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A thesis submitted for the degree of Doctor of Philosophy

Introgression and the current status of the Scottish wildcat (*Felis silvestris silvestris*)

Kerry Anne Kilshaw
Lady Margaret Hall
Hilary Term, 2015

Dedication

To my parents,

for giving me the wings to fly,

and to James,

who helped me find a direction to fly in.

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Abstract

Baseline data on a species' distribution and abundance are essential for developing practical conservation management plans. Such data are difficult to obtain for many low density cryptic carnivores. The Scottish wildcat, *Felis silvestris silvestris,* is no exception with <400 individuals thought to remain. Its conservation has been further complicated by extensive hybridisation and introgression with the domestic cat (*F.s.catus*). Hybridisation has also resulted in difficulties in discriminating between wildcats, wildcat x domestic hybrids (hybrids) and tabby coloured feral domestic cats. This has inhibited survey efforts, leading to a lack of general ecological information.

Using the most recent identification tools available, extensive surveys using various methods including camera trapping were carried out across Northern Scotland in order to examine the current status of the Scottish wildcat. Current distribution indicates a more restricted range than recent studies. Wildcats are at risk of hybridisation from feral domestic cats and in particular, hybrids, throughout their current probable range. The distribution of hybrids overlaps with both feral domestic cats and wildcats, pointing to a significant threat from hybrids acting as a bridge between wildcats and feral cats. Mean density estimates of 3.5 (SD=0.7) wildcats/100 km^2 were comparable with those from other studies in Scotland using different survey methods. Total population size estimates ranged between 115-314 individuals depending on local densities and home range size. Population viability analysis (PVA) indicated the current population is not viable unless management actions are undertaken in the near future (Mean time to extinction = 48.2 years (SD = 9.39), probability of extinction=1, SE = 0), and that reducing mortality rates and/or supplementing populations from captive bred cats are likely to be necessary to achieve viability. Based on these data, the Scottish wildcat may be more endangered than many other species classified as Endangered and the current status of the Scottish wildcat should be reviewed.

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Statement of Contribution

As Principle Investigator I, Kerry Anne Kilshaw, contributed the primary intellectual input to design, data collection and data analysis for the contents of this thesis. Dr. Rob Ogden and Dr. Ross McEwing at the Wildgenes laboratory, Royal Zoological Society of Scotland, Edinburgh, UK contributed resources and carried out genetic analysis of the scat samples collected. Dr. Robert Montgomery, University of Missouri, USA assisted with the data analysis for Chapter 3.

Signed:

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Kerry Anne Kilshaw

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Chapter 1

1.0 Introduction

1.1. Species background

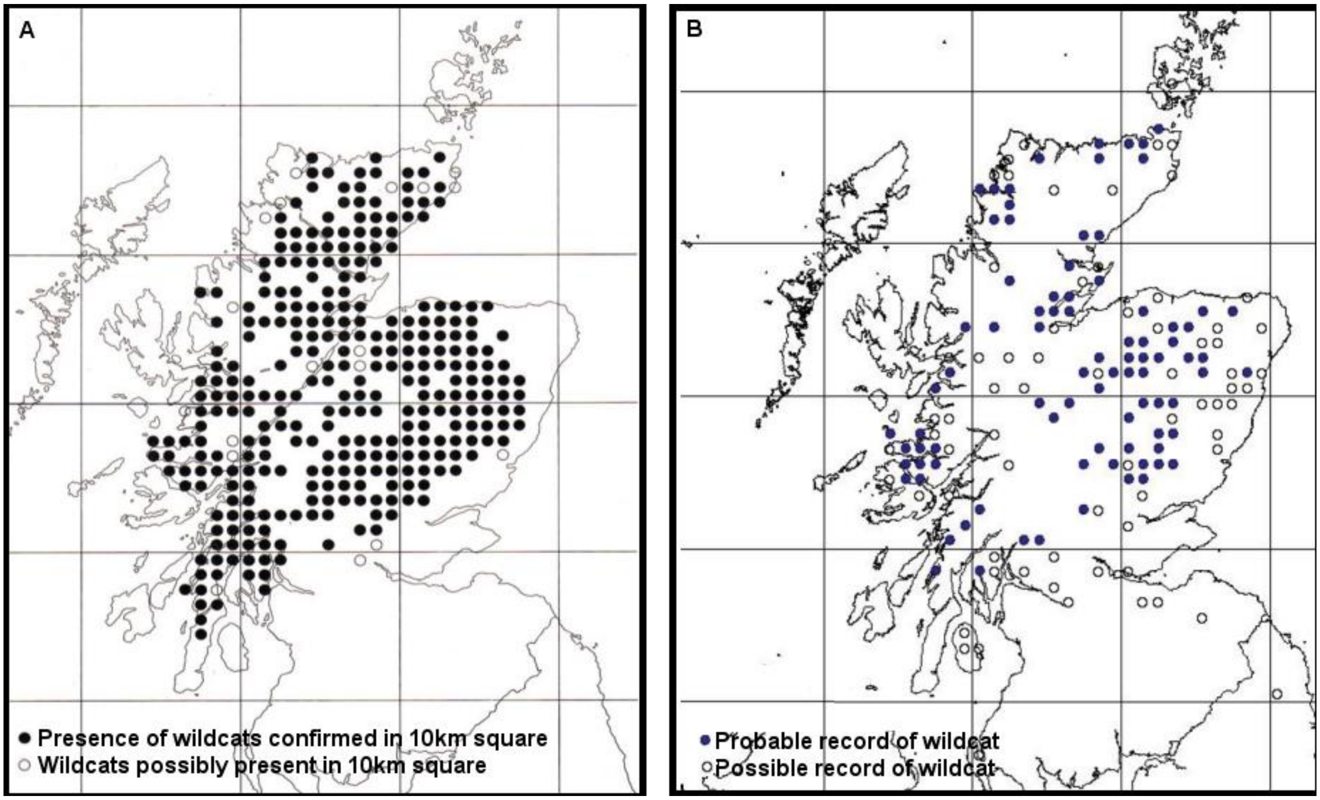
The Scottish wildcat (*Felis silvestris silvestris*) is Britain's only surviving native felid (Macdonald *et al.*, 2004). Previously classified as a separate Scottish species, *Felis grampia* (Miller in 1907) (and later reclassified as a subspecies *F. s. grampia*, Miller 1914, Pocock, 1951), following recent genetic studies, the Scottish wildcat is now considered to be part of the European wildcat subspecies *F. s. silvestris* (Pierpaoli *et al.*, 2003; Driscoll *et al.*, 2007). Palaeo-geological, morphological, and genetic evidence indicates that the Scottish wildcat is descended from continental European ancestors, believed to have separated from the European wildcat population some 7,000 – 9,000 years ago when Britain was isolated after the last glacial maximum (Yalden, 1982; Yamaguchi *et al.*, 2004b; Driscoll *et al.*, 2007). The wildcat is likely to have existed in England and Wales for a long period before it was first recorded in Scotland, with records of it being hunted for sport or as a pest species (vermin) as far back as the 12th Century (Hamilton, 1897). However, the wildcat began to disappear from much of its southern range in the 1700s, and by 1800, the wildcat was restricted to northern England, Wales (where it was scarce) and Scotland, by 1850 it had almost disappeared from west central Wales and was scarce in Northumberland. By 1880, the wildcat survived only in Scotland, and by 1915 it was restricted to the north-west of the Highlands (Langley & Yalden, 1977; Tapper, 1992).

The initial decline of the Scottish wildcat is attributed partially to habitat loss, in particular the loss of forested areas, and partially to hunting for fur and persecution (Kitchener, 1995; Lovegrove, 2007). Persecution was particularly rife in the 16^{th}-18^{th} centuries as a resulted of the Preservation of Grain Act, passed in 1532 by Henry VIII and strengthened by Elizabeth I in 1566. This act made it compulsory for every man, woman and child to kill as many creatures as possible that appeared on an official list of 'vermin'. Communities that failed to kill enough animals were punished with fines. As a result, during this period, millions of birds and mammals were slaughtered, and the wildcat was no exception with the bounty on the head of a wildcat fixed at 1 penny (Lovegrove, 2007). In the 17th century alone, almost 5000 bounties were paid for wildcat heads in England and Wales (Lovegrove, 2007). The development of sporting estates in Scotland from the mid-19th century led to a further decline because wildcats were considered very destructive to game and lambs and were consequently heavily controlled (Langley & Yalden, 1977; Tapper, 1992; McOrist & Kitchener, 1994a). For example, data from the Game Conservancy's National Game Bag Census return for 1984/85 recorded the killing of 274 wildcats on 40 shooting estates in central, eastern and north-eastern Scotland (Harris *et al.*, 1995), indeed Kitchener (1995) stated the development of sporting estates and consequent persecution was the "catalyst for final extirpation" of the wildcat.

The decline of the wildcat is thought to have abated during the First World War with the associated decline of gamekeepers (Tapper, 1992), and numbers rapidly increased, although it is unclear how much of this population expansion can be attributed to the presence of feral domestic cat (*F.s.catus*) x wildcat hybrids. Recolonization was aided by reforestation by the Forestry Commission (established in 1919) and by the 1950s the wildcat had recolonized most of the area north of the central belt of Scotland (Jenkins, 1962; Kitchener, 1995). In 1991, Easterbee *et al.* (1991) produced a distribution map based largely on a questionnaire survey carried out in the 1980s (1983–87) which was based on 499 ten-km^2 units with more than 400 people supplying information. This suggested that wildcats were restricted to the area north of a line between Edinburgh and Glasgow (known as the Central Belt), and the main populations appeared to occur in the east, north-east, and south-west. In the 1990s (1992–94), Balharry and Daniels (1998) carried out a further survey based on carcass location, live trapping and road traffic accident (RTA) surveys which suggested that the Scottish wildcat was restricted to the east of Scotland.

The most widely published population estimate indicated that the number of individuals left with "pure" wildcat pelage may be as low as 400 (Macdonald *et al.*, 2004). However this estimate was obtained from applying the morphological characteristics associated with wildcats (e.g. larger skull, larger body size, coat pattern, longer limb bones and shorter intestine; Kitchener & Easterbee, 1992; Daniels, 1997; Yamaguchi *et al.*, 2004a) to the samples collected by Balharry and Daniels (1998) and then extrapolating the percentage of this sample found to have a "pure" wildcat pelage onto the Harris *et al.* (1995) estimate of 3500 wildcats. The actual number of wildcats in the "wild-living" cat population in Scotland today is therefore, unknown and some studies have suggested it may be as low as 35 individuals (www.wildcathaven.co.uk), However, a recent population survey carried out by Scottish Natural Heritage between 2006-2008 (Davies & Gray, 2010) using interviews and questionnaires has updated the current distribution of this species, indicating that very little change has occurred since the Balharry and Daniels (1998) survey except that there were more records further south (Figure 1.1).

Figure 1.1 Probable and possible wildcat records from A) Balharry and Daniels (1998) survey 1983-1987 and B) Scottish wildcat survey 2006-2008 (Davies & Gray, 2010).



Currently, the biggest threat facing the European wildcat across its range is hybridisation with the domestic cat (Stahl & Artois, 1995; Driscoll & Nowell, 2009). This threatens the genetic integrity of the species through genetic erosion, where the limited gene pool of the species becomes further diminished as individuals die before having a chance to reproduce with one another, and may result in its genetic extinction (Suminski, 1962; Randi *et al.*, 2001; Pierpaoli *et al.*, 2003). Extensive hybridisation in the Scottish population has led to difficulties in identification of wildcats from hybrids and feral tabby domestic cats (Daniels, 1997; Daniels *et al.*, 1998). This complicates both study of the species and enforcement of conservation legislation (Macdonald *et al.*, 2004). The mechanisms and extent of the problem are poorly understood (discussed below). Consequently the current status of the Scottish wildcat population is unknown.

1.2. Hybridisation and introgression

Hybridisation, "the interbreeding of individuals from genetically distinct populations regardless of their taxonomic status" (Woodruff, 1973; Rhymer & Simberloff, 1996) can also result in introgression hybridisation (Rhymer & Simberloff, 1996). Introgression occurs when the backcrossing (crossing of a hybrid with one of the parent species) of inter-specific hybrids causes gene flow from one species into the gene pool of another (Anderson, 1949). It is a long term process, taking many generations of hybrids before backcrossing occurs. The resulting individuals have a complex mixture of parental genes and morphological characteristics compared to those resulting from simple hybridisation (where an individual has 50% of genes from each parent; Anderson, 1949).

Hybridisation and introgression occur naturally between many species and are thought to be an important aspect of evolutionary diversification which may eventually result in speciation (Arnold, 1997; Dowling & Secor, 1997; Smith *et al.*, 2003). Although primarily studied in plants (e.g. Arnold, 1997; Abbott & Lowe, 2004; Hegarty & Hiscock, 2005), it also occurs in many mammal species. For example; between sable (*Martes zibellina*) and pine marten (*M. martes*) (Grakov, 1994), between many deer species (e.g. Goodman *et al.*, 1999) and between grey wolves (*Canis lupus*) and coyotes (*C. latrans*) (Lehman, 1991). Hybridisation may not always result in genetic erosion of one or both of the parent populations; in some cases the hybrid offspring are infertile e.g offspring of donkeys and zebra (*Equus* spp.) (Gray, 1972) or fail to produce offspring e.g. mating between European mink (*Mustela lutreola*) and American mink (*M.vison*) (Romanov, 1993) and in some cases, hybridisation between native taxa can save one of them from extinction by increasing the genetic diversity of the endangered population (Dowling & Secor, 1997).

In other cases, hybridisation or introgression may present a significant extinction risk by causing the elimination of one or both parental species such that no genetically pure individuals remain (Rhymer & Simberloff, 1996; Levin, 2002). Extinction of parental species can occur in only a few generations (Wolf *et al.*, 2001). For example, the translocation of the Tatra mountain ibex (*Capra ibex ibex*) from Sinai and Turkey into a Czechoslovakian population resulted in outbreeding depression; offspring inherited a mid-winter calving date, thereby losing their young. The recipient population went extinct as a result (Greig, 1979).

In addition to threatening the genetic integrity of endangered populations, hybridisation and introgression affect the legal aspects of conservation. The identification of definable taxonomic units is fundamental to much current conservation. Whether hybrids should be protected or not is still under debate (Allendorf *et al.*, 2001). It has been recommended that hybrids arising from natural causes, which can influence the evolution of a species, should be given protection, but not where interbreeding arises not-naturally (Allendorf *et al.*, 2001), such as from the transport of species by humans or where habitat change leads to range expansion of previously allopatric species (Rhymer & Simberloff, 1996). This may be difficult to assess, and it seems advisable that each situation should be examined separately to determine the importance of the hybrid population to the long term viability of either parent populations. If the number of parent populations remaining is small, then the value of the hybridized population is greater (Allendorf *et al.*, 2001). In other cases, introgression may be so extensive that complete admixture or hybrid swarming has occurred such that few if any of the parental population remain. In such cases, conservation of the hybrids should be considered (Allendorf *et al.*, 2001).

There has been a recent increase in the number of species threatened by hybridisation and introgression, largely as a result of anthropogenic activities (Rhymer & Simberloff, 1996). The European wildcat is threatened across its range by hybridisation with the domestic cat (Randi *et al.*, 2001; Pierpaoli *et al.*, 2003; Oliveira *et al.*, 2008). The genetic integrity of European wildcat populations is threatened both by the loss of allelic variation due to genetic drift and by the introgression of genes from roaming or feral domestic cats (Stahl & Artois, 1991). Hybridisation, therefore, has been identified as one of the greatest threats to this species (Stahl & Artois, 1994), having already resulted in the local extirpation of some European wildcat populations (Suminski, 1962). The extent of introgression across the wildcats' geographical range appears to vary considerably however. Introgression is thought to be particularly prevalent in the Scottish and Hungarian wildcat populations compared to other European wildcat populations (Parent, 1975; McOrist & Kitchener, 1994b; Beaumont *et al.*, 2001; Daniels *et al.*, 2001; Randi *et al.*, 2001; Pierpaoli *et al.*, 2003; Lecis *et al.*, 2006; Oliveira *et al.*, 2008; O'Brien *et al.*, 2009). The potential for hybridisation is exacerbated by habitat loss and fragmentation, by urbanization and by reduced prey availability. These can result in decreased wildcat numbers or fragmentation of the wildcat population and consequently increased reproduction with domestic cats (Oliveira *et al.*, 2008). Some authors have observed differences in body sizes between populations of *F. s. silvestris* along an east-west gradient (e.g. Kratochvil & Kratochvil, 1970; Platz *et al.*, 2010). Originally these differences were thought to be due to variation in habitat quality and climate along an east-west gradient but more recently, authors have suggested that these morphometric differences may be due to the differing levels and history of introgression in different populations (Platz *et al.*, 2010). Introgression in general has resulted in wild-living cat populations across Europe exhibiting a range of morphological and genetic characteristics of both *F.s.silvestris* and *F.s. catus,* making identification between these two species difficult. This problem is particularly prevalent in Scotland where unequivocal identification is difficult because of the high levels of introgression. As a result of the differences between and within different populations of *F.s.silvestris* no single set of characteristics can be used to distinguish between wildcats and domestic cats across their range, instead, diagnostic characteristics need to be identified for each population separately (Yamaguchi *et al.*, 2004a; Platz *et al.*, 2010).

1.2.1. Hybridisation and Introgression in the Scottish wildcat population

The Scottish wildcat is thought to have been interbreeding with the closely related domestic cat for at least 2-3000 years, although not in all areas at the same time (Hamilton, 1897; Maltby, 1979; Noddle, 1987). The risk of the Scottish wildcat breeding with domestic cats was first documented in 1820 (Bewick, 1820) and later by Darwin (1875). The potentially negative impact of hybridisation was recognised by Cocks (1876), with later evidence that inter breeding occurred (Pitt, 1939; Gray, 1971; Corbett, 1979). Although hybridisation is thought to have been occurring for some 2-3000 years, the first cat classified as *F. grampia* based on its pelage wasn't collected until 1904 (Pocock, 1951). This "type specimen" was the bench-mark against which all future specimens have been compared (e.g. Corbett, 1979; French *et al.*, 1988; Easterbee *et al.*, 1991). Population surveys provided evidence that hybridisation was occurring (Langley & Yalden, 1977; Easterbee *et al.*, 1991). Daniels *et al.* (1998) morphological analysis of 333 "wild-living" cats from the north-east of Scotland identified two groups. These were categorized as Group I cats, which had the characteristics typically associated with wildcats, and Group II cats, which generally represented domestic cats. There was, however, overlap between the two groups, Genetic analysis using microsatellites of a sub-sample of 230 “wild-living” cats found a bimodal distribution, with two clear groups but with a high degree of genetic overlap between them, indicating introgression was occurring (Beaumont *et al.*, 2001; Daniels *et al.*, 2001).

In addition to threatening the genetic integrity of the species, hybridisation has resulted in a range of practical problems for this species. Difficulties in identifying between wildcats, wildcat x domestic hybrids and wild-living tabby coloured feral cats have resulted in problems surveying and a consequent lack of ecological information. The complications in identification have made surveys and population estimates difficult (Macdonald *et al.*, 2004), but have also led to legal difficulties because, in the UK, the Scottish wildcat is legally protected and the feral cat can be legally controlled (Daniels *et al.*, 1998). Most recent studies have therefore focused on a classification method for the wildcat to try and resolve these difficulties. A variety of features have been used to differentiate wildcats, ranging from intestinal and limb bone length, skull size, cranial index, physical size and coat pattern (Schauenberg, 1977; French *et al.*, 1988; Daniels *et al.*, 1998; Yamaguchi *et al.*, 2004a) to genetic differences (Beaumont *et al.*, 2001; Daniels *et al.*, 2001; Driscoll *et al.*, 2007).

In 2005, Kitchener *et al.* developed a practical pelage based diagnostic method which uses 7 key pelage characteristics (7PS: extent of dorsal line, shape of tail tip, distinctness of tail bands, broken stripes on flanks and hindquarters, spots on flanks and hindquarters, stripes on nape, and stripes on shoulder) to separate wildcats from hybrids and domestic cats. Recent developments in genetic research focus on the use of Single Nucleotide Polymorphisms (SNPs) which are particularly useful for low DNA yield samples. Diagnostic SNPs have been found on both mitochondrial DNA (mtDNA) (Driscoll *et al.*, 2007) and the Y-chromosome (C. Driscoll pers comm., 2013) and nuclear DNA SNP markers have also recently been identified to allow the identification of wildcats, domestic cats, their hybrids and backcrosses (Nussberger *et al.*, 2013). McEwing *et al.* (2011) developed a real time PCR assay for the rapid assessment of mtDNA introgression, allowing quick identification of European wildcat mtDNA lineages from domestic lineages in wild-living cat samples. Currently identification is based on both the mtDNA assay and 14 nuclear DNA SNP markers selected from a subset of the SNP markers identified by Nussberger *et al.* (2013). Identification of more SNP markers should allow more effective identification of hybrids. There are therefore, tools which can help to clarify the status of the Scottish wildcat specifically and the European wildcat in general.

It is unclear how widespread introgression is across Scotland however. Hybridisation is thought to be more likely to occur in areas of high human habitation, where there are high population densities of domestic and feral cats (Macdonald *et al.*, 2004). For example, in Hungary, male European wildcats were shown to shift their home ranges in the breeding season to cover the territories of female farm cats (Szemethy, 1993). This suggests hybridisation may also be sex-biased with male wildcats playing a larger role than female wildcats in the process. It is not known whether this is also the case for the Scottish wildcat. Studies in Europe suggest that rates of hybridisation could locally increase in rural areas with a widespread and abundant presence of domestic cats, if wildcat populations decline strongly as a result of direct persecution and/or habitat loss (Pierpaoli *et al.*, 2003). It is likely therefore, that hybridisation between the Scottish wildcat and feral cat increases in relation to proximity of human habituation and in areas where the availability of suitable habitat for wildcats has become fragmented or lost.

1.3. Study species and research rationale

F. s. silvestris is currently considered by the IUCN to be Least Concern. If it were to be confirmed that few genetically pure wildcats remain in Scotland with a high risk of extinction in the wild then the Scottish population will be re-classified as Critically Endangered (Driscoll & Nowell, 2009).

Baseline data on the distribution and densities of a species is essential for developing practical conservation management plans. The complications associated with hybridisation render such data for Scottish wildcats rather elusive. Currently only limited density estimates exist for the Scottish wildcat; 0.3 individuals/km^2 on the Glen Tanar estate in Deeside (Corbett, 1979), 0.01 individuals/km^2 in Ardnamurchan, Western peninsula (Scott *et al.*, 1993), and more recently, density estimates of wildcats and hybrids combined of 0.68 (SE=0.09, CI=0.50-0.80) individuals/km^2 in the north-eastern Cairngorms National Park (Kilshaw *et al.*, 2015a) and 0.02 (SE=0.01, CI=0.01-0.06) individuals/km^2 on the Morvern peninsula on the western coast of Scotland (Littlewood *et al.*, 2014). The earlier estimates may no longer be accurate, particularly in the Glen Tanar estate where rabbits have been eradicated since research on the wildcat was carried out there (D. Hetherington pers comm., 2009). Survey methodology issues also complicate interpretation of density estimates. Surveys have generally used questionnaires and interviews (e.g. Easterbee *et al.*, 1991; Davies & Gray, 2010), road traffic accident surveys, carcass collection and live trapping (e.g. Balharry & Daniels, 1998) or a combination of these. These methods have their limitations. For example, sightings data collected using interviews and questionnaires can cover large survey areas but may be biased because they may reflect the distribution of interviewees rather than species distribution (Lozano *et al.*, 2003) and there is clearly a high risk of misidentification of wildcats whatever species 'definition' is used (Davies & Gray, 2010). In addition, most of these surveys were carried out before the recent pelage (Kitchener *et al.*, 2005) and genetic tools (2007 to present) were developed. More recently, studies have shown that camera trapping is also a feasible methodology (Kilshaw *et al.*, 2015a). There is therefore a need to carry out a large scale survey across Scotland using these new diagnostic tools and recent survey techniques to examine the distribution of wildcats, hybrids and domestic cats and to identify areas of the highest risk of hybridisation.

Here, I use large scale surveys across Northern Scotland to examine the current status of the Scottish wildcat. The following objectives are outlined; *i*) establish the current distribution of wildcat, hybrids and feral domestic cats, *ii*) map potential hybridisation risk for the wildcat and discuss the implications this has for future management actions, *iii*) produce density estimates and use these to provide a revised population size estimate, *iv*) compare different survey methods and make recommendations on how to improve detection methods, *v*) examine long term population viability.

Chapter 2

2.0 Study areas and methodology

2.1. Northern Scotland: Overview

The study was carried out across various sites in northern Scotland, north of the Central Belt which lies between Glasgow and Edinburgh (Figure 2.1).

Scotland was once largely covered in forest Godwin (1975), largely oak (*Quercus* sp.), ash (*Fraxinus excelsior*) and birch (*Betula* sp.) in the south and Scots pine (*Pinus sylvestris*) forming much of the Caledonian forests covering the Highlands to the north (McVean & Ratcliffe, 1962; Summers *et al.*, 1999). By the Middle Ages, the lowlands had largely been cleared for sheep farming, and by the 18th Century the introduction of widespread sheep farming in the Highlands kept the upland landscapes free of woodland. The rapid growth of sporting estates in the 19th Century also meant management for grouse (*Lagopus lagopus)* shooting has kept the moorlands free of trees. Pine forests were exploited to meet the needs of industrial growth (Forestry Commission, 1998). By 1905 only an estimated 350 000 ha (4.5% of Scotland) of woodland, native and planted, remained (Statistics, 2008). Overall, deforestation has removed 99% of Scottish woodlands, leaving only small, highly fragmented patches across Scotland (Steven & Carlisle, 1959). Nowadays, some 25% of Scotland's landscape is dominated by bog with a further 13% consisting of improved grassland, some 12% of coniferous plantations and another 12% composed of dwarf shrub heath land (McGowan *et al.*, 2002), a stark difference to the forested landscape that once dominated much of Scotland.

Today, moorland areas are intensively managed for grouse. Predators and ticks are controlled and heather (*Calluna vulgaris*) is frequently burned to generate new growth resulting in a mosaic of young and mature plant growth. Hunting is an important economic activity in northern Scotland (estimated £200 million/year) with some 56% of land in Scotland influenced by shooting sports to some degree (SGA, 2011). Hunting is focused on wild rabbits (*Oryctolagus cuniculus*), grouse and deer stalking (roe deer *Capreolus capreolus* and red deer *Cervus elaphus*). The introduced pheasant (*Phasianus colchicus*) is also reared in high numbers as a game species. In spite of their hunting, deer are highly abundant (Clutton-Brock *et al.*, 2004) with a mean of 12.34 deer/km^2, twice as high as the desired objective of six deer/ km^2 identified by the Deer Commission, Scotland in order to reduce their impact on both the environment and other species (DCS, 2010). Other primary human activities include animal husbandry (namely cattle and sheep), intensive agriculture that is mainly related with cereal crop production and, recently, with biofuels production. Recently, areas previously considered as remote are increasingly being subjected to human pressure, due to a boost in different recreational activities, like outdoor sports (Habron, 1998).

Scotland supports approximately 75% (455 species) of the UK priority species (BAP, 2010). Nine carnivore species are supported (weasel *Mustela nivalis*, stoat *M. erminea*, polecat *M. putorius*, American mink *Neovison vison*, pine marten *Martes martes*, otter *Lutra lutra*, badger *Meles meles*, red fox *Vulpes vulpes* and wildcat (Arnold, 1993). Mammal prey species available across the study site include field vole *Microtus agrestis*, bank vole *Myodes glaureolus*, water vole *Arvicola terrestris*, wood mouse *Apodemus sylvaticus*, house mouse *Mus domesticus* and brown rat *Rattus norvegicus*) and three lagomorphs species (European rabbit, brown *Lepus europaeus* and mountain hare *L. timidus*).

Topography, climate, land use and habitat across northern Scotland vary from east to west and north to south with large bodies of water (Lochs) breaking up the landscape. The main geographic features comprise the Grampian Mountains and the northern Highlands, which rise steeply from the glens and fjord-like sea lochs. The study area can be categorized into four main climatic and topographic areas; the Highlands (excluding the Islands) in the north; Grampian, (Morayshire and Aberdeenshire) to the east, the Central uplands to the south and Argyll and Bute (excluding the Islands) to the west. A summary of the main features of interest for each region are shown in Table 2.1.

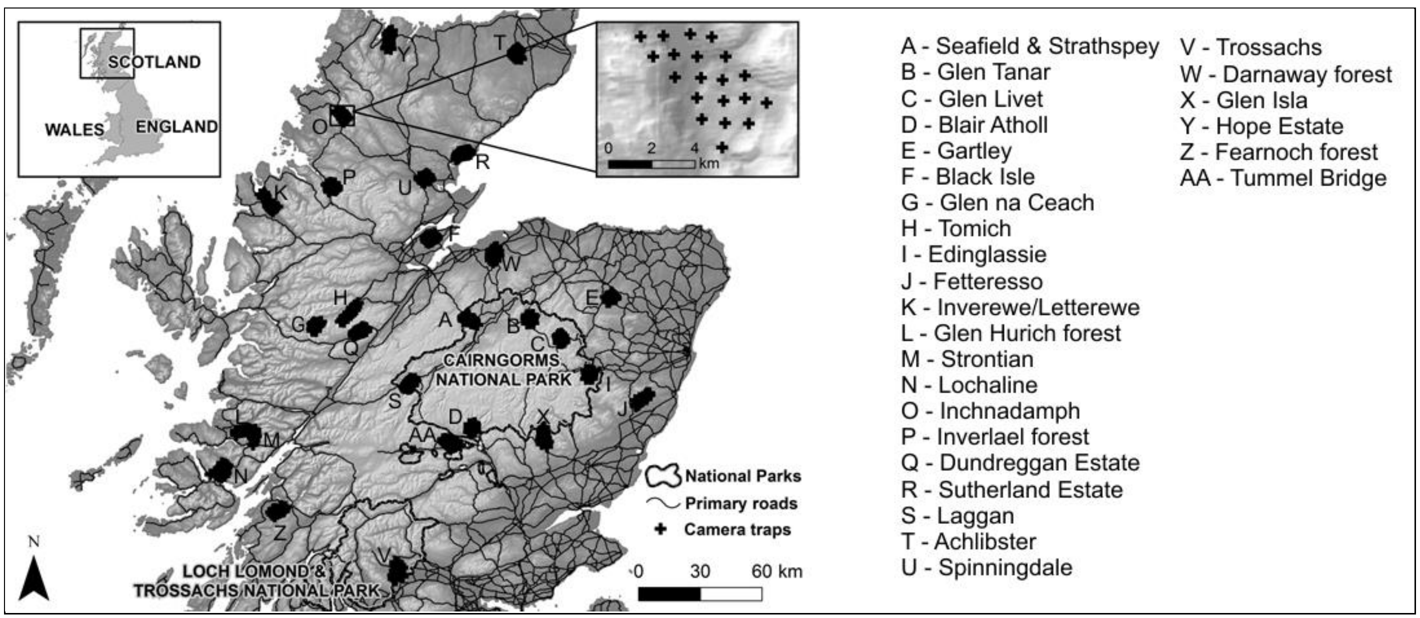
Table 2.1 Summary of the different regions surveyed during this study (Data collated from MLURI (1993); SCROL (2011); MET (2012)).

	Highland	**Grampian**	**Central**	**Western**
Population Density ind/km^2	8	36.6	58.2	19
Main habitats				
Heather moorland	44%	20%	21%	11.5
Coniferous/broadleaved	9%	13%	15%	17%
Rough grassland	2.40%	2%	7%	11%
Improved grassland	4.40%	12.60%	18%	10
Arable	2.10%	36.50%	47%	0.7
Annual rainfall (mm)	700-1700	700-1500	<700	1000-3500
Annual snowfall (days)	40-100+	20-100+	20-60	10-60
Mean annual temp (Celsius)	0-8C	6-9C	9	8-9.4

2.2. Specific study sites

Between October 2010 – July 2013, 23 sites were surveyed for wildcat, hybrid and feral domestic cats (Figure 2.1). Data from an additional 4 sites for use in Chapter 3 were provided by the Royal Zoological Society of Scotland (RZSS) which was collected as part of the Highland Tiger Project and are also shown on Figure 2.1. Sites were chosen primarily to survey a range of different habitats across Northern Scotland. A brief overview of the 23 primary survey sites is provided below.

Figure 2.1 Map of northern Scotland showing location of study sites A – AA for the detection of wildcats, hybrids and feral domestic cats, 2010-2013. Sites B, C, D and I were surveyed by RZSS.



2.2.1. A - Seafield and Strathspey estates, Highland

The Seafield and Strathspey Estate site (57°16'29"N, 3°50'21"W) is located in the northwest of the Cairngorms National Park in the Highlands. Privately owned, approximately 23 815 hectares of the estate lies within the Cairngorms National Park, of which 5324 hectares has been designated a Site of Special Scientific Interest (SSSI). Largely composed of a mixture of heather moorland (39%), Scots pine plantations (41%), birch woodland, mainly bordering the numerous rivers (5%) and areas of rough grazing and gorse scrub (15%) which is mainly grazed by sheep and in some areas supports healthy rabbit populations; the estate supports a variety of predators including the Scottish wildcat. The estate has been traditionally used for red grouse (*L. l. scotica*) shooting and deer stalking and as a result predator control has played a part in the management of the estate. Although the estate is now primarily used for tourism and deer stalking, predator control is still carried out, particularly because parts of the estate are recognised as important lek sites for Capercaillie (*Tetrao urogallus*) (Estates, 2011). The survey site encompassed an area of $35km^2$. The river Spey runs through the site. A busy primary road runs alongside and through some of the north/north eastern edge of the study site. A couple of secondary roads run through the southern edge of the study site as well as local estate roads running through the study site. The nearest village, has a population of approximately 700 inhabitants (SCROL, 2011). The area is a popular tourist destination for walkers and part of the site is used by cross country skiers during heavy snowfall.

Wildcats are known to be present in the area and were last recorded in 2010 by Kilshaw and Macdonald (2011) during a pilot camera trap study. This study also noted a large population of rabbits on site, although the population subsequently crashed after two consecutive bad winters in 2009 and 2010.

2.2.2. E - Gartly Forest/Leith Hall, Grampian

Gartly Forest (57°21'37"N, 2°45'53"W) is owned by the Forestry Commission Scotland and is managed for timber and deer. The forest is largely composed of a mosaic of Norwegian Sitka spruce patches (34%) of varying ages including recently felled areas. Among these patches smaller areas of heather (12%) and rough grass can occur. The forested area is surrounded by grassland covered areas (22%) and arable fields (17%), mainly used by the surrounding farms for livestock rearing, particularly cattle and sheep. Deer control is currently carried out on the site but not predator control. The south of the forest is bordered by Leith Hall, a property owned and managed by the National Trust of Scotland (268 acres). Approximately 6 acres are dominated by ornamental trees and shrubs but large areas are composed of rough pasture with patches of gorse (30%) which support rabbits and some of the site is leased to a farmer who grazes cattle and sheep and broad-leaved woodlands are found along the river at the southern edge of the site (3%). The forest is popular with dog walkers and no motorized vehicles are allowed within the forest or gardens. Human population surrounding the site is ~144 (SCROL, 2011). Leith Hall in particular is a popular tourist attraction in summer.

Last records for wildcats at Gartley are from 2008 (Gateway, 2014a) although wildcats were reported by Forestry Commission staff and National Trust of Scotland immediately before the survey work. Rabbits were found at the northern end of the site in adjoining pasture/gorse scrubland and in the pasture bordering the site.

2.2.3. F - Black Isle, Highland

The Black Isle is a small peninsula located in Ross-shire, Northeast Inverness. The peninsula is mainly used for agriculture, with large arable fields. The study site **(**57°36'40"N, 4°13'24"W) was situated in the eastern half of the peninsula, in Forestry Commission land. The site is dominated by Norwegian spruce plantation (45%) with some dwarf shrub areas (11%) and surrounded by pasture (22%) and arable fields (17%) which is mainly used for sheep and cattle grazing and grain production including winter barley and oats. The forest is managed for deer and predator control, specifically fox control, has been carried out in the past (C. Leslie pers comm. 2011). The Black Isle in general has historically been heavily populated by rabbits and the peninsula was considered to be one of the main areas where wildcats could still be found in the recent Scottish Natural Heritage survey carried out in 2006-2008 (Davies & Gray, 2010). However, since the survey was carried out, the rabbit population has suffered from myxomatosis and most rabbits are now found to the west of the peninsula (KK observation from this study). Local human population around the study site is 231 individuals (SCROL, 2011).

The last recorded wildcat sighting within 2-3 km of the site was in 2008 (Gateway, 2014a) and rabbits in 2007 (Gateway, 2014b). Local residents commented on the abundance of rabbits around this time that were then subsequently wiped out by disease.

2.2.4. G - Glen na Ceach, South Glen Affric, Highland

This site lies in the southern edge of the great Glen Affric (57^{o}12’44”N, 5 ^{o}06’42”W) which stretches some 30km from the west coast up towards the north east coast by Inverness. Dominated by high craggy peaks (up to 1000m), rivers and valleys. The site was once covered in Caledonian pine forest and birch, most of which was removed for sheep grazing and crofting. During the clearances, crofters were removed from the area and the site has been heavily grazed by deer in the past. Now some of the old forested areas have been fenced off and regeneration is occurring. In the valleys the area is mainly heather moorland (45%), rough grassland (15%) and areas of woodland primarily birch (10%), with montane habitat (35%) dominating the higher areas. The site is fragmented by several large rivers which often go into spate during periods of heavy rain or during the snowmelt.

Historically, rabbits were common in the area and wildcats were also regularly shot on part of the old estate (R. McGaskill pers comm. 2011). Vole populations can reach high numbers in some years (R. McGaskill pers comm. 2011). Currently, no rabbits are found across the site and only one recent cat sighting has been recorded (Davies & Gray, 2010; Gateway, 2014a; Gateway, 2014b). No people reside permanently within 5km of the site, although a local youth hostel is found in the adjoining valley which is popular with walkers and mountaineers.

2.2.5 H - Tomich, North Glen Affric, Highland

The Tomich site (57°17’06”N, 4°50’15”W) lies either side of the village of Tomich in the Great Glen of Glen Affric. The forest surrounding the village is owned and managed by the Forestry Commission and areas of rough grazing and improved grassland (15%), mainly used for sheep grazing run in the valley between the forest patches (50%), along river edges. The village of Tomich is a popular tourist destination in the summer. Wide expanses of open heather moorland (40%) sit high above the forested areas. Patches of broadleaved woodland, mainly birch and oak (10%) are interspersed among the habitat. The forest is mainly used for timber extraction and is heavily managed for deer. Historically, rabbits were common in the area and wildcats were also regularly shot as part of the old estate (R. McGaskill pers comm. 2011). Currently, no rabbits are found across the site and only a one wildcat sighting has been recorded in the recent past (Davies & Gray, 2010). The human population across the site is 139 (SCROL, 2011).

2.2.6. J - Fetteresso/Drumtochty Forest, Grampian

Drumtochty forest (56^{o}54’59”N, 2 ^{o}30’42”W) lies some 16 miles south west of Aberdeen. The forest is contiguous with the larger Fetteresso Forest with an overall area of approximately >100 km^2, timber extraction in Fetteresso was ongoing at the time of survey. The forest is owned by the Forestry Commission and managed for deer, and predator control is not currently carried out. To the east of the forest lies a deer park and to the north east a privately owned grousing estate where predator control is likely to be carried out. The forest is mainly pine plantation patches of varying ages. Habitat immediately surrounding the forest is large patches of scrub and rough pasture, arable and pasture to the south, heather moorland to the west and improved grassland and arable to the north and east. The majority of the site lies between 200-400m above sea level and as a result often has lying snow even when the surrounding farmlands do not. The site is often exposed to very high winds which have resulted in extensive tree fall in the past. Local human population estimate is 69 (SCROL, 2011), the majority of which are located in farms around the forest. Wildcats have been sighted here in the past.

Last recorded wildcat sighting within Drumtochty forest was in 1968 (Gateway, 2014a) although hybrids had recently been collected from Road Traffic Accident surveys suggesting some wildcats may remain in the area. The last rabbit sighting within Fetteresso Forest was in 1982 (Gateway, 2014b) although rabbits were seen during the survey period on the crop fields bordering the survey area.

2.2.7. K - Inverewe/Letterewe, Highland

The Letterewe estate is a privately owned estate encompassing some 60 000 acres of land and the neighbouring Inverewe gardens managed by the National Trust of Scotland (2000 acres) both sit on the western coastline of the Highlands. Across the whole study site (57°45'30"N, 5°34'22"W) heather moorland/peatland mosaic dominates the landscape (75%); there are several small coniferous forest plantations (10%), and patches of birch woodland. An area of mature oak forest interspersed with rough grassland lies along the south-western edge of the site which sits on the edge of Loch Maree. Inverewe gardens (50 acres), is full of exotic plants and trees. Along the eastern edge of the site sits an area of craggy slopes rising to >300m in places.

Deer stalking and predator control occurs on the Letterewe estate and deer are controlled in Inverewe gardens. The Letterewe estate has an estimated 6000 red deer, Highland cattle and sheep are found on both areas (Estate, 2012). Deer stalking and fishing are the main activities on the estate and tourists can visit the gardens in the summer months (NTS, 2012). Local resident population is 149 (SCROL, 2011).

No recent records of wildcats exist for the site and the rabbits were last recorded within 1km north of the site in 1968 (Gateway, 2014b) although the odd rabbit has been reported at Inverewe Gardens.

2.2.8. L - Glen Hurich Forