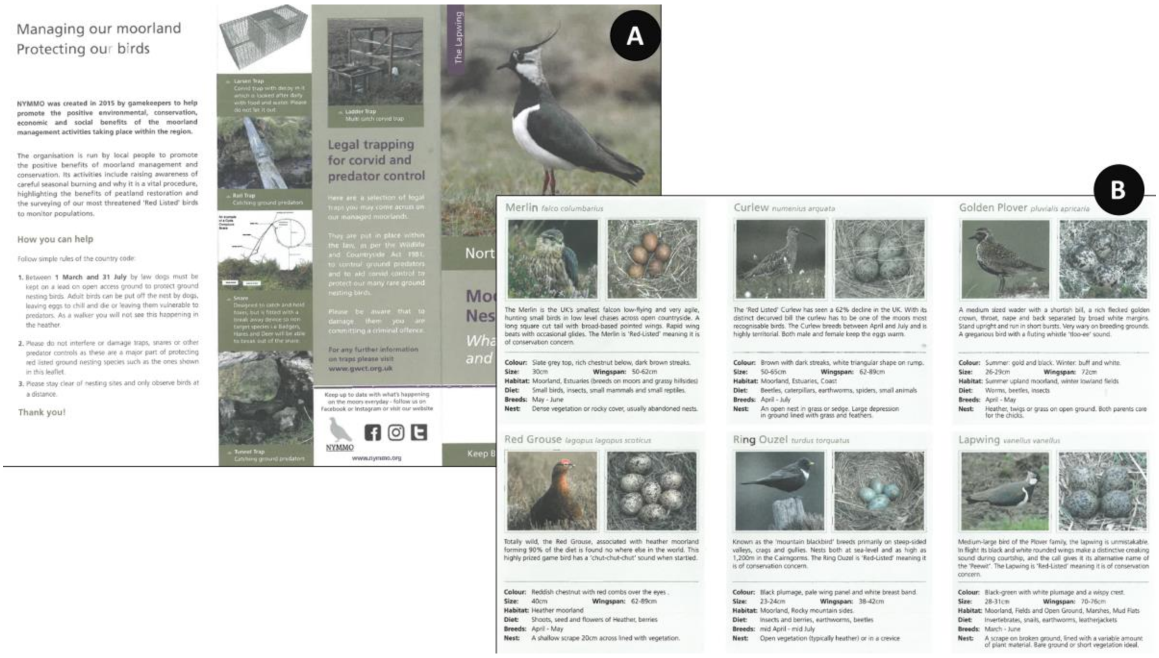
[13] The Tudor Vermyn Acts were first introduced in 1532 by Henry VIII and subsequent laws enacted by Elizabeth I in 1566 were aimed at protecting grain from pest species.

centuries of controls (Reynolds & Tapper 1996). Viewed through a twenty-first century lens, the near eradication of certain species to protect sporting interests is ethically difficult to justify, even before considering the fundamentals of shooting for sport, the ethics and social acceptability of which continue to be hotly debated topics in their own right.

Game management is associated with the ethic 'conservation through wise use', which is a belief that conservation occurs from intelligent sustainable use of natural resources achieved through appropriate human intervention (Tapper 2005). Culling predators remains central to game management (Tapper 1992), but due to a combination of legal protections and regulations stipulating the use of more discriminate and humane traps and restricting the use of some poisons, gamekeepers no longer pose the generalised threat to predator populations that they once did. Indeed, Britain's native mammalian carnivore populations are now more numerous and widely distributed than at any time in the last 150 years (Sainsbury et al. 2019). Most of the growth in numbers of native species has occurred through natural increase and spread, but in some cases, notably pine marten and otter, populations have been translocated to support the recovery process. Carnivores are literally 'being brought back into' the countryside (Wolch & Emel 1995). How gamekeepers interact with predators in keeping the balance is therefore of particular interest.

Since the introduction of legal protections, some keepers have been prosecuted for illegal killing of predators, leading to negative coverage and perceptions of the gamekeeping profession more generally (Britten 2008, North Yorkshire Police 2018, Carrell 2018). Conflict between conservation groups and shooting interests over management of hen harrier *Circus cyaneus* predation of red grouse has become one of the most intractable human-wildlife conflicts in Britain (e.g. Sotherton et al. 2009, Redpath et al. 2010). At the same time, the gamekeeping profession is keen to promote understanding of the positive benefits of their countryside management (Fig. 6.2). Studies comparing the effects of keepered versus unkeepered land show the benefits of keepered land for biodiversity (Tapper 2005). This includes, for example, the preservation of heather moorland, a globally rare habitat (Thompson et al. 1995), elevated wading bird abundance on grouse moors (Tharme et al. 2001), improved plant and butterfly diversity in woodlands (Ludolf et al. 1984, Clarke & Robertson

1993) and increased abundance of overwintering birds in game crops compared to arable fields (Parish & Sotherton 2004). At a national scale, the evidence for the benefits of game management are less conclusive, as this incorporates areas that are also managed for biodiversity conservation (Mustin et al. 2011).



Managing our moorland
Protecting our birds

NYMMO was created in 2015 by gamekeepers to help promote the positive environmental, conservation, economic and social benefits of the moorland management activities taking place within the region.

The organisation is run by local people to promote the positive benefits of moorland management and conservation. Its activities include raising awareness of careful seasonal burning and why it is a vital procedure, highlighting the benefits of peatland restoration and the surveying of our most threatened 'Red Listed' birds to monitor populations.

How you can help

Follow simple rules of the country code:

1. Between **1 March and 31 July** by law dogs must be kept on a lead on open access ground to protect ground nesting birds. Adult birds can be put off the nest by dogs, leaving eggs to chill and die or leaving them vulnerable to predators. As a walker you will not see this happening in the heather.
2. Please do not interfere or damage traps, snares or other predator controls as these are a major part of protecting red listed ground nesting species such as the ones shown in this leaflet.
3. Please stay clear of nesting sites and only observe birds at a distance.

Thank you!

Larsen Trap
Corvid trap with decoy in it which is looked after daily with food and water. Please do not let it out

Rail Trap
Catching ground predators

Snare
Designed to catch and hold foxes, but is fitted with a break away device so non target species i.e Badgers, Hares and Deer will be able to break out of the snare

Tunnel Trap
Catching ground predators

Ladder Trap
Multi catch corvid trap

Legal trapping for corvid and predator control

Here are a selection of legal traps you may come across on our managed moorlands.

They are put in place within the law, as per the Wildlife and Countryside Act 1981, to control ground predators and to aid corvid control to protect our many rare ground nesting birds.

Please be aware that to damage them you are committing a criminal offence.

For any further information on traps please visit www.gwct.org.uk

Keep up to date with what's happening on the moors everyday - follow us on Facebook or Instagram or visit our website

NYMMO
www.nymmo.org

Merlin *falco columbarius*

The Merlin is the UK's smallest falcon low-flying and very agile, hunting small birds in low level chases across open countryside. A long square cut tail with broad-based pointed wings. Rapid wing beats with occasional glides. The Merlin is 'Red-Listed' meaning it is of conservation concern.

Colour: Slate grey top, rich chestnut below, dark brown streaks.
Size: 30cm **Wingspan:** 50-62cm
Habitat: Moorland, Estuaries (breeds on moors and grassy hillsides)
Diet: Small birds, insects, small mammals and small reptiles.
Breeds: May - June
Nest: Dense vegetation or rocky cover, usually abandoned nests.

Curlew *numenius arquata*

The 'Red Listed' Curlew has seen a 62% decline in the UK. With its distinct decurved bill the curlew has to be one of the moors most recognisable birds. The Curlew breeds between April and July and is highly territorial. Both male and female keep the eggs warm.

Colour: Brown with dark streaks, white triangular shape on rump.
Size: 50-65cm **Wingspan:** 62-89cm
Habitat: Moorland, Estuaries, Coast
Diet: Beetles, caterpillars, earthworms, spiders, small animals
Breeds: April - July
Nest: An open nest in grass or sedge. Large depression in ground lined with grass and feathers.

Golden Plover *pluvialis apricaria*

A medium sized wader with a shortish bill, a rich flecked golden crown, throat, nape and back separated by broad white margins. Stand upright and run in short bursts. Very wary on breeding grounds. A gregarious bird with a fluting whistle 'tloo-ee' sound.

Colour: Summer: gold and black. Winter: buff and white.
Size: 26-29cm **Wingspan:** 72cm
Habitat: Summer upland moorland, winter lowland fields
Diet: Worms, beetles, insects
Breeds: April - May
Nest: Heather, twigs or grass on open ground. Both parents care for the chicks.

Red Grouse *lagopus lagopus scoticus*

Totally wild, the Red Grouse, associated with heather moorland forming 90% of the diet is found no where else in the world. This highly prized game bird has a 'chut-chut-chut' sound when startled.

Colour: Reddish chestnut with red combs over the eyes .
Size: 40cm **Wingspan:** 62-89cm
Habitat: Heather moorland
Diet: Shoots, seed and flowers of Heather, berries
Breeds: April - May
Nest: A shallow scrape 20cm across lined with vegetation.

Ring Ouzel *turdus torquatus*

Known as the 'mountain blackbird' breeds primarily on steep-sided valleys, crags and gullies. Nests both at sea-level and as high as 1,200m in the Cairngorms. The Ring Ouzel is 'Red-Listed' meaning it is of conservation concern.

Colour: Black plumage, pale wing panel and white breast band.
Size: 23-24cm **Wingspan:** 38-42cm
Habitat: Moorland, Rocky mountain sides.
Diet: Insects and berries, earthworms, beetles
Breeds: mid April - mid July
Nest: Open vegetation (typically heather) or in a crevice

Lapwing *vanellus vanellus*

Medium-large bird of the Plover family, the lapwing is unmistakable. In flight its black and white rounded wings make a distinctive creaking sound during courtship, and the call gives it its alternative name of the 'Peewit'. The Lapwing is 'Red-Listed' meaning it is of conservation concern.

Colour: Black-green with white plumage and a wispy crest.
Size: 28-31cm **Wingspan:** 70-76cm
Habitat: Moorland, Fields and Open Ground, Marshes, Mud Flats
Diet: Invertebrates, snails, earthworms, leatherjackets
Breeds: March - June
Nest: A scrape on broken ground, lined with a variable amount of plant material. Bare ground or short vegetation ideal.

Figure 6.2. *Trifold educational leaflet created by the North Yorkshire Moors Moorland Organisation (NYMMO) entitled 'Moorland nesting season: what you need to know and how you can help'. The outside cover (A) provides information about the organisation, predator controls and public responsibility. The interior (B) contains information about ground nesting birds on the moor.*

Here, we examine how keepers practice countryside management in order to maintain what they see as an important balance between sustainable use of natural resources and conservation of wildlife. We consider how keepers maintain a balance through gamebird, predator and habitat management. We conclude by highlighting how the keepers' balance may differ from other popular conceptualisations of the natural world, and the implications of this for social conflict surrounding wildlife management.

Methods

In the course of this research, the first author carried out twenty-three semi-structured interviews with gamekeepers from across Great Britain[14]. Six keepers mainly produced red grouse or grey partridge[15] and the remainder produced primarily reared game[16]. Most interviews were conducted at the keeper's home and while walking or driving around their beat. Conducting interviews *in situ* enabled keepers to talk about what they do in relation to features of the estate and explain or demonstrate the use of objects relating to their daily work. The researcher was able to observe the keeper interacting with gamebirds and carrying out other day-to-day activities on their rounds. The observations made during 'go-along' interviews provide a richer contextual understanding of keeper perspectives and practices (Carpiano 2009). Interview questions focused on finding out what gamekeepers do at different times of year and why, but the semi-structured format enabled simultaneous exploration of broader themes and concerns (Appendix 6.1 provides an example interview guide).

All interviews were carried out between April and August 2018. This timing enabled the researcher to observe keeper activity and the situation of estates through the early life of reared and wild birds. The breadth of participation was maximised by having a broad base (n=9) of starting interviewees, who were identified from a diverse range of informants with varied perspectives, including members of gamekeeper and conservation organisations, academics, and attendees of a county fayre and a shooting event. Thereafter a snowball approach to identifying more interviewees was employed, through which participating keepers assisted with the recruitment of others. All participants provided written consent to participate in the study (Appendix 6.2 contains a sample consent form). All interviews were anonymised and here participants

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[14] Keepers interviewed were based at shoots in the counties of Cornwall, County Durham, Devon, Dorset, Hampshire, Powys, West Sussex, Wiltshire, Gloucestershire, Herefordshire, Hertfordshire and Yorkshire. Four keepers had also worked in Scotland.

[15] Some wild game shoots also produced pheasants and / or red-legged partridge, but wild game was the main focus of the shoot.

[16] Some keepers were also involved in producing wild grey partridge on their shoots as part of a conservation initiative.

are referred to by pseudonyms to protect their anonymity. All but two interviews were audio recorded in their entirety and transcribed. When permission to record was not given, detailed notes were taken, and written up as soon as possible after the event. Exploratory analysis of transcripts using NVIVO (Version 12) identified and developed themes for discussion, including balance, the balance of nature, habitat management, bird husbandry, predator management and how gamekeepers felt about gamebirds, predator species and other prey species. More participants were interviewed until no new themes were identified and therefore theoretical saturation was reached.

Results

The keepers' Balance

Almost without exception keepers volunteered unprompted to speak of their role in maintaining 'the balance'. As it quickly became clear that the keepers' use of 'the balance' was as a way of collectively organising multiple related narratives and experiences, from here on we refer to the keepers' balance as The Balance. As Harry articulated:

> 'That's what keepers do. They're there to keep the balance.'

Keeping The Balance is based on an assumption that there is a cause and effect within nature, that 'as one thing goes up, something has to go down' (Michael). A keeper of wild game (Alan), explained that the role of a keeper is to prevent prey populations from cycling downwards. The combination of habitat management and predator controls allowed him to manage The Balance:

> 'You're keeping it in balance. And that's what you get on a game keepered or a managed shoot… You've always to look after the environment, get the prey species fairly abundant and never let the predators get to the point where they make the prey species go down or get to the point where they then have to start coming down. And that's keeping a balance.' (Alan)

The Balance is not limited to the interactions between predators and gamebirds, but also includes the wider connections between potential prey and predators in the ecosystem. Killing too many pest species, such as rabbits, may cause predators, like stoats and weasels, to 'kill loads of little chicks and have a massive knock on effect on everything. Wagtails, pied flycatchers, bullfinches, everything that's endangered they'll just keep hammering it as well' (Luke)[17].

The Balance is more than a hypothetical concept, it is a guiding principle for a way of being. Ideas of 'a balance' or being 'balanced' flowed through the everyday language that keepers used to explain decisions about time and resource management. For example, Harry said, when talking about managing their personal life with work, 'I just know how to balance things'.

Keeping The Balance presumes that a long history of intervention by humans in the British countryside has created a dependency on continued management, without which 'opportunists' (i.e. predators) would overtake 'underdogs' (i.e. ground nesting birds). The keeper's intervention is therefore required to control the nature under their auspices. Without management, the system would 'get out of control' (Dean) as 'the wildlife doesn't manage itself' (Harry). In this way, the management of The Balance is presented as a moral duty to be corrected, as humans have 'made a such a rickets' (Dougal) of the countryside and it is the keeper's role to redress the imbalance that has been created as a result.

If The Balance isn't kept, opportunistic predators in a human-dominated environment may decimate prey numbers:

> 'I've seen areas which haven't been keepered and nothing's fed and there's nothing there. Because the vermin of life are opportunists… there has to be a balance.' (Nigel)

In this context, keeping The Balance is justified on the basis of a need to address inequalities between species, which are judged as more or less able to capitalise on human practices:

> 'You hear … "Let nature do it." …But you're not letting nature do it if nature's living off dustbins, roadkill, farming activity and any other human

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[17] In ecology, this phenomenon is known as 'hyperpredation' (e.g. Blanco-Aguiar 2012).

> activity that keeps the predator species in abundance and never letting the prey species ever come into fruition.' (Alan)

Each keeper is principally concerned with The Balance in their locality:

> 'I've got no interest in foxes over there. Whereas a lot of people would be like "fucking hell, do this, do that." If it's over there, it's over there. Until it crosses the boundary across the road I've got no interest in it.' (Luke)

While keepers might limit most of their activity to the areas directly relevant to them, wild animals didn't adhere to these defined areas. Wild animals were described as being free to move into areas being 'balanced'. This freedom of movement perpetuated the need to maintain The Balance, otherwise reductions in predators through controls would be sustained:

> 'If we were having an impact on the population you'd have nothing, nothing, nothing and then up again... Because we're killing a regular amount of stoats ... they're coming from somewhere, breeding from somewhere. We haven't wiped them out. Kept them low enough that the prey species thrive and then obviously we take our share of the prey species like the grouse.' (Alan)

Additionally, the focal areas prioritised by the keepers were fluid and subject to change as the layout and size of rearing areas, pens and drives evolved with the shoot itself. Where the footprint of shooting activity on an estate had grown, the space available for predators to roam unchallenged declined with the inevitable consequence of increasing the likelihood of interactions between keepers and predators:

> 'Over the years the pens have got bigger, there's more pheasants going in and now unfortunately if the fox wants to go in that wood, he's got to be in my pen. And so I've created a problem for myself. Because the pen is so big he comes to it, looks that way 100 yards, looks that way 100 yards and he's got to dig in, jump over, or go through the fox gate… I do get a little bit of problems from that. It's par for the course.' (Leslie)

The very fact that to achieve The Balance requires human intervention indicates that is not a 'natural' state, rather something that is humanmade:

> ‘Some people say there’s a balance in nature. There is a balance in nature. Some things have to be balanced by humans to keep that balance in nature.’ (Jesse)

It cannot therefore constitute *the* balance-of-nature, rather is *a* balance-of-nature:

> ‘If they [keepers] are naïve enough to think they’re trying to maintain some sort of natural balance… they’re maintaining an unnatural balance, but a different sort of unnatural balance to what there would be if they weren’t out there doing it.’ (John)

This, then, begs the question: what exactly is the balance that is being kept?

> ‘I am trying to seasonally reduce the population of this, that and the other at the time of year when they are going to impact on what I am trying to achieve. So I am taking effectively a sustainable harvest out of them to produce a larger sustainable harvest of the game.’ (John)

Thus what the right balance is depends on what comprises a sustainable harvest of game. Setting the desired shootable surplus is subject to local differences and, ultimately, commercial and / or private goals as sufficient game surplus for one individual or estate may be insufficient to meet the needs of another. It also means that the management required to keep The Balance locally will differ by shoot type, with a clear distinction between wild and reared game shoots, as Michael, a gamekeeper on a reared-bird shoot explained:

> ‘There are many sorts of keepers though. We are a shoot that rears and releases pheasants. The grey partridge keepers and grouse keepers, totally different because they’re reliant on wild birds. So the only thing they can do is protect their stock by traps or that sort of thing and manage the habitat.’ (Michael)

As reared keepers can ‘top up’ their stock there was more value in their focussing on fox control than spending time setting and checking spring traps set for smaller predators, when it was just easier to ‘let him [the stoat or weasel] have the pheasant’ (Michael). Whereas for wild game, there wasn’t that option:

‘if you didn’t do it, you wouldn’t have any.’ (Ali). This creates an imperative to try to minimise losses, as any losses are irreplaceable:

> ‘you only get one shot at it. You can’t release a handful more to compensate for the litter of cubs, something scoffing a few. What you have has to produce. And you have to keep the vermin off its back and make sure it is there to produce’ (Mark).

Mark, a wild gamekeeper, estimated that 90% of his time was spent on predator control. Most keepers did not pursue carnivores all year round; keeping The Balance needs the greatest intervention during egg production in the spring, or when the juvenile birds are most vulnerable after they’ve been released, whereas others disagreed with this approach as they were concerned that predators would recovery over the rest of the year.

This means that The Balance is variable in relation to the status of the extractable resource, game, and subject to individual differences in management approach. In addition, many keepers spoke about The Balance as something that applied more broadly to the management of nature:

> ‘I think everything should be balanced. If there’s too much of one thing they need getting rid of and not enough of another thing they need protecting. Everything needs keeping in balance.’ (Leslie)

The Balance was tied to keeper experiences, knowledge and perceptions of nature. Having too many predators in particular was perceived as unnatural:

> ‘I don’t think at the moment that things are particularly in balance … There’s different rules and regulations that say what you can and can’t do. Like the red kite population. Lovely to see, don’t get me wrong. But where you’ve got hundreds of them, that’s not natural. So it should be balanced, I feel… I’m very much we want a little bit of everything. Not a great load of pheasants or a great load of red kites. We want everything balanced … And if I can create that, I’d love it.’ (Leslie)

In this broader view of The Balance, it is not the existence of predators that is problematic *per se*, but their abundance. Some keepers spoke of achieving personal wildlife management aspirations in terms of maintaining numbers of rare birds, which included raptors such as merlins *Falco columbarius* and hen harrier. When arriving at one keeper's residence, four juvenile buzzards were perched on fence posts in the field opposite. The keeper remarked on how he enjoyed watching them through the early summer. The level at which a predator becomes too abundant was informed by keepers' past experiences as to how many they might expect to see at different times of year. This is similar to the findings of Swan et al. (in prep.), where keepers judged the amount of management intervention necessary based on perceived population trends.

Gamebirds in The Balance

In general, gamebirds were conceptualised by keepers as 'stock', 'crop' and a 'harvest' and, after providing sporting entertainment, their ultimate utility was to become part of the food chain (without which keepers said they would find it hard to justify the scale of shooting). Paul was not alone in comparing keepers of reared birds to 'livestock farmers':

> 'They rear their birds. Their animals for slaughter. For the food chain. It is exactly what we do. ... It's the same end product… When it's loaded on a trailer and taken and killed, or pushed out a bit of game cover and killed. It's same thing.'

Some keepers spoke of 'loving their stock' as a collective, while others volunteered stories of recognising and looking forward to seeing individual birds:

> 'You get attached to pheasants. I expect all the keepers have told you that. I've put one in feed bins before now. Put him in the bin so's it doesn't get shot [during the shoot]… and then got him out at the end of the day.' (Murray)

Here keepers differed from livestock farmers. A study of poultry farmers in Europe by Bock et al. (2007) found that, in the main, poultry farmers did not have an emotional attachment to their birds as individuals but connected with the flock.

Keepers spend considerable time with their birds to monitor their health and general wellbeing, watching them 'play', seeing 'how they're feeling' and if they're 'happy' or 'mopey' (Jesse). On the keepers' rounds, we spent time sitting quietly and observing the birds and their behaviour. We listened to cock birds alarm calling and waited to observe the cause: in one case it was a fox, in another a goshawk. We crept up to grey partridge hens on the nest to check on their wellbeing, careful not to leave flattened vegetation for predators to follow. We watched red grouse hens leading their broods across tracks in the moor and counted the brood sizes. We stopped at wet mud patches to look for signs of predator tracks. We watched for corvids 'egging'[18] along beetle banks and hedgerows. We picked up any dead birds that had been predated upon and looked for signs of what animal or bird might have killed it. When we found a dead sheep, the keeper touched its eyes to approximate how recently it had died before calling the farmer. When we smelled a fox, the keeper explained how he would go about setting snares in the vicinity that evening. We checked Larson traps to make sure that call birds were watered and fed and several keepers explained how they take steps to prevent corvids from eating feed out of feed drums, or hoppers, in order to prevent disease transfer. Good husbandry was described as very important to mitigate diseases and prevent birds pecking one another, both a major source of mortality. One keeper picked up numerous dead birds that had died from disease, although he had been treating them. Though saying little, the keeper's dismay as we found each corpse was evident in his body language. We cleaned water drinkers and made sure that watering systems functioned. We topped up feed hoppers and hand fed birds to a whistle, watching as the birds strode into the release pen from some distance away in response to the keeper's call. Collectively, these experiences demonstrate just how intimately and corporeally keepers are involved in the day-to-day practice of protecting and caring for their birds.

Another way that gamekeeping differs to livestock farming is that 'wildness' is unlikely to be considered a desirable attribute in most domestic livestock (indeed docility is often a defining characteristic of domesticated species (Price 1984)). Unlike gamebirds, there is no point in the lifecycle of domestic poultry at

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[18] Hunting for birds on nests.

which demonstrating wildness is required. In contrast, to provide 'good sport' on a shoot day, reared birds must be raised to be as wild as possible:

> 'It's knowing that your bird that's coming, it's not wild but it's as close to that as reared keepers can get... It's all a little bit false. We get birds, we put 'em into a wood in a pen. But as soon as they go to wood fully winged, fully beaked they are wild, they can go where they like. It's up to us to keep 'em there.' (Paul)

Realising this wildness in the reared birds was a source of pride for Leslie:

> 'I get quite a thrill to think that a little bird like that, I can get him up to adult and he's totally self-sufficient and can survive in the wild without me.'

It is therefore expected that the birds will show a degree of autonomy and it is up to the keepers to 'keep them'. The gamebirds go where they want to go, some turning up miles away from their original point of release, others migrating to the neighbouring shoot. Some keepers spend hours every day 'dogging in' - rounding the birds up with dogs and shepherding them back to drives. Walking and exercise leads to strong, healthy birds. Mostly, however, birds wander during the day and return 'home' at feeding times: 'as long as they've got food and water and they're safe from predators they'll be here' (Luke). The requirement to foster wildness, the birds' natural inclination to roam, and the importance of minimising the threats from other birds and disease caused by keeping too many birds in close proximity to one another, means that the birds cannot be completely shut away and protected from predators.

Habitat management in The Balance

While raising gamebirds is a keepers' primary role, managing the 'environment'—or habitat—is the foundation of keeping The Balance:

> 'I've got to create the environment in which the pheasants and partridges can successfully complete their whole life cycle. So I've got to have the right basic environment for them. I've got to have a food source … And I've got to have reasonable freedom from being eaten by something else.' (John)

Habitat provides cover from predators and inclement weather, gives natural forage for the different life stages of birds and ensures sufficient birds can be held[19] on the estate to provide for the desired number of shoot days. The exact habitat management activities carried out differ between shoot types and the richness of the environment provided varies across the landscape of the estate, but the underlying principles are the same (Appendix 6.3). In the uplands, Alan explains that a healthy environment is the foundation for everything on the moor:

> ‘You know the heather's more important than the grouse. The grouse are only a barometer for the health of the moor. The key thing you want is healthy land. Healthy environment and, if that's right, everything else comes round.’

In the lowlands, keepers were keen to talk of the change in emphasis towards habitat enrichment over the preceding decades, which has become necessary as the number of birds released has increased (Mitchell & Manning 2014).

> ‘People are changing… Somebody’s turned around and gone, “We put down ten thousand pheasants, we only shoot a thousand. Where’s the other nine [thousand]?” They’ve wandered off because they don’t want to stay there. All that wood there, it’s drafty, it’s cold. Where you’ve got your bit of game crop … the wind blows. So, if we thicken the hedge up, if we planted a nice bit of kale on one side to stop the wind and a bit of maize so they can feed. Do you know, we’d shoot more pheasants?’ (Michael)

As a result, a significant amount of effort goes into drilling, spraying and maintaining large quantities of game or cover crops for pheasants and partridges (both red-legged and grey). As an example, Leslie runs a lowland shoot over 5500 acres of mixed farmland, in which he plants 35 acres of maize and 150-170 acres of mixed game crops. Larger estates plant crops that flower and seed at different times so there is always cover and additional forage available. Most lowland estates provided food all year round. The provision of,

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[19] Holding the birds involves keeping them near the woods and drives that are designated to them for the purpose of shooting.

and investment in, habitat and food provide a bottom-up improvement that cascades through the whole food chain:

> ‘People really do underestimate the whole food chain and ecosystem and all the rest of it. … if you can … reinstate the habitat for the insects …, it’s funny how everything further up the food chain does well as well.’ (Ali)

Several keepers demonstrated the invertebrate counts that they carry out regularly. They walked through wild seed crops sweeping with a large net to collect insects, estimating the amount of natural food available for birds to eat and providing an indication of the health of the environment. When visiting the estates, the wider benefits of the game crops and field margins were very visible, even to the inexpert eye. Summer flowering species provided an oasis for invertebrates, vibrating with bees and teeming with a variety of butterflies. Merlin, curlew *Numenius arquata*, lapwing *Vanellus vanellus,* skylark *Alauda arvensis* and brown hare *Lepus europaeus* were observed while carrying out interviews, as well as raptors such as buzzard *Buteo buteo,* red kite *Milvus milvus,* peregrine *Falco peregrinus* and goshawk.

The “Catch-22” for keepers is that their environmental enrichment for game birds also creates a ‘honeypot’ for carnivores, which is undesirable, as carnivores move in to take ‘advantage of the food source that we create’ (Daryl). This then distorts The Balance. Many keepers spoke of the inevitability of this (‘you set the table, everyone’ll come’: Mark) and, while they may take action to curb predation, they did not ‘begrudge’ or ‘blame’ predators for taking advantage of the benefits of ‘increased management’. As Dean described:

> ‘We're only getting nailed more because we have more. It’s the point I'm trying to make to the boss. … The more we have, the more we are going to get punished.’

Predators in The Balance

The increased forage and richer habitat in keepered areas may present an opportunity for predators, but this can be accompanied by increased mortality risk as keepers take steps to counter predation. Modern predator controls applied by gamekeepers comprise a mixture of lethal and non-lethal methods

(Appendix 6.4). Where lethal control of a species is prohibited, the lack of ability to control them is a source of frustration, but also leads to creative solutions.

This raises an interesting question about source-sink[20] dynamics for predators on and around game estates. The high reproductive rate and mobility of small ground predators like stoat and weasels have enabled them to persist in areas managed for game throughout periods of intensive controls (McDonald et al. 2002), in line with Pulliam's (1988) hypothesis that 'active dispersal from source habitats can maintain large sink populations and that such dispersal may be evolutionary stable'. The revival of fox, stoat and weasel numbers each year (based on the regularity of numbers killed) indicates to keepers that these animals are 'survivors' and will always be there. As Paul said, 'we've always got foxes, always will have'. The difficulty for slower-to-breed carnivores like the polecat[21] is that gamekeepers may create an ecological trap[22] (Robertson & Hutto 2006) where the risk of mortality outweighs any increase in productivity afforded by provision of high-quality habitat on the shoot. Over time this might lead to a reduction in numbers at the landscape scale. Harry, who runs a large lowland shoot, recounted how buzzards and red kites can starve when shooting has finished:

> 'We are absolutely overrun by buzzards and kites, there is hundreds and hundreds… if there is any [shot] game that hasn't been found, which is very minimal, the buzzards and kites will clear that up. So we are a massive food source for them. Massive. Once the season finishes and we stop shooting and - I've spoken to people from the nature reserve and the RSPB[23] who work just alongside us - … buzzards and kites starve to death because their food source has been taken away.'

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[20] Source areas are where reproductive potential is high and 'sink' areas are where mortality rates outweigh reproductive potential (Pulliam 1988).

[21] It is legal to shoot polecats but not legal to catch them in traps without a licence under the Wildlife and Countryside Act (1981). However, polecats can be and are accidentally caught in traps set for stoats and weasels (Packer & Birks 1999).

[22] An ecological trap is when an animal 'settles preferentially in a habitat where it then does poorly relative to other available habitats' (Robertson & Hutto 2006). Lapwings are an example of this, as they nest in arable fields where nests are more likely to be destroyed by ploughing (Galbraith 1989).

[23] Royal Society for the Protection of Birds.

It is self-evident that keepers 'don't want' predators because they reduce the shootable surplus of game (see also Sage et al. 2018), or in the words of Dean:

> 'Every time that you've seen a fox it's alive. Every day it's alive it's eating something to stay alive and that's going to be your partridges.'

All keepers had lost birds to foxes. Of all the ground predators, foxes, or 'Charlie', were seen as the worst killers for all types of shoots, particularly in the spring and summer when there were cubs. This is because 'instead of feeding their mouth, they have five mouths to feed' (Luke). Foxes on wild game shoots can 'wipe out a drive' in a period of weeks (Alan). Dean recounted what would happen if they became aware of fox cubs on their beat:

> 'You'd have dinner at home with the kids, keep your boots on. In, out, "see you in a bit". I'd drop everything for cubs. Because they're just causing so much damage all the time. All the time they [adult foxes] are feeding young, they're feeding hard. They're killing everything as quick as they can to get back. More, more, more, more.'

Predation is not just one or two birds being taken at a time. Every keeper had experienced some kind of mass kill event where a predator had killed tens or hundreds of birds in one go without eating them; mostly these were carried out by fox or badger. Foxes were described as experiencing a 'red mist' or 'kill[ing] for pleasure and 'go[ing] mental' in a pheasant pen. These 'surplus killing' events have long been described in carnivores in general and foxes, in particular[24] (Kruuk 1972). It is perhaps not surprising, then, that some gamekeepers characterised foxes as 'hellbent killer[s]'. Conversely, polecats were described as 'lazy killers' who 'don't do us much damage' (Daryl). Daryl explained a polecat mass kill that he experienced on the rearing field:

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[24] The carnivore biologist Hans Kruuk describes one such a scene that he personally observed in a seabird colony at night: 'Foxes might merely walk through the colony and stumble on to a sitting bird, grab and kill it, or they might take a bird after a short stalk and run. After grabbing and shaking the victim, it was then dropped and abandoned, sometimes not even properly killed...' (Kruuk 1972: 235).

> 'I think as a killer they kill two or three what they want to eat and that's about it. I think even when they killed 40 odd [birds] in a pen, I was a bit of a realist. 20 of those had smothered themselves in panic.'

'Foxes happily travel 3-4-5 miles in a night' (Dougal) and give keepers 'a fair run around' (Geoff). Predators 'especially the foxes' are often represented by keepers as 'sly' and 'clever', not to be underestimated. This is evidenced through the fact that foxes may learn to avoid being hunted using lamps[25], jump over or go around traps and snares and may also use keepers to track prey, for example, by following paths through trodden vegetation to nests that are being monitored. Geoff provided a vivid account of the persistence of a fox:

> 'Last year when my birds was in the pen, I come down that track … and poults were coming out of the bit of the wood on the left. Flying in, hitting the side of the pen and running out. I was like "something's not right, there's something in there". I just sat there quietly and I had the rifle in the truck ... a fox come out of there across to the pen. … there was a lower bit under the electric fence. He dipped under that and was walking between the electric fence and the pen following the poults. I said "oi, what are you doing?" and he lifted up his head and I sent him back to his maker. So you've got to give him some respect for that. I got the electric fence tester out of the glove box and put it on there. It's sitting at 8000 volts ... You can't underestimate them.'

As a result of their persistence, foxes are held 'in awe', given 'respect' as something for the keeper to 'outwit', creating a competition between human and animal in terms of who will best who. Some keepers match the persistence of foxes with their own efforts in order to do a good job:

> 'I was obsessed to be honest. Probably unhealthily obsessed. I'm not so much like that now. But you just want to be the best. Want to produce the best.' (Dean)

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[25] Hunting at night with lamps involves locating foxes (or other ground predators) at night with a bright lamp and then shooting them based on the location of the eyeshine. Has been replaced to a certain extent by night vision or thermal sensors.

The effect of predators on game estates is greater than just the number of birds they may kill in a season. As Leslie explains, ‘it’s not so much what they kill, it’s the disturbance.’ The very presence of a predator (including domestic dogs or humans) can ‘drive them away’. Nigel explained pheasants’ response to foxes:

> ‘If you’ve got a wood and a fox walks that wood every day, slowly those pheasants won’t go in there because they know that’s danger so they’re not daft, they’ll stay in a different wood.’

Disturbance was a primary concern expressed about the return of pine martens by Daryl, a keeper who used to work around them in Scotland:

> ‘The biggest problem with pine martens was early ... late autumn early winter … They’ll move into a wood. Because they hunt in the trees at night the pheasants just move out. They won’t stay there. So you didn’t actually lose your pheasants but you’d end up with a drive that you couldn’t shoot. They’ve moved to another drive. Which like with us, we shoot 4 days a week. We have 16 drives. If you lose a drive all of a sudden, you’re in trouble.’

This anecdote highlights a number of interesting points. Firstly, we see the ‘transgression’ of the pine marten, ‘moving in’ to the pheasants’ ‘home’ at a certain time of year. Next we see the pheasants – usually described as ‘homely’ – ‘moving out’ or ‘resisting’ the keeper’s desire for them to stay in a wood or on a drive. The wholesale departure of birds from a drive is the worst outcome for keepers. We also see the keeper express commercial concern about the impact of predators (which we return to below). This keeper represents the birds as effectively ‘evading human attempts to place them in space’ (Philo & Wilbert 2000: 14) as a functional response to the threat of being hunted, whether by predator or by humans, is played out in the landscape. Adjusting spatial and temporal use of a landscape in response to predation pressure, also known as a ‘landscape of fear’, has been observed in other wild animals (Laundré et al. 2001). Interestingly, though, reared gamebirds in particular are presented by keepers as behaving in this way; this was reinforced by observation. We arrived at one pen and all the birds were hiding away – none in sight and not a noise to be heard. As we went into the pen, you could see the poults were all hiding, jugging low down under the shelter of the ground cover provided. The keeper explained that this is usually what he will find when a bird of prey has recently flown over the pen. In a few cases keepers spoke of making use of the landscape of fear via birds of prey:

> ‘The buzzards and kites I just use to my advantage. Like I have to control the rabbits and the squirrels for the crops and for everything. So what I’ll do is go and put ‘em in a freezer and go and lay ‘em down by that boundary. And there’ll be 40-50 buzzards and kites over them on a good day. They’ll take them off to their chicks. I never see my partridges down there. They’ll always be up here.’ (Luke)

As Sebastian expressed in his concerns about pine martens, commercial aspects of predation are important to keepers. Many keepers talked about commercial concerns as a justification for killing predators:

> ‘From a commercial side when you’re a full-time keeper every one counts… it’s a numbers game.’ (Jesse)

Keepers cannot, therefore, ‘afford’ predators (Alan). Sometimes the pressure comes from the bosses putting pressure on keepers to get any foxes that may harm their returns. As Luke said,

> ‘[From] September those birds go from being £4.50 each to £50 each and if you put it in that perspective to anyone if someone was taking £50 out of your back pocket every time they visited you, you’d want to stop it. And that’s what I do. I treat my boss’s money like its mine. And that’s why I am where I am and why he trusts me to do what I’ve got to do.’

This narrative echoes that of otter hunters in England, where otters were presented as ‘predators on commercial value’ (Matless et al. 2005). Matless et al. (2005) aligned this perspective to a hunting discourse, in which animals are given respect but killing is justified by the need to protect human interests. An extension of the commercial implications of predators is the potential impact on the keeper’s own livelihood. By eating prey species, predators have the potential to make the ‘job unviable and then if we cease to be then they’ll cease to be cos they’ll have nothing too.’ (Alan). This is exemplified by the Langholm

Moor Joint Raptor Study (1992-1999) which tested the effects of hen harriers on a grouse moor and in which grouse shooting ceased due to levels of hen harrier predation (Langholm Moor Demonstration Project n.d., see also Tapper 2005). Several keepers mentioned the Langholm project as an example of what might happen to them if they weren't able to control increasing numbers of predators. This presents an interesting contrast between the moral consideration afforded to birds and carnivores by keepers. In the keeper's view, it is the utility to humans that defines the hierarchy of value placed on the animals. Gamebirds are afforded greater status because of their commercial and / or recreational value. This makes the killing of carnivores justifiable in the pursuit of The Balance.

This being said, the relationship between keepers and predators is not as simple as predators eat gamebirds and gamekeepers kill predators. Predators can redress the balance of opinion towards themselves by being useful to keepers. Once the shooting season starts, predators 'clean up the ground' of weaker or dead birds and 'tidy up' pricked[26] birds on shoot days. In doing so predators do keepers 'a world of good' (Sebastian). This is received as helpful because keepers want to do the right thing by their birds and minimise any suffering. Predators also provide an aesthetic pleasure. Many keepers described their pleasure at watching stoats, weasels and foxes. Paul explained, 'I still appreciate what it is. A fox it is an amazing animal, an apex predator. But we have a job to do.' In this way keepers separated what an animal does in terms of The Balance from its innate characteristics, which may still be appreciated.

The overall sentiment is that as frustrating, and difficult, as it can be to endure losses, these are part of nature's process and a 'healthy balance' (Dean) includes the presence of predators. As Leslie said, 'we know they're not all gonna make it, you know.' Paul explained:

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[26] Birds that are wounded but not killed outright when shot.

> ‘If I was given a license to go out and shoot and control all the vermin that I’m not allowed to shoot, I wouldn’t kill ‘em all. There’s that nice little balance you can get.’

The Balance thus becomes a guiding principle for being proportionate in predator management, a “sweet spot” in terms of killing enough predators for a successful shooting season, without ‘wiping out’ everything in the area. In fact, if there were no predators at all, the role of the gamekeeper would be diminished (Cowan 2009), as predator controls are central to the keepers’ identity and something that many enjoy the process of doing. In this way, The Balance creates a dependency between predator and gamekeeper, in which each, to some extent, relies on the existence of the other (Cowan 2009).

Gamekeepers in The Balance

Alan contrasted the gamekeeper’s approach to managing nature to that of conservationists or ‘nature people’:

> ‘We want wildlife, the countryside thriving. We both want the same thing. It’s just that their existence tends to rely on them saving things from being extinct rather than balancing the environment for everything.’

Some keepers did not, though, see The Balance as solely their preserve:

> ‘In a perfect world, we’d all work together. At the moment you’ve got keepers that do their bit on their ground. Nature people that do their bit on their ground. If it was all to come together... you know there's things that they do that we don't like. And there’s things, a lot of things, that we do that they don’t like... it’s not a perfect world. [If] people gave in a bit more to other peoples’ opinions … the balance would be better.’ (Harry)

One of the obvious ‘things’ that conservationists ‘don’t like’ is killing of predators. Keepers spoke in very matter of fact terms about killing, even when talking about levels of killing in a reasoned way:

> ‘I’m dead against the killing of everything all the time. I think when it can do you harm, get rid of it’ (Sebastian).

One keeper recounted a maxim for moorland management practices ‘if it flies, it dies. If it hops, it drops’ (Geoff). When asked about this phrase others were quick to defend the profession:

> ‘I think possibly in the olden days, you know that’s the classic old boys [a] hundred years ago ... that’s when gamekeeping was ruthless and brutal. ... And some people might still be ruthless and brutal.’ (Dean)

There is probably a gap between how keepers define ‘ruthless and brutal’ and what lay people, who are not directly involved in killing animals, might perceive this to be. Killing fox cubs, for example, might be seen as ruthless to an outsider, but to a keeper it is an essential practice in keeping The Balance. Keepers go to extraordinary lengths to kill problem individuals, staying up night after night until they have caught them. Keepers do have to balance the need to control predation while staying within the law. There have been high profile cases of individual keepers failing to manage this, either due to a perceived or actual threat to their birds or livelihood. When asked, keepers were quick to state that they felt the profession was tainted by a minority creating a bad impression, rather like in the police force where ‘there’s the odd bad copper’ (Des). Des said, ‘in every walk of life there’s someone that doesn’t toe the line… why should every gamekeeper be branded with that?’

As alluded to by Dean, use of best practice provides a counterbalance to accusations of impropriety:

> ‘You know we move with the modern times… We all use codes of practice. Best of this. Best of that. Because, long story short, it’s your arse that’s on the line if anything goes wrong ... So why not be above board?’ (Dean)

He was not alone; many keepers talked about following the rules, using best practice guidelines and not being able to be seen to be outside of the law. Even so, keepers perceive that there is a gap between how they believe other people perceive the work they do, versus their reality: ‘all people see is us naughty gamekeepers poisoning stuff. That doesn’t happen.’ (Paul).

Returning protected species like polecats do create a grey area for keepers because they are not able to be taken in a trap without a licence but may still get caught in traps set for smaller species like stoats and weasels as ‘there’s not a lot you can do to set a trap for a stoat that won’t catch a polecat’ (Murray). As Murray, a keeper working in a polecat area for 40 years puts it, ‘we’ve always said you can’t put a sign ‘polecats that way!’ cos they’re not going to read it.’ Part of the problem with polecats is that keepers may not realise they are in the area until they have caught one ‘you don’t see ‘em and then you get one [polecat] in a trap and say “Christ, I didn’t know there was one there!”’ (George).

Although keepers are used to killing predators and other pests[27] and seeing dead birds, they were not inured to it. The premature death of birds caused by predators was a source of emotion. When asked how it feels to find dead birds in a release pen, Michael replied:

> ‘It’s like coming home and finding your wife in bed with another man …It just deflates you. Absolutely deflates you.’

The damage is therefore received personally:

> ‘I know the damage they have caused. They’ve hurt me. To the point where you know. Keep you up at night. Can’t sleep. You’re worried. You can’t sleep cos you know it’s killing stuff and you can’t do nothing so when I do catch it, I am going to shoot you because you’ve caused me [hurt].’ (Dean)

For others, the prospect of any birds being eaten was a constant concern:

> ‘It’s worrying that when you’re there asleep there’s something out there trying to eat ‘em and I know that sounds really funny, but it worries me to death to be honest. I can never just relax.’ (Ali)

It is perhaps not surprising that when birds are taken, keepers experience an emotional reaction given the amount of time and effort that goes into rearing

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[27] Rabbits or deer, for example.

them. However, keepers recognised that other ‘people don’t understand’ the ‘damage’ and why it is so painful and frustrating that carnivores should take some gamebirds, of which there are perceived to be an abundance and which are destined to be shot. This highlights a gap in perceptions between what keepers experience and know from first-hand knowledge and what they perceive others think about predators. The distress at premature demise of animals under human care is analogous to the apparent contradiction revealed by Tovey (2002) in research on farmers’ views during the mass slaughter of their livestock following a Foot and Mouth Disease outbreak. Tovey (2002) describes the profound emotional response of farmers to the mass killing of the animals, which the general public struggled to comprehend as the animals were always destined for slaughter and the farmers were being paid for them anyway. From the farmers’ perspective, keeping the animal ‘alive’, ‘well and healthy’ was ‘everything that he works for’ (Tovey 2002). To see it killed prematurely was described as very upsetting. Also, just as the farmers in Tovey’s (2002) study understood that others could not comprehend their angst when the animals are born destined for slaughter anyway, the keepers understood that others would not appreciate the damage to them caused by predators:

> ‘Unfortunately, the general public do not see this damage. And don’t understand it. They just see a friendly old billy [badger] ambling along.’ (Luke)

Geoff asked:

> ‘Why don’t people get out their living room and come out here and actually see what they do? What damage they do. Don’t sit there … They want to get out here and experience it and see what it is.’

It follows that if others do not perceive the damage that predators cause, they will not understand the necessity of killing predators to maintain The Balance.

While the killing of birds on shoot day was a source of emotion, the killing of predators is ‘one of them things that’s got to be done’ (Paul). That is not to say that some keepers did not express feelings of remorse at killing predators, but this was secondary to the necessity of killing them as part of the job of keeping The Balance:

> ‘There are times when you kill a predator. And you get that “yes I’ve got it [feeling], you know …they’re safe now, that lot”. And then afterwards you feel a bit of… whether it is remorse or just sort of. I don’t know. Difficult to describe to be honest. But it’s a necessary job and you think that you’re kind of there to try and restore the balance a bit.’ (Ali)

Given time and resource that keepers invest in protecting their birds, being ‘their guardian and their saviour’ (Ali) and maintaining The Balance, it may seem contradictory to others that keepers can then accept putting the birds through shoot day:

> ‘They say “you have a fluffy little pheasant and then you rear it up and look after it and nurture it and then you shoot it.” Well, yes we do. But there is a lot involved in it. But if you try and explain that to somebody, you can look back at yourself and think if “I was a bystander you’d think how ever could you do that?” But there’s so much involved which is almost impossible to explain.’ (Jesse)

The shooting of the birds is accepted by keepers because ‘that’s what they’re there for’ (Luke). How well the birds perform on shoot day is also ‘the mark of how well you’ve done’ (Alan). What is important is that the end is ‘done right… the respect should be there for what's happening for the bird’ (Paul). Here we see a distinction in the way that death is achieved for the birds that is important to the keepers. This is reminiscent of Marvin’s (2000) description of the role of performance in foxhunting where it ‘is the manner of realizing that death that is fundamental’. A clean shot over the open sky over a drive is a clinical way to die, whereas a premature death at the jaws of a predator is messy and undignified. Nevertheless, the death of the birds on shoot day, while it is the realisation of their intended purpose, is still a profound experience for keepers: a ‘funny feeling’; ‘difficult to explain’; ‘like the shepherd with his sheep, he loves his sheep, but when they go off for slaughter…’ (Ali). Several keepers admitted to ‘melancholic’, ‘emotional’ feelings and visiting the birds hung up in the cool room at the end of the day to reflect on what they have achieved together with ‘a fag and a beer’ (Paul).

Overall there are similarities in the way that keepers experience the deaths of gamebirds and predators – they appreciate what both are and also accept that the deaths of both are necessary for the pursuit of sport shooting. The difference is that one (predator death) is the means to an end and the other (gamebird death) is an end in itself. It is the realisation of the end point that is most important and provides a justification for killing predators as a practice of keeping The Balance.

Discussion

We have seen The Balance presented by gamekeepers as a guiding principle for their countryside management, in which all species stand to benefit from habitat enrichment, but also where opportunistic predators need to be reduced in number in order that vulnerable prey species are able to thrive in the right place, until they meet the right ending. The keeper’s Balance is built around creating a shootable surplus of game and maintaining ancillary species that do not conflict with that objective. However, The Balance as a lived concept is also more than this—it describes a way of being that is pragmatic and is concerned with making necessary choices in wildlife management and addressing perceived inequalities between species that arise in a human-dominated landscape.

The Balance that keepers described initially is a relatively simple concept that involves maintaining an equilibrium, or a steady state of harvestable prey species where the competing pressures of predation and disease are contained by habitat management, husbandry and predator controls (Fig. 6.3a). The keeper’s Balance is distinct from a balance-of-nature that would be realised without any intervention, or a balance-of-nature that would be realised purely with conservation objectives in mind, because it primarily seeks to create a sustainable harvest for human recreation and consumption (Fig. 6.3b). These nuances are important because the existence of multiple perceptions of balance could be a cause for misunderstanding between different groups of people invested in managing, preserving and utilising nature.

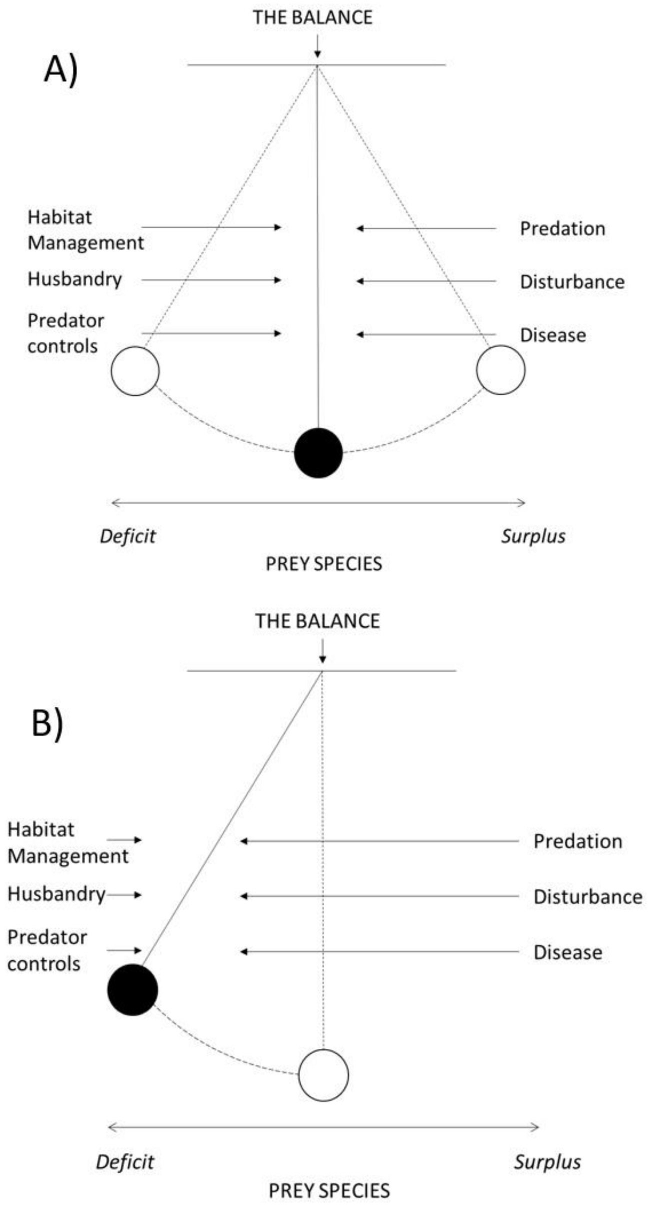


Figure 6.3. *A visualisation of The Balance as described by gamekeepers. A swinging pendulum illustrates the counteracting forces on prey species populations. In A) the forces of predation, disturbance and disease are counteracted with habitat management, husbandry and predator controls and so The Balance is achieved as a sustainable abundance of game for harvesting. When predation, disturbance and disease effects outweigh habitat management, husbandry and predator controls, prey populations will be negatively impacted such that they decline. In B), an excess of predation, disturbance and disease push the pendulum towards a deficit in prey species. Interventions such as habitat management, husbandry and predator controls need to be increased in order to swing the pendulum back towards the equilibrium.*

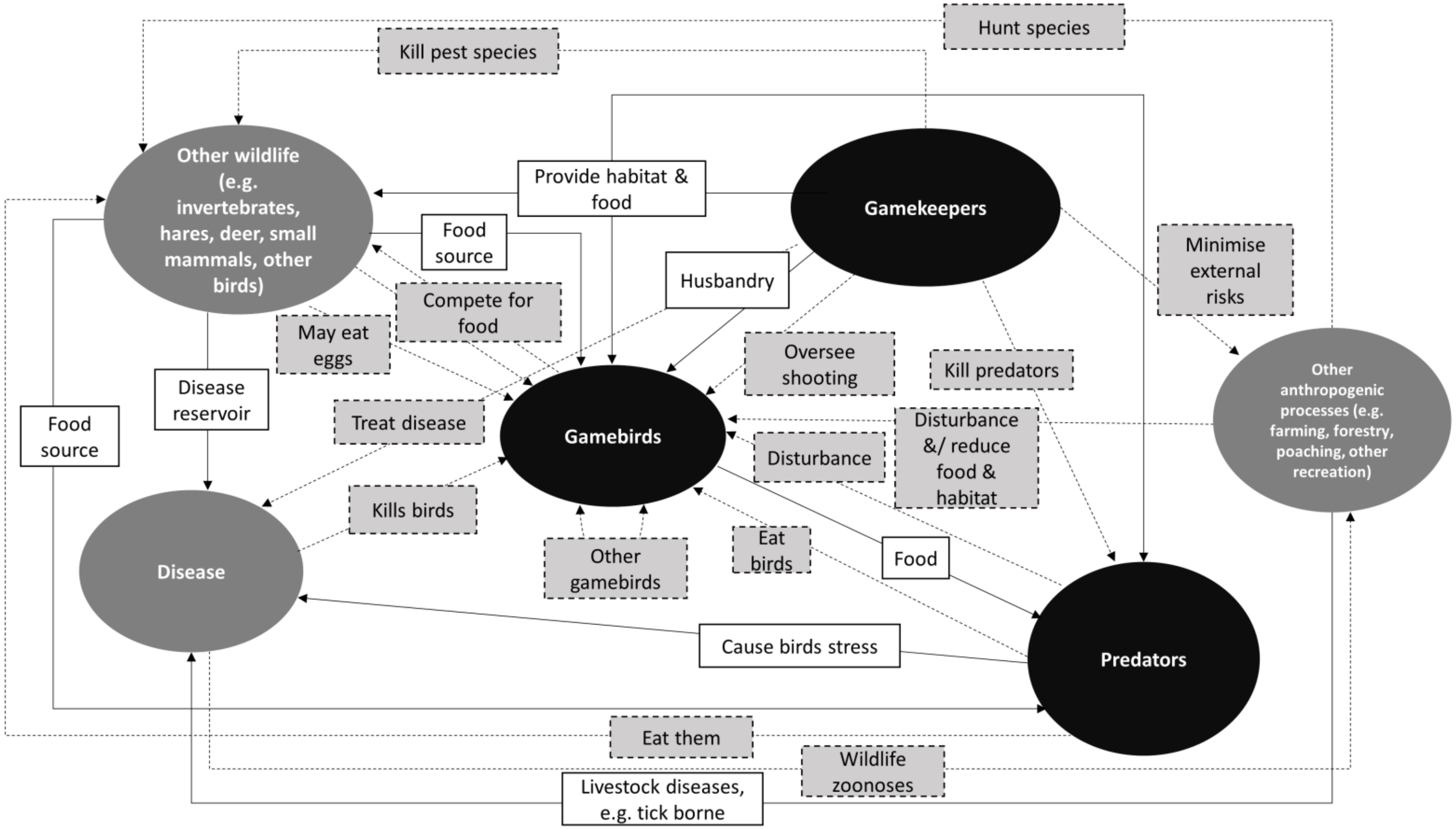


Figure 6.4. *Diagram illustrating the main interactions and effects between keepers, predators and gamebirds (black circles) and the indirect effects on disease, other wildlife and other anthropogenic processes (grey circles) as they relate to keeping The Balance. Arrows indicate the direction of effect. Negative effects (described in grey boxes) on recipients of interactions are indicated by dashed lines. Positive effects (described in white boxes) on recipients of interactions are indicated by solid lines.*

From the keepers' narratives, it is clear that keeping The Balance captures a complex system of interacting anthropogenic and ecological processes (Fig. 6.4). The complexity involved echoes the conundrum encountered by ecologists when considering the balance-of-nature and seeking to prove its existence, namely, that the complexity and dynamism of social-ecological systems mean that maintaining any form of balance-of-nature is always going to be a challenging endeavour.

There are, however, precedents in wildlife management for targeting sustainable harvests in complex systems, of which marine fisheries provide a good example. An important difference between fishers and gamekeepers, though, is that fishers are part of the harvest and largely external to the system of production whereas keepers are integral to game production and not usually involved directly in, but rather facilitate, the harvest. Creating a sustainable harvest is arguably different from realising a balance-of-nature, as although they both involve managing natural resources, they are in fact independent outcomes. In the keepers' worldview, it is their dual role as stewards of game and countryside that allow the alignment of The Balance with both harvestable surpluses and a broader concept of environmental balance. The ambiguity of The Balance is constructive in this context because it allows keepers to capture and communicate all of the diverse aspects and interpretations of their approach to wildlife management under a single umbrella. In this respect, it is similar to Deary and Warren's (2017) exploration of the discourses relating to 'rewilding' in Scotland, in which the researchers identify that participants conceptualise 'many wilds' of wildness and nature that can all be understood as part of 'rewilding' and that this multiplicity is central to the term's broad appeal.

Ideas of a balance-of-nature might be discussed by wildlife managers but ways of maintaining this will depend on perspectives on intervention. Some forms of wildlife management are purposeful: for example, active conservation of species and habitats, or the management of fisheries to ensure sustainable harvests from stock in the long-term. Other approaches emphasise non-intervention and animal autonomy (DeSilvey & Bartolini 2019). For example, in the United States, wilderness is often idealised as a pristine nature that should not be intervened with by humans (Cronon 1996). Equally, however, the conservation movement in North America is grounded in a long tradition of interventionist wildlife management that originated with widespread and popular hunting activity (Organ et al. 2010) and continues with the use of a hunting quota system for the management of certain species. In Great Britain there is little, if any, comparable wilderness (or indeed any concept of wilderness as part of the British landscape) and wildlife management is not rooted in hunting tradition. The conservation approach is that some level of intervention is required in order to create a version of nature that can be sustained alongside meeting human needs, including food and recreation, but there are no quotas or regulations relating to the offtake of species that are not protected by law. The keepers' Balance is one of ritualised management to maintain a locally desired state on their patch of the countryside. A particular cadre of people are integral to managing this Balance in perpetuity. The keepers are integral to the process because of their active role in predator and habitat management for the benefit of wildlife. This contrasts with conservation interventions which aim to produce self-sustaining populations that require minimal ongoing management.

There are similarities with the views expressed by gamekeepers and those engaged in killing introduced species, in a study by Crowley et al. (2018) in which participants expressed a 'moral duty' to address imbalances caused by humans. Crowley et al. (2018) consider that this narrative fits with the ethical assumptions underlying the process of biodiversity conservation, which prioritises the preservation of one or more species (which may be native, or rare) at the expense of (which may be non-native) others (e.g. Biermann & Mansfield 2014, Srinivasan 2014, van Dooren 2015). Where keepers are fostering game species such as red grouse (native) or grey partridge (native and rare), the comparison between keepers and introduced species controllers is apt. However, the comparison is less convincing for keepers that rear and release pheasants and red-legged partridge, which are both non-native and abundant. In this scenario, unprotected native carnivores are killed to encourage higher survivorship of non-native birds whose value is tied into their utility and whose existence is short term as they are themselves are killed, only to be replaced the following year. This is offset, however, by the fact that predator controls are generally less intense on shoots founded on reared game, a subtlety that may not be appreciated by groups outside of the shooting community.

Although gamekeepers and conservationists in Britain share the same broad goals and engage in some similar practices, there is an apparent disconnect between the two communities, of which the keepers are acutely aware. Some mistrust may undoubtedly be attributed to decades-long conflicts between conservationists and shooting interests over raptor predation of gamebirds. Whilst there are undoubtedly areas of difference in practices and perspectives between gamekeepers and other wildlife management groups, there are also many areas of similarity. Keepers want a thriving countryside that includes a diversity of species (they'd just rather not see too many predators on their patch). They, knowingly or otherwise, observe and use ecological language and phenomena, providing some common foundations for communication with conservation ecologists. Trapping and hunting quarry requires an intimate knowledge and appreciation of the habits of their subjects, much like traditional naturalists. Keepers are required to adhere to environmental regulations regarding predator and habitat management and are incentivised to adopt environmental stewardship incentives, like any other land manager. Therefore, for the most part, the practices of The Balance are constrained by a framework set out in UK law. Although predator control activities are carried out by other conservation NGOs, for example the RSPB, these are not publicised and keepers carry the burden of being associated with generalised killing. Even then, differences in values are apparent, as conservation NGOs are killing, ostensibly reluctantly, only for conservation purposes whereas keepers are killing in support of recreational or economic interests. This may reduce the value of the keeper's Balance in the eyes of those who question whether the costs, as well as the drivers, of maintaining The Balance undermine any benefits that might it might bring. Recognising that there may be different perceptions of what 'balance' in natural environments consists of, as well as different perspectives of both what is required and deemed acceptable to maintain these balances, is important for understanding the politics of the countryside and working to achieve conservation goals in conflicted arenas.

Chapter 7

Discussion

Chapter 7: Discussion

In this thesis I have explored the recovery of the polecat in Great Britain between the 1960s and the late 2010s, with the aim of reviewing the recovery itself, exploring some of the mechanisms underpinning that recovery and improving understanding of contemporary anthropogenic processes that may affect the species' future prospects. More broadly, I have aimed to situate polecat recovery in the context of the population trends of other British carnivores and carnivore management in general.

To this end, in Chapter 2, I carried out a review of all of Britain's mammalian carnivores, which found that badger, fox, otter, pine marten and polecat were more numerous and/or widespread in 2015 than in the 1960s, although the fox is currently experiencing a period of decline. Stoat and weasel were data deficient, although the evidence from the GWCT's National Gamebag Census suggests that stoat is increasing relative to weasel. Care should be taken when interpreting game bag data trends. Biases may occur through variations in trapping effort in both space and time, trapper experience and trapping methods (McDonald & Harris 1999, Ruette et al. 2003). In this thesis, I have only used game bag data where it can either be validated by other survey data (e.g. foxes), or as a way of elucidating relative population trends rather than absolute abundance or population change (e.g. the relative fluctuations of stoats and weasels records). Wildcat is a cause for conservation concern due to the prevalence of extensive hybridisation with domestic cats. Of those species that have been recolonising following historical range contractions, otter has been recolonising the fastest, followed by polecat and then pine marten. Environmental pollution, hybridisation, predator controls and disease are among the anthropogenic processes limiting carnivore populations in Britain, whereas legal protections, conservation interventions, e.g. translocations and habitat management, are supporting increases in species' populations and ranges.

In Chapter 3, I explored resource use through the polecat's expansion between the 1960s and 2010s. Resource use by polecats differed depending on whether polecats were in the core of their range or at the frontline of expansion, and this difference was greatest in the 1960s when rabbits, an important resource for polecats, were limited in availability. I also found that resource use was more variable over time for female than male polecats. When exploring polecat diet more explicitly in Chapter 4, I found that consumption of mammals and lagomorphs had increased (as a proportion of total diet) between the 1960s and 2010s, which is in line with the recovery in rabbit numbers following the myxomatosis epizootic that began in the 1950s (Sumption & Flowerdew 1985, Aebischer et al. 2011). The increase in the numbers of rabbits may also explain some of the temporal differences in resource use by polecats between the 1960s and later decades that I reported in Chapter 3. The proportion of lagomorphs in polecat diet between the 1990s and 2010s did not change, despite declines in lagomorphs recorded during surveys over the same period of time (Harris et al. 2018). Although lagomorphs remained an important food source for polecats between the 1990s and 2010s, in Chapter 5, I found that levels of secondary exposure to second generation anticoagulant rodenticides (SGARs) had increased 1.7 fold between the 1990s and 2010s. Both the extent of secondary exposure (presence or absence of liver residues) and the severity of exposure (number of SGARs and total concentrations of SGARs detected) in polecats increased between the decades. The severity of exposure increased with polecat age, reflecting the greater likelihood of older animals to encounter contaminated prey over time and, as a result, bioaccumulate SGAR residues in the liver. The probability of exposure varied with values of $\delta^{15}N$, indicating that resource use influences whether or not a polecat is likely to be exposed to SGARs, but it does not affect the severity of that exposure.

The statistical analyses in this thesis were limited by the sampling approach, which, due to the cryptic nature of the study species, necessarily relied heavily on road-killed animals. It is possible that some bias was introduced relating to detectability, collectability, and persistence of carcasses (Guinard et al. 2012), as well as the limited presence of roads in some areas of the polecats distribution – such as central Wales. The sample sizes in Chapters 3, 4 and 5, while comparatively large for a study of polecats, restricted the power of the analyses undertaken. For example, it was not possible to test three-way interaction effects in Chapter 5 and it may be that the three-way interaction effect tested in Chapter 3 may have been present, but may not have been detectable due to sampling power. Not having enough power in the model to detect signals in the data may lead to type II statistical errors (false negatives). Missing relevant variables from models would reduce the fit, or explanatory power, of resulting models. Adopting an information-theoretic approach to modelling will have improved the chances of including variables with the largest biological effects in models where I had sufficient power to detect them.

Finally, in Chapter 6, I investigated The Balance, the grand narrative used by gamekeepers to describe their approach to wildlife management that also encapsulates their way of being. I found that enacting The Balance necessitates that gamekeepers carry out a highly interventionist approach to management of the countryside. I identified that The Balance may have positive (in terms of provision of habitat and food) and negative (in terms of predator controls) implications for carnivores. The polecat, while killed by gamekeepers as part of predator controls by accident or design (see also e.g. Packer & Birks 1999), is not considered as much of a threat to game as the fox. The extent of predator control practices differs between shoot types. The interventionist approach to management will predispose countryside managers like gamekeepers to want to control carnivores, or indeed avian predators, as they recover their populations.

Implications for polecats

My research findings provide an understanding of the drivers of polecat recovery and for carnivore management in Britain and elsewhere. My studies have highlighted that, in spite of polecats facing a diverse array of risks (Table 7.1, Chapter 2), some of which (such as rodenticide exposure) have only become apparent since the 1980s and have continued to increase in frequency and extent (Chapter 5), polecat recovery has continued unabated since the 1960s. Polecats are now present across much of south, central and eastern England as well as the whole of mainland Wales. The extent of recolonisation is such now that assessing the polecat’s distribution alone is unlikely to be a sufficient measure of population status. Future monitoring should include analysis of variation in polecat population densities from a cross-section of habitats and locations in the polecat’s range if it is to provide a true measure of the species’ status and ongoing recovery. However, measuring polecat density is difficult and time-consuming due to the elusive nature of these animals. The trapping protocols tested by Birks and Kitchener (1999) provide a useful starting point for measuring polecat density using volunteers. Overall, however, my analysis based on changes in distribution alone (Chapter 2) indicates that polecats have recolonised more quickly in Britain than either of Langley and Yalden's (1977) other "rarer carnivores", the pine marten, or the wildcat, which is now facing extinction by hybridisation. This suggests that the life history traits of polecats may provide greater population resilience than is the case for pine martens and wildcats and/or that the severity of the threats to survival and recruitment are lower than for these other species. Given this, it seems likely that the original causes for the eighteenth and nineteenth century reductions in polecat numbers must have been very intense and widespread to have caused the severity of decline that occurred.

Effective wildlife management relies on some form of assessment of the risks to species' persistence (Fletcher 2005). Risk assessments aid identification of which risks to populations require management intervention, how much effort is required to mitigate said risks and in what order they should be addressed, ultimately leading to better management decisions (Fletcher 2005). The risks to polecats in Britain are now quite well defined and described, unlike in parts of the rest of the polecat's range where the species is in decline (Croose et al. 2018). The main risks in Britain have been identified as: secondary exposure to SGARs, predator controls by gamekeepers, declines in rabbit populations, road-induced mortality and hybridisation. It is possible to undertake a qualitative summary assessment of these main contemporary risks, based on the findings of this thesis and information on the wider literature (Table 7.1).

Table 7.1. *A qualitative assessment of the risks to further polecat recovery using the dimensions of i) potential consequences (impacts) associated with an issue assessed in terms of effect on population and time to recover; and ii) the likelihood (probability) of the consequences occurring. Impact on polecat populations was assessed as: Low = negligible to minor impact. Little impact on populations size or dynamics and, if detected, recovery time required would be within 1-2 years; Medium = moderate to severe impact. Long term population growth and dynamics not adversely impacted, although may cause localised extinctions. Recovery would be measured in 3-10 years if stopped; High = major to catastrophic. Likely to cause regional extinctions if it continues and recovery would take place over decades if it stopped. Probability of consequences occurring was assessed as: Low = remote to rare. Not heard of, but not impossible; Medium = possible. Evidence suggests it may take place, although may not be widespread; High = likely. It is expected to occur and will be widespread across the population. Both measures are adapted from Fletcher (2005).*

Risk	**Impact**		**Probability of occurrence**		**Source(s)**
	Assessment	**Evidence**	**Assessment**	**Evidence**	
Rodenticide exposure	Low	There is currently no evidence of population level effects of rodenticide exposure. The range of total rodenticide concentrations detected was wide. Instances of very high concentrations being detected were not frequent. It is possible that those with the highest concentrations died out of sight and were not recorded.	High	79% of polecats are secondarily exposed to at least one rodenticide.	Chapter 5, Shore et al. (2003).
Predator controls by gamekeepers	Medium	In the uplands of northern England and Scotland where controls are most intensive and which polecats are now moving into, it is likely that intensive controls will mean that polecats are unlikely to be able to establish themselves in some localities.	Medium	Although gamekeepers are responsible for game over a large proportion of the countryside, coverage is not contiguous and control intensity is variable by season and type of quarry; wild	Chapter 6, Packer & Birks 1999.

Risk	Impact		Probability of occurrence		Source(s)
	Assessment	Evidence	Assessment	Evidence	
				game requires the most intensive controls.	
Reduced rabbit availability	Medium	Rabbits feature heavily in polecat diet. Rabbit recovery post myxomatosis between 1960 – 1990s aided stoat populations and it may have assisted polecat recovery in the same way. When rabbit populations were very restricted in the 1960s, there is some evidence that polecat resource use differed between the sexes. This is not the case in the 2010s after a decade of rabbit declines. This may mean that polecats are restricting their resource use to areas that are more abundant with rabbits, or that they are occurring at lower densities in response to reduced rabbit availability.	Medium	Rabbit records indicate that rabbits are declining but this appears to be a patchier decline than myxomatosis epizootic.	Chapters 3, 4, McDonald et al. 2000 and Harris et al. 2018.
Road density	Low	Although, there are large road barriers in the north of England and the urban conurbations of central Scotland may impede polecat recolonisation of these areas.	High	Most polecats collected in all monitoring surveys were road casualties. Patterns of carcass collection imply this risk changes seasonally and is greatest in spring and autumn when polecats are dispersing.	Chapter 2, Croose 2016.
Hybridisation	High	Hybridisation could lead to the genetic extinction of the species.	Low	31% of polecats are introgressed with ferrets, but the genetic evidence suggests that hybridisation occurred in previous generations of polecats and that current levels of hybridisation are a legacy of this occurring.	Costa et al. 2013.

Risk	Impact		Probability of occurrence		Source(s)
	Assessment	**Evidence**	**Assessment**	**Evidence**	
Intraguild effects	Low	Polecats may experience intraguild effects from foxes, badgers, pine martens, stoats, otters and American mink, but there is no evidence to confirm any population level effects on polecats in Britain. There is no evidence of intraguild resource partitioning by prey size between British mustelids, although there is some evidence that polecats and American mink may alter their activity schedules in areas where they are sympatric. Polecats have been sympatric with fox, badger, American mink, otters, stoats and weasels (and more recently pine martens again in Wales) and this has not appeared to affect their ability to recolonize, although it is possible that it might affect local population densities and / or speed of expansion.	High	As polecats continue to expand and other carnivores such as otters and pine martens continue to recolonise and reach carrying capacity in the same areas, their distributions increasingly overlap and intraguild interactions may occur.	McDonald 2002, Harrington 2008

This qualitative risk assessment finds that secondary exposure to SGARs and road mortality are the risks most likely to occur, but that these risks are unlikely to have the greatest impact in limiting future population expansion. Predator controls, rabbit abundance and roads may affect expansion in some areas. While secondary exposure to rodenticides is the primary chemical control agent considered in this thesis, other chemical control agents have been prevalent in wildlife management in Britain. Use of poisons such as strychnine and, more recently, the pesticides carbofuran or alpha-chlorolose have been associated with game management in the UK (Reynolds & Tapper 1996, Whitfield et al. 2003). It is reasonable to suppose that such practices may have been more widespread historically and that these, alongside trapping, may have contributed to the extirpation of some predator species. Fumigation (or “gassing”) of rabbit burrows to manage rabbit numbers is a common practice on game estates and may affect non-target species that make use of rabbit burrows (such polecats, stoats and weasels) through indiscriminate killing of burrow inhabitants (Packer & Birks 1999, McDonald & Harris 2000).

This assessment is a point-in-time estimate of the known risks to polecats, which are unlikely to be static. Should SGAR exposure continue to rise (as has happened in the last 25 years), then SGAR mortality may become more important to polecat expansion. In addition, if rabbit abundance continues to decline to a point where polecats need to diversify their diet, it is possible that SGAR exposure may increase further and the “low” impact status of SGAR exposure would need to be upgraded. Harris et al. (2018) provides long-term trends of rabbit records but finer scale information on rabbit distributions are not available. Given the prevalence of rabbits in polecat diet (Chapter 4) and the evidence that polecats have adapted their resource use when rabbits were very scarce (Chapter 3), the status of rabbit populations and the nature of polecat dependency on them are important. There is a need to carry out a finer scale analysis of polecat diet using stable isotopes to reconstruct diet in areas of varying rabbit abundance and thereby understand the extent of any dietary dependency on rabbits in greater detail.

Given the characteristics of the areas that polecats are now recolonising, which includes the uplands and eastern counties of Britain, where predator controls are more intense (Chapter 6) and areas with significant road and urban barriers, it is possible that it will take polecats longer to establish themselves in northern England and Scotland. It is also possible that there may be some areas where polecats do not become established where historically they were once common. In order to validate these conclusions, particularly with regards to predator controls, an analysis of the source-sink dynamics of carnivores around game estates would be invaluable in terms of understanding the dynamics around a large highly seasonal food source. The updated information about risks to polecats presented in this thesis could now be used as the foundations for a quantitative spatial model of the risks to polecats across the landscape and to project their maximum future distribution extent in Britain. Such a model could be extended to estimate range and / or abundance changes in other British carnivores, such as the pine marten or fox.

Implications for carnivores and wildlife management in Britain

The polecat is not alone in experiencing improvements in population status in Britain since the 1960s. In most cases, a relatively low level of intervention has accompanied population increases in the form of legal protections to control levels of killing and, in the case of the otter, restrictions/bans on the use of some environmental pollutants and translocations of animals (Chapter 2). Natural recovery of rabbit populations may have supported population growth (Chapter 4, McDonald et al. 2000).

Overall, though, the broadly positive picture for carnivore populations in Britain implies that although the countryside might be fragmented (Thomas 1995), and environmental pollutants pervasive (Chapter 5, Pountney et al. 2015), there has been sufficient habitat and food to support increasing numbers of carnivores. Caution should be exercised, though, when using small carnivores as ecological indicators to make generalisations about overall ecosystem health (Landres 1992). It cannot be presumed that increasing numbers of carnivores is indicative of any more than an adequately functioning ecosystem for these species. Carnivores play an important regulatory role in ecosystems and an interesting next research step would be to explore the community dynamics in areas where all British carnivores are now present (because of the recovery of certain species) to understand any trophic cascades and intra-guild interactions that may occur. For example, Hebblewhite et al. (2005) found that the reintroduction of wolves to Banff National park led to changes in elk *Cervus elaphus* population density, female survival and calf recruitment. Similar evidence of trophic cascades has been observed following wolf reintroduction in Yellowstone National Park (Ripple et al. 2012). Furthermore, wolf recovery on Isle Royale in the 1960s led to the collapse of coyote *Canis latrans* populations as coyotes competed with wolves for the same prey (Mech 1966, Smith et al. 2003). Studies by Harrington et al. (2008, 2009b) found that otter and polecat recovery lead to behavioural changes in sympatric invasive American minks *Neovison vison* and it is possible that there may be some intra-guild cascading effects of returning polecats on stoat populations, given the similarities in their diet.

The apparent ongoing change in Britain in the numbers of rabbits, a major food source for British carnivores (Chapter 4, Sumption & Flowerdew 1985, McDonald et al. 2000), and its effect on carnivore populations is also uncertain. Research in countries such as Spain where rabbit haemorrhagic disease has led to significant rabbit population declines found that generalist predators like foxes switched their diet to prey upon more rodents and birds (e.g. Villafuerte et al. 1996). In Britain, the current decline in rabbit populations could lead to an increased risk of secondary exposure to SGARs if carnivores compensate by eating more rodents (Chapter 5). This could increase the risk of both poor nutrition/starvation and poisoning in some carnivore populations. There is a need to understand how carnivore populations and carnivore-prey community dynamics are affected by variation in rabbit abundance.

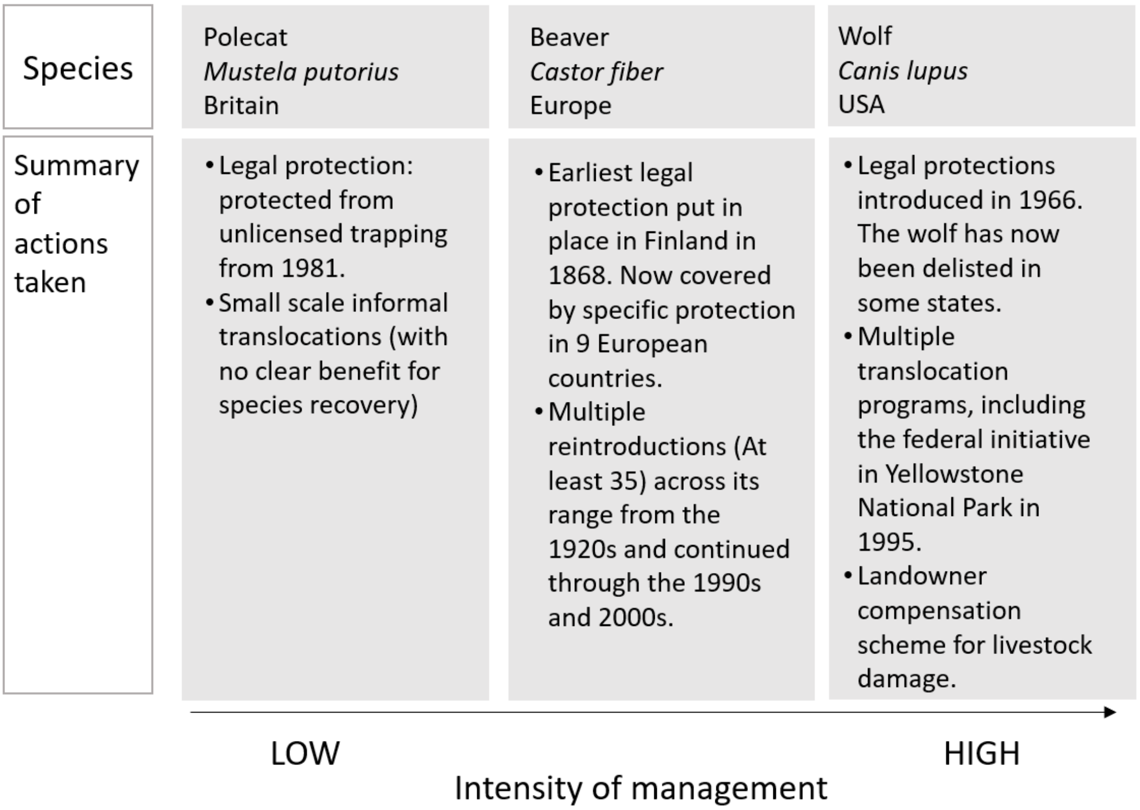
The population status of polecats, otters and eventually pine martens is such that at some point their legal status may need to be reviewed. Proponents of a more interventionist style of wildlife management, such as gamekeepers, will be inclined towards seeing such a review earlier than other groups (Chapter 6). The likelihood of a review of predator protection legislation being pursued is likely to depend on the species in question. Gamekeepers mainly did not seem to think that polecats were a problem although they do sometimes kill them (Packer & Birks 1999), but they were all aware of the potential threat of pine martens in terms of disturbing gamebirds in woodlands. The effect of any reduction in legal protection is likely to be more severe for some species than others, depending on availability of suitable habitat, plasticity in resource use, time to breeding, average annual reproduction rates and the likelihood of other mortality factors occurring which may put pressure on populations. In Chapter 3 we highlight potential differences in resource use in different parts of a recovering species range, which indicate that the distinct ecological requirements of males and females of dimorphic species may need to be considered during the process of range expansion.

In summary, my research findings suggest that any policy decisions concerning reducing the level of species protection should take into account both the state of the recolonisation process and the extent to which animals pose a problem. At the moment it is possible to control polecats by shooting them. As a Schedule VI species under the Wildlife and Countryside Act (1981) they are not protected against all forms of killing. Unintentional killing is recorded in the Game and Wildlife Conservation Trust's National Gamebag census, but it is likely that this underestimates levels of killing due to both the presence of hybrid individuals, which may mean that gamekeepers count animals as ferrets, and to the fact that it is illegal to trap them.

General implications for carnivore management

My study of polecats highlights that species recoveries may occur in dynamic social-ecological systems. One of the challenges with polecat declines elsewhere in Europe is that the potential causes of the decline are not well understood (Croose et al. 2018). In the case of polecats in Britain, events in the first part of the twentieth century (e.g. the combined effects of the wars on predator management and the banning of the gin trap) were key factors in initiating polecat recovery. These changes were not directed at benefitting small ground predators at that time, although this has been the outcome. My research also shows the importance in recognising that the original causes of the decline may not be the same ones that are restricting population recovery at a later date. It is therefore important for wildlife managers not only to be aware of the causes for past declines but also to investigate novel risks that recovering species will encounter as they expand their population range. Gamekeeper practices continue to change with the development of the shooting industry and practices are not the same as they were historically (Chapter 6). Secondary exposure to rodenticides is a relatively new risk in the context of polecat recovery, but has also has emerged as a risk within the time that rodenticides have been used to manage rodents (Chapter 5).

In a comparison of the way that polecat recovery has been managed compared with other species, such as beavers *Castor fiber* across Europe and wolves *Canis lupus* in the USA, we can see that the approach has been quite low in intensity (Fig. 7.1).



Species	Polecat *Mustela putorius* Britain	Beaver *Castor fiber* Europe	Wolf *Canis lupus* USA
Summary of actions taken	• Legal protection: protected from unlicensed trapping from 1981. • Small scale informal translocations (with no clear benefit for species recovery)	• Earliest legal protection put in place in Finland in 1868. Now covered by specific protection in 9 European countries. • Multiple reintroductions (At least 35) across its range from the 1920s and continued through the 1990s and 2000s.	• Legal protections introduced in 1966. The wolf has now been delisted in some states. • Multiple translocation programs, including the federal initiative in Yellowstone National Park in 1995. • Landowner compensation scheme for livestock damage.

Figure 7.1. *Comparisons of wildlife management approaches associated with the recovery of polecats in Britain, beavers in Europe and wolves in the USA. Sources: Bath 1989, Halley & Rosell 2002, Naughton-Treves et al. 2003, Guertin 2016, Sainsbury et al. 2019.*

Apart from some basic legal protection and some small-scale translocations, polecat recovery has largely taken place without specific interventions, and has gone largely unnoticed. Nonetheless, the outcome for polecats has been positive and could be seen to vindicate the view that, once human threats are removed, at risk species can recover by themselves with minimal direct intervention. It is difficult to state with conviction that the polecat's recovery in Britain is a validation of that view as there is no counterfactual scenario to which the outcome can be compared (Ferraro & Pattanayak 2006). We also cannot say how many polecats have been killed illegally since their inclusion under the protection of the Wildlife & Countryside Act (1981) and therefore it is also not possible to know whether fewer have been killed than would have been killed had the legislation not been in place.

This minimal intervention approach for aiding population recovery may not be an appropriate strategy for polecats elsewhere in their range in Europe, as the causes of decline in European populations is not known. Furthermore, it would not work with all other carnivore species. In Great Britain, pine marten and wildcat experienced similar declines to the polecat in the eighteenth and nineteenth centuries, but neither have recovered to the extent of the polecat. This is despite both receiving more intervention in the forms of translocations and trap-neuter-release programmes to reduce the threat of hybridisation (Chapter 2). Minimal intervention would also be less successful for larger carnivores, such as wolves *Canis lupus* or brown bear *Ursus arctos*, which are more visible and may create greater opportunities for human-wildlife conflict over livestock (e.g. Breitenmoser 1998). However, the polecat case study does indicate that it can be appropriate to prioritise management efforts towards species that need more support, as long as there is sufficient understanding of the species in question. Chapter 3 highlights that even with a generalist species, assumptions about resource use during recolonisation need to be made carefully.

Polecats mature and breed relatively quickly. They are flexible in their resource use (Chapters 3 & 4). However, even 100 years after their population reached its nadir in Britain and the reduction of the main threats to their persistence, they are still to fully recover their former range (Chapter 2). This indicates that even for a flexible, quick to breed species like the polecat, management planning needs to take place over extended time frames and that the benefits of any investment may not be realised within the lifespan of a conservation intervention, which are often typically short-lived (Ferraro & Pattanayak 2006). Finally, while the need for monitoring and evaluation of wildlife management is not new, this case study underlines the utility of long-term monitoring of species of interest (including carcass collection and preservation), their prey and threats to their persistence.

Appendix

Appendix 2.1. Changes in the ranges of wildcat Felis silvestris*, European pine marten* Martes martes *and European polecat* Mustela putorius*. A) Distances (in km) from the central points of species ranges in 1975 to all positive hectads using 95th percentile gamma statistic (after Preuss et al. 2014) and B) results of linear models analysing the rates of expansion (in km).*

A] **Decade**	**Wildcat** ***Felis silvestris***	**European pine marten** ***Martes martes***	**European polecat** ***Mustela putorius***
1975	144.9	122.0	119.7
1985	153.7	127.0	123.9
1995	117.9	149.6	221.3
2005	164.4	n/a	246.3
2015	n/a	188.1	302.8

B]		**Coefficient summary**				**Model statistics**		
Species	**Parameter**	**Coefficient**	**Standard Error**	**t value**	**p value**	**Adjusted R^2**	**F statistic**	**Degrees of freedom**
Wildcat	*(intercept)*	*141.8*	*20.2*	*7.0*				
Felis silvestris	Year (0-30)	0.2	0.1	0.2	0.852	0.47	0.04	1,2
European pine	*(intercept)*	*116.4*	*5.0*	*23.2*				
marten ***Martes martes***	Year (0-40)	1.7	0.2	7.9	0.015	0.95	62.7	1,2
European	*(intercept)*	*105.1*	*17.3*	*6.1*				
polecat *Mustela putorius*	Year (0-40)	4.9	0.7	6.9	0.006	0.92	48.1	1,3

Appendix 2.2. Recent population estimates for native mammalian carnivores in Great Britain. Population estimates are the combined totals for England, Scotland, and Wales unless otherwise stated. Reliability is scored differently by Mathews et al. (2018), where <=1 indicates very poor reliability of estimate and 4= very good reliability of estimate, and Harris et al. (1995), where 1 is most reliable estimate and 5 the least reliable estimate.

Species	**Source**	**Population estimate (95% Confidence Interval)**
Wildcat *Felis silvestris*	Mathews et al. 2018 Kitchener et al. 2005 Harris et al. 1995	200 (30 – 430). Scotland only. Mathews reliability = 2. 400-1800, depending on wildcat definition. Scotland only. ~3500. Scotland only. Harris reliability = 3.
Red fox *Vulpes vulpes*	Mathews et al. 2018 Webbon et al. 2004 Harris et al. 1995	357,000 (104,000 - 646,000). Mathews reliability = 2.5. 225,000 (179,000-271,000) rural foxes. 33,000 urban foxes (Harris et al. 1995). Total = 258,000. ~240,000. 195,000 in England, 23,000 in Scotland, 22,000 in Wales. Urban fox population: total 33,000 of which 30,000 in England, 2,900 in Scotland, 100 in Wales. Harris reliability = 4.
European otter *Lutra lutra*	Mathews et al. 2018 Harris et al. 1995	11,000 (NA). Mathews reliability = 1. ~7,350. 350 in England, 6600 in Scotland (of which 3,600 on mainland and 3000 on islands), 400 in Wales. Harris reliability = 3.
European badger *Meles meles*	Mathews et al. 2018 Judge et al. 2017 Harris et al. 1995 Cresswell et al. 1990	562,000 (391,000 - 1,014,000). Mathews reliability = 4. 485,000 (391,000–581,000) in England and Wales. ~250,000. 190,000 in England, 25,000 in Scotland, 35,000 in Wales. Harris reliability = 1. 250,000.
European pine marten *Martes martes*	Mathews et al. 2018 Balharry et al. 1996 Harris et al. 1995	3,700 (1,600 - 8,900). Mathews reliability = 2. 2,600 in Scotland only. ~3,650. <100 in England, ~3,500 in Scotland, <50 in Wales. Harris reliability = 2.
Stoat (ermine) *Mustela erminea*	Mathews et al. 2018 Harris et al. 1995	438,000 (NA). Mathews reliability = 1. ~462,000. 245,000 in England, 180,000 in Scotland, 37,000 in Wales. Harris reliability = 4.
Weasel (common weasel, least weasel) *Mustela nivalis*	Mathews et al. 2018 Harris et al. 1995	450,000 (NA). Mathews reliability = 0. ~450,000. 308,000 in England, 106,000 in Scotland, 36,000 in Wales. Harris reliability = 4.
European polecat *Mustela putorius*	Mathews et al. 2018 Harris et al. 1995	83,300 (68,000 - 99,000). Mathews reliability = 4. ~15,000; 2500 in England, Scottish introductions unknown, 12,500 in Wales. Harris reliability = 3.

Appendix 2.3. National distribution surveys of native mammalian carnivores in Great Britain, 1960–2017.

Species	1960-1979	1980-1989	1990-1999	2000-2009	2010-present
Wildcat *Felis silvestris*	1960-75 (Langley & Yalden 1977)	1983-87 (Easterbee et al. 1991)	Live trapping: 1992-1993 (Daniels et al. 1998)	2006-08 (Davis & Gray 2010)	2010-13 (Kilshaw et al. 2016)
Red fox *Vulpes vulpes*	No specific surveys of national distribution have been published. See Battersby 2005 for a summary of surveys including red fox, Aebischer et al. 2011 for GWCT's National Gamebag Census trends and Harris et al (2018) for BBS trends.				
European otter *Lutra lutra*	England 1977-79 (Lenton et al. 1980) Scotland 1977-79 (Green & Green 1980) Wales 1977-78 (Crawford et al. 1979)	England 1984-86 (Strachan et al. 1990) Scotland 1984-85 (Green & Green 1987) Wales 1984-85 (Andrews et al. 1986)	England & Wales 1991-94 (Strachan & Jefferies 1996) Scotland 1991-94 (Green & Green 1997) Wales 1991 (Andrews et al. 1993)	England 2000-02 (Crawford 2003) Scotland 2003-04 (Strachan 2007) Wales 2002 (Jones & Jones 2004)	England 2009-10 (Crawford 2010) Scotland 2011-12 (Findlay et al. 2015) Wales 2009-2010 (Strachan 2015)
European badger *Meles meles*	1960-70 (Neal 1972, 1977, 1986, Clements et al. 1988)	1985-88 (Cresswell et al. 1989, 1990)	1994-1997 (Wilson et al. 1997)	Scotland 2006-2009 (Rainey et al. 2009)	England & Wales 2011-13 (Judge et al. 2014, 2017)
European pine marten *Martes martes*	Great Britain 1960-1975 (Langley & Yalden 1977) England & Wales 1960-1988 (Strachan et al. 1996)	Great Britain 1980-82 (Velander 1983) England & Wales 1960-88 (Strachan et al. 1996)	Scotland 1994 (Balharry et al. 1996) England & Wales 1996-2007 (Birks & Messenger 2010) 1993 (Bright & Harris 1994), 1994-95 (McDonald et al. 1994)	Scotland NA England & Wales 1996-2007 (Birks & Messenger 2010)	Scotland 2012-13 (Croose et al. 2013, 2014) England & Wales VWT unpublished data
Stoat (ermine) *Mustela erminea*	No specific surveys were carried out. See Aebischer et al. 2011 for the National Gamebag Census trends.				
Weasel (common or least weasel) *Mustela nivalis*	No specific surveys were carried out. See Aebischer et al. 2011 for the National Gamebag Census trends.				
European polecat *Mustela putorius*	1960-75 (Langley & Yalden 1977)	1986 (Blandford 1987) 1981-85 (Tapper 1992)	1993-97 (Birks & Kitchener 1999)	2004-06 (Birks 2008)	2013–16 (Croose 2016)

Appendix 2.4. National and international legislation providing protection for native mammalian carnivores in Great Britain.

Species	**GB legislation**			**International Legislation**			**Other**
	Wildlife & Countryside Act (1981)	**UK Biodiversity Action Plan**	**Conservation of Species & Habitats Regulations (2010)**	**Bern Convention (1982)**	**EU Habitats Directive (1992)**	**EC CITES**	
Wildcat *Felis silvestris*	Schedule 5 (as per 1988)	Priority species	Schedule 2	Appendix 2	IV	Annex A	NA
Red fox *Vulpes vulpes*	NA	NA	NA	NA	NA	NA	Hunting Act (2004).
European otter *Lutra lutra*	Schedule 5	Priority species	Schedule 2	Appendix 2	II, IV	Annex A	Hunting Act (2004); Natural Environment and Rural Communities Act (2006); Scottish Biodiversity List.
European badger *Meles meles*	NA	NA	NA	Appendix 3	NA	NA	Protection of Badgers Act (1992); Agreement on International Humane Trapping Standards.
European pine marten *Martes martes*	Schedule 5	Priority species	Schedule 4	Appendix 3	V	NA	Agreement on International Humane Trapping Standards; Natural Environment and Rural Communities Act (2006); Scottish Biodiversity List.
Stoat (ermine) *Mustela erminea*	NA	NA	NA	Appendix 3	NA	NA	Agreement on International Humane Trapping Standards

Species	GB legislation			International Legislation			Other
	Wildlife & Countryside Act (1981)	**UK Biodiversity Action Plan**	**Conservation of Species & Habitats Regulations (2010)**	**Bern Convention (1982)**	**EU Habitats Directive (1992)**	**EC CITES**	
Weasel (common or least) *Mustela nivalis*	NA	NA	NA	Appendix 3	NA	NA	NA
European polecat *Mustela putorius*	Schedule 6	Priority species	Schedule 4	Appendix 3	V	NA	Natural Environment and Rural Communities Act (2006); Scottish Biodiversity List.

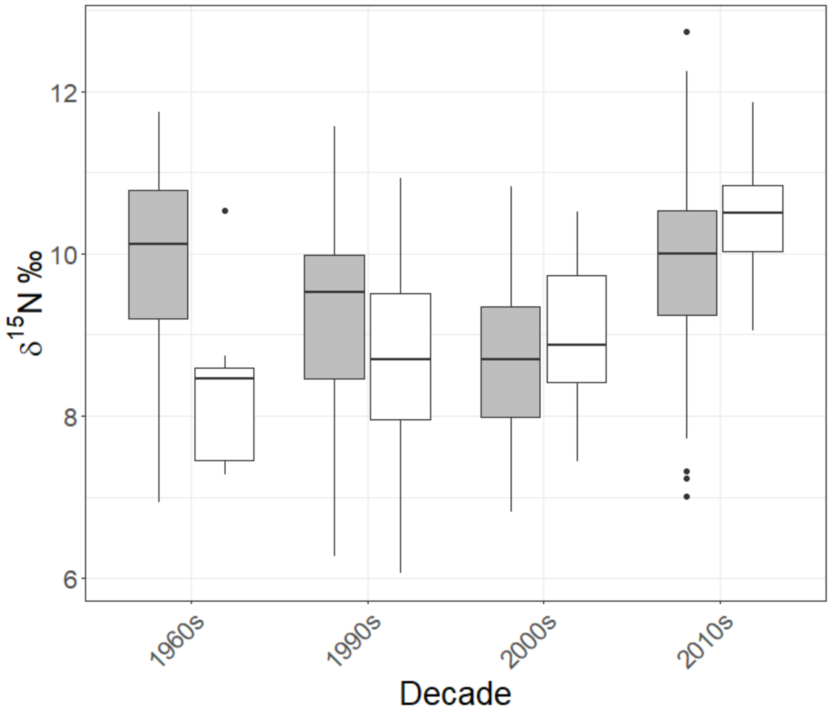
Appendix 2.5. Incidences of secondary exposure to contaminants in native British mammalian carnivores in Europe.

Species	**Country**	**Organochlorine pesticides**	**PCBs**	**PDBEs**	**Second generation anticoagulant rodenticides**	**Toxic metals (including lead and mercury)**
Wildcat *Felis silvestris*	Great Britain	Hamilton et al. 1981			Taylor et al. 2011	
Red fox *Vulpes vulpes*	Great Britain	Blackmore 1963			Tosh et al. 2011 (includes Northern Ireland)	
	Belgium	Voorspoels et al. 2006				
	Germany				Geduhn et al. 2015	
	Poland					Kalisiñska et al. 2009
	Spain	Mateo et al. 2012	Mateo et al. 2012		Sánchez-Barbudo et al. 2012	
European otter *Lutra lutra*	Great Britain	Mason et al. 1986, Chadwick 2007	Pountney et al. 2015	Pountney et al. 2015		
	Finland					Lodenius et al. 2014
	Spain				Sánchez-Barbudo et al. 2012	
European badger *Meles meles*	Great Britain	Jefferies 1969				
	Poland		Tomza-Marciniak et al. 2014			Kalisiñska et al. 2009
	Spain	Mateo et al. 2012	Mateo et al. 2012			
	Great Britain				Sharp et al. 2013	

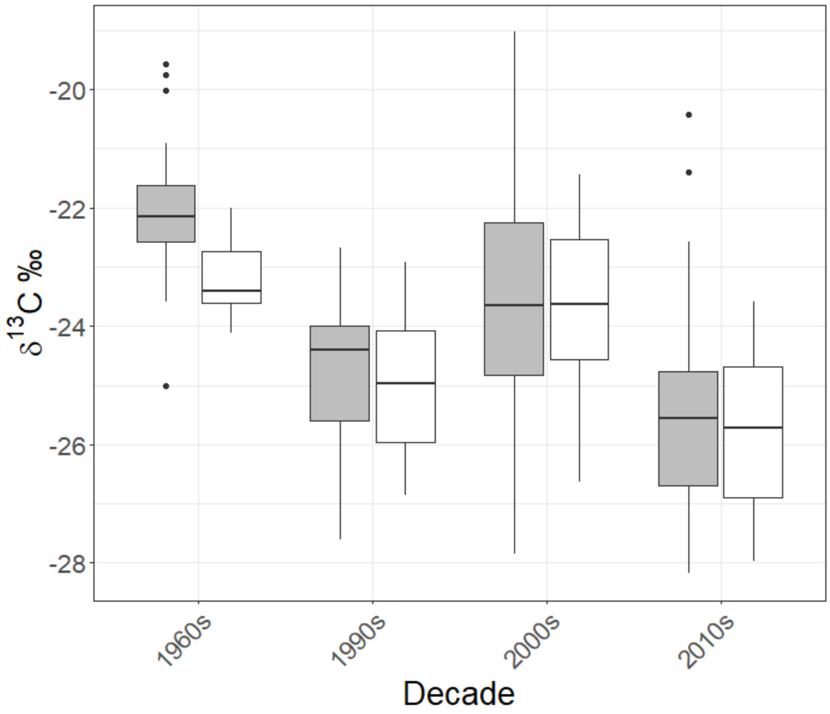
Species	**Country**	**Organochlorine pesticides**	**PCBs**	**PDBEs**	**Second generation anticoagulant rodenticides**	**Toxic metals (including lead and mercury)**
European pine marten *Martes martes*	Ireland	Mason & O'Sullivan 1992	Mason & O'Sullivan 1992			Mason & O'Sullivan 1992
	Poland					Kalisiñska et al. 2009
	Sweden		Bremle et al. 1997			
	Finland					Lodenius et al. 2014
Stoat (ermine) *Mustela erminea*	Great Britain	Jefferies & Pendlebury 1968			McDonald et al. 1998	
	Denmark				Elmeros et al. 2011	
Weasel (common weasel, least weasel) *Mustela nivalis*	Great Britain	Jefferies & Pendlebury 1968			McDonald et al. 1998	
	Denmark				Elmeros et al. 2011	
	Italy	Alleva et al. 2006	Alleva et al. 2006			Alleva et al. 2006
	Spain				Sánchez-Barbudo et al. 2012	
European polecat *Mustela putorius*	Great Britain				Shore et al. 1999, 2003; Sainsbury et al. 2018	
	Denmark				Elmeros et al. 2018	
	Italy	Alleva et al. 2006	Alleva et al. 2006			Alleva et al. 2006

Species	Country	Organochlorine pesticides	PCBs	PDBEs	Second generation anticoagulant rodenticides	Toxic metals (including lead and mercury)
	Germany		Engelhart et al. 2001 Skumatov 2016	Skumatov 2016		
	Poland					Kalisiñska et al. 2009
	Switzerland		Mason & Weber 1990			Mason & Weber 1990
	Finland					Lodenius et al. 2014

Appendix 3.1. Comparison of mean values of (A) δ^{15}N and (B) δ^{13}C from polecat whiskers between all data and a subset where polecats were present continuously between 1960 and 2016. The whole dataset, excluding the subset, is coloured grey, and the subset, where the samples are taken from an area (Grid square OSGB SO) where polecats were present for all decades, is coloured white.

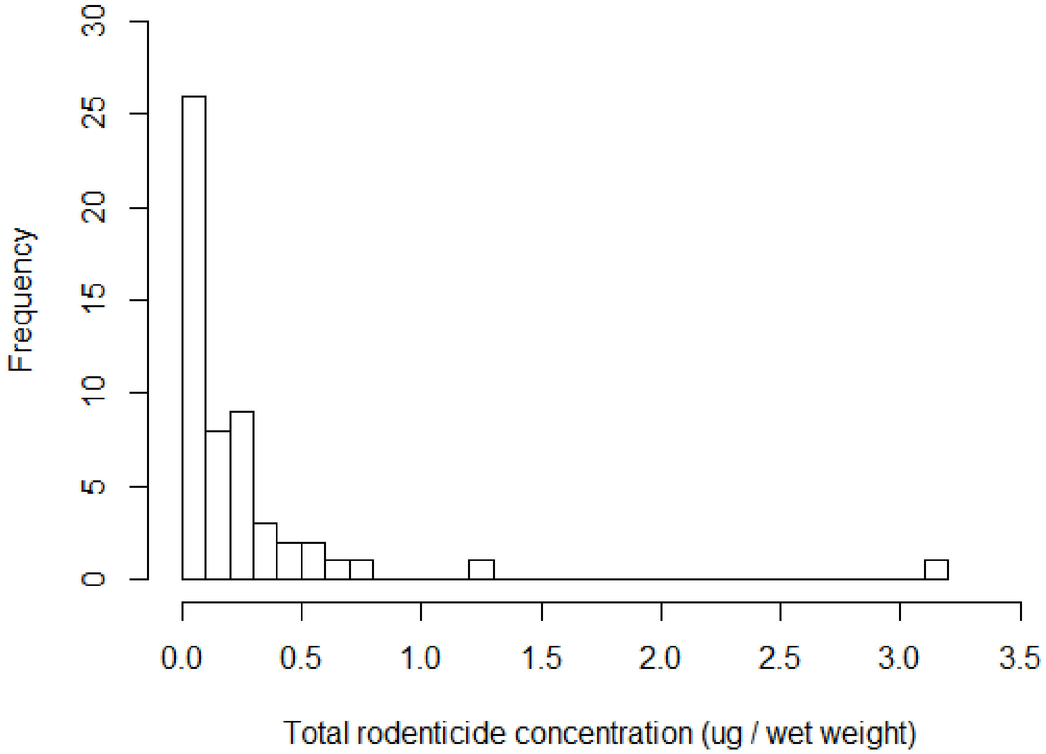


(A)



(B)

Appendix 5.1. Histogram of distribution of total rodenticide concentrations detected in polecats collected 2013-2016. Frequencies are grouped into 0.1 µg/g wet weight intervals. If a lethal level of secondary exposure is assumed to be 0.2 µg/g wet weight (Newton et al. 1999), 38% (n=20) of polecats with detectable levels of rodenticide in their liver residues would be above this threshold.



Appendix 6.1. Example of semi-structured interview guide.

This guide was used for interviews with gamekeepers. Interviews took place at either the participants home, or in the field while visiting their rounds or (most commonly) a combination of the two locations. The order of questions was adapted so that participants could show the location of their activities and demonstrate them (where appropriate) as they described carrying them out.

Background

- How long have you been a gamekeeper?
- How did you get into it?
- Have you always worked here?
- How big is your patch compared to others?
- How many days shooting are there for a year?
- What do you enjoy most about the job?

What

- What does being a gamekeeper involve?
- How does this change through the year, starting in the spring?
- What is a typical day like for you?
- Do you have objectives/targets that you have to meet?
- How do you know if you're doing well?
- Which part of the job takes up the most time/effort?

How

- How do you carry out predator controls?
- How do you go about rodent and rabbit controls?
- How do things you do shape the countryside?
- How have things changed over the time you've been doing the job?

Why

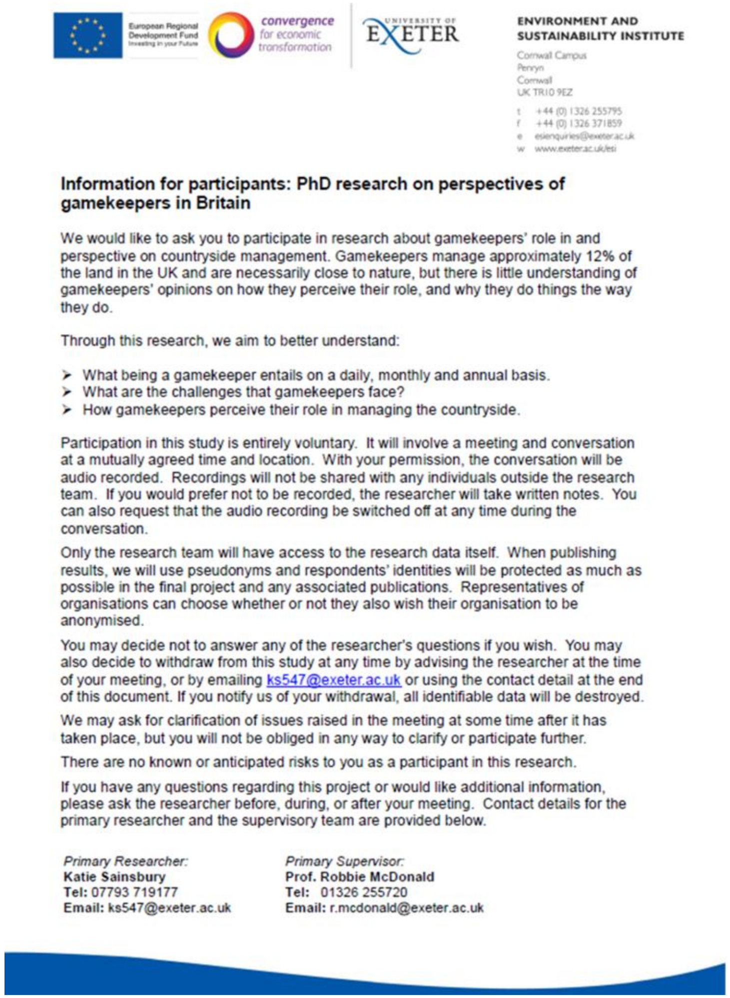
- Do other keepers do things the way you do? If not, why not?
- Is there a community around keeping, where you share what you know and what works/doesn't?

- Why do you manage this kind of shoot rather than grouse or wild game? Would you manage wild game or grouse preferentially?
- What principles guide your work as a gamekeeper?
- What is the biggest risk to your birds?
- What is more of a problem, disturbance or kills?
- If you were to go about minimising disturbance what would you do?
- How do you know what predator is getting at the birds?
- What is more of a problem, vermin on the ground, or from the air?
- To what extent do you target any control activity against specific birds or animals?

Perceptions, values and norms

- What is the most difficult thing about what you do?
- What changes have you made that wouldn't be there otherwise
- Are there any external influences on you to do things the way you do?
- What is a desirable way to behave as a gamekeeper?
- If you were hiring someone, what qualities do you look for?
- Some organisations describe keepers as conserving the countryside. What do you think about that?
- What do other people who aren't keepers think about what gamekeepers do?
- Have you ever experienced any negativity personally towards what you do?
- How would you go about addressing some of the conflict between keepering communities and those who have other interests?
- How do you think the profession will be in 10-20 years?
- What do more predators recovering mean to you?
- How does the community internally handle things like raptors being poisoned?

Appendix 6.2. Example information for participants and consent form.



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Information for participants: PhD research on perspectives of gamekeepers in Britain

We would like to ask you to participate in research about gamekeepers' role in and perspective on countryside management. Gamekeepers manage approximately 12% of the land in the UK and are necessarily close to nature, but there is little understanding of gamekeepers' opinions on how they perceive their role, and why they do things the way they do.

Through this research, we aim to better understand:

- What being a gamekeeper entails on a daily, monthly and annual basis.
- What are the challenges that gamekeepers face?
- How gamekeepers perceive their role in managing the countryside.

Participation in this study is entirely voluntary. It will involve a meeting and conversation at a mutually agreed time and location. With your permission, the conversation will be audio recorded. Recordings will not be shared with any individuals outside the research team. If you would prefer not to be recorded, the researcher will take written notes. You can also request that the audio recording be switched off at any time during the conversation.

Only the research team will have access to the research data itself. When publishing results, we will use pseudonyms and respondents' identities will be protected as much as possible in the final project and any associated publications. Representatives of organisations can choose whether or not they also wish their organisation to be anonymised.

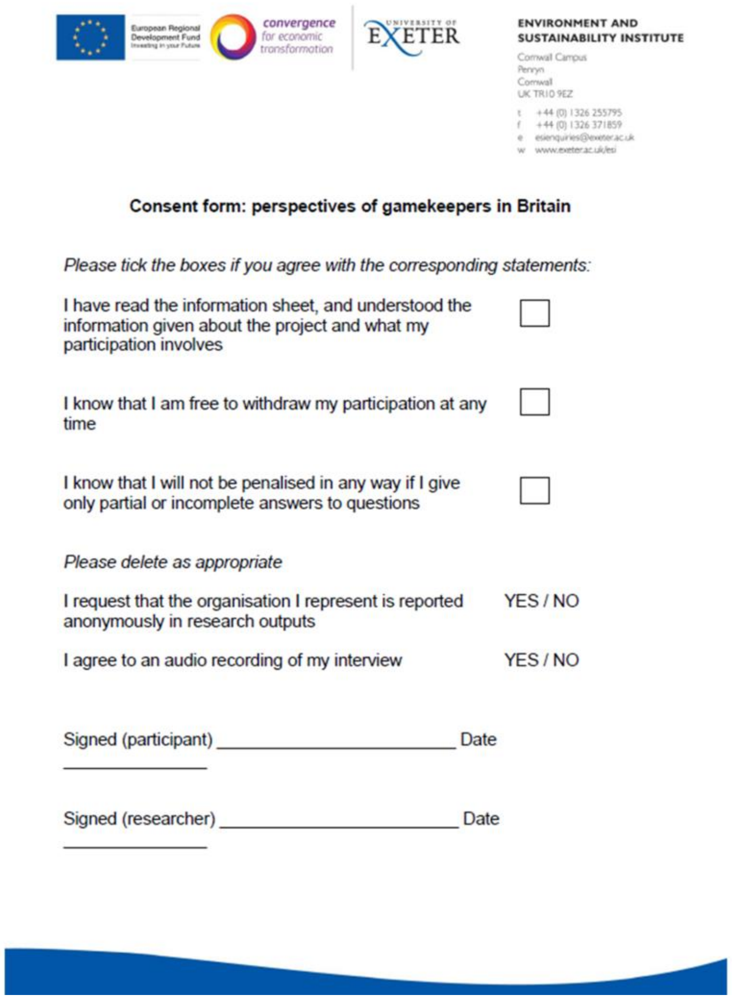
You may decide not to answer any of the researcher's questions if you wish. You may also decide to withdraw from this study at any time by advising the researcher at the time of your meeting, or by emailing ks547@exeter.ac.uk or using the contact detail at the end of this document. If you notify us of your withdrawal, all identifiable data will be destroyed.

We may ask for clarification of issues raised in the meeting at some time after it has taken place, but you will not be obliged in any way to clarify or participate further.

There are no known or anticipated risks to you as a participant in this research.

If you have any questions regarding this project or would like additional information, please ask the researcher before, during, or after your meeting. Contact details for the primary researcher and the supervisory team are provided below.

Primary Researcher:	*Primary Supervisor:*
Katie Sainsbury	**Prof. Robbie McDonald**
Tel: 07793 719177	**Tel:** 01326 255720
Email: ks547@exeter.ac.uk	**Email:** r.mcdonald@exeter.ac.uk



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Consent form: perspectives of gamekeepers in Britain

Please tick the boxes if you agree with the corresponding statements:

I have read the information sheet, and understood the information given about the project and what my participation involves ☐

I know that I am free to withdraw my participation at any time ☐

I know that I will not be penalised in any way if I give only partial or incomplete answers to questions ☐

Please delete as appropriate

I request that the organisation I represent is reported anonymously in research outputs YES / NO

I agree to an audio recording of my interview YES / NO

Signed (participant) ______________________ Date ______________

Signed (researcher) ______________________ Date ______________

Appendix 6.3. Overview of activities carried out by gamekeepers to manage habitat in The Balance.

Gamebird	**Examples of habitat management to maximise gamebird production in The Balance**	**Primary objectives**
Red grouse *Lagopus lagopus scotica* (wild game)	• Controlled heather burning • Sheep grazing (by tenant farmers) • Peat hag restoration • Provide medicated and unmedicated grit	Create a 'mosaic' of habitat that maximises the: • Amount of forage available to birds (insects, heather and seeds) • Number of territories available to cockbirds, thereby producing as many breeding pairs as possible • To aid digestion and manage worm burdens
Grey partridge *Perdix perdix* (wild game)	• Planting cover crops around field margins • Building 'beetlebanks' to break up fields • Planting cover crops • Managing hedgerows • Woodland management • Dew pond restoration • Feed supplemented by hoppers	Provide a rich and diverse natural habitat for birds that: • Provides a natural food source for adults and chicks (insects and seeds) • Regularly distributed hoppers ensure adult birds don't have to leave the nest for long • Provide shelter from inclement weather • Provide cover from predation
Red-legged partridge *Alectoris rufa* (reared game[28])	• Planting cover crops • Food provisioned by hoppers and / or spinners and / or by hand • Water provided in drinkers	• Regular feeding encourages birds to specific locations at desired times of day. Also provides opportunity to check birds overall health and demeanour • Provide natural food source to supplement feed provided by keeper • Provide shelter from inclement weather • Provide cover from predation • Discourage the birds from leaving drives • Water drinkers can be used to provide birds with medication if required

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[28] Most red-legged partridge and pheasants are reared from captive stock for driven shooting, but some shoots do maintain feral populations.

Gamebird	**Examples of habitat management to maximise gamebird production in The Balance**	**Primary objectives**
Pheasant *Phasianus colchicus* (reared game)	As for red-legged partridge, plus: • Woodland management, including cutting in rides, creating dappled light and shade, encouraging understory growth, ‘pleaching’[29] and coppicing	• As for red-legged partridge

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[29] Woodland management practice where lower branches are part cut and laid on the ground so that they continue to grow and provide ground cover.

Appendix 6.4. Predator management activities carried out by gamekeepers as part of keeping The Balance.

Activity	Description	Reared game	Wild game
Lethal controls			
Trapping	Aimed at trapping small ground predators such as stoats and weasels, our primary focus here. Keepers may also target rats and squirrels in cage traps which are dispatched later. Spring traps (Fenn Mark 4) are set in tunnels and on rails over ditches and streams.	Trapping effort varies between shoots depending on keeper priorities. Some only trap around rearing fields, pens and holding crops, others carry out more widespread controls with traps situated along routes the keeper regularly travels. In general, most keepers stated that as by the time pheasants *Phasianus colchicus* / red-legged partridge *Alectoris rufa* are released they are big enough to deter smaller ground predators and so their time is better spent focusing on fox control, which is where the larger risk to their birds lies. Trapping may take place over a month period in the spring while keepers are preparing for poults to arrive.	Grey partridge *Perdix perdix*: Predator controls start in January and carry on through to August. Systematic trapping of field edges and beetle banks, with traps usually set every 100-200 yards. Excluder sticks are used in traps to guide the quarry over the trap treadle and to discourage non-targets from entering traps. Red grouse *Lagopus lagopus scotica*: timing of controls as for grey partridge, with a peak when the hens are sitting on eggs and chicks are hatching. Trap lines are set along routes that the keepers follow as part of their regular routine and make use of linear features such as stone walls.
Snaring	Method to hold foxes before they are shot. Snares are set in field tramlines and on animal trails.	Typically set around pens and holding areas. Varies between keepers.	Grey partridge: used extensively as a way of catching foxes when the keeper can't be there. Effort put in depends on the number of foxes in an area.

Activity	Description	Reared game	Wild game
			Red grouse: the number of foxes on estates interviewed were far fewer than in the lowlands, so snaring effort was lower.
Shooting	Carried out at night with night vision and thermal imaging sensors, or in a team with a lamp. Usually targeting foxes, although sometimes polecats may be shot this way.	Peak activity in spring and summer when cubs are born and birds are released. Keepers will 'sit out from dawn 'til dusk to catch a fox' (Frankie). Some keepers are out 3 days a week year round, others focus their activities to where risk is highest or when they have a problem. Once the shooting season starts, fox control effort reduces.	As for reared game. In the uplands, keepers may use snow to track animals.
Non-lethal controls			
Electric fencing	Electrified wires of up to 8000 volts. To discourage fox, badger and deer from entering pens.	All keepers had electric running around pens and release areas without exception. Sometimes secondary fences were put up around fields adjacent to pens to provide a second line of defence for when birds were flushed to ground.	N/A
Diversionary feeding	Encouraging predators to areas such as the estate boundaries or away from drives by distributing carcasses/remains of other pest species (rat, rabbit, deer) when birds are younger. May also include not eradicating all pest species, e.g. rabbits, so	Talked about by partridge keepers only as a way to keep birds from wandering.	N/A

Activity	Description	Reared game	Wild game
	that predators have an alternative source of prey to game. Mostly useful for birds of prey.		
Other deterrents	Playing radios, flashing lights, flapping plastic bags, leaving human scent markers, and displaying mannequins	Used in pheasant pens in spring / summer to deter predators.	N/A

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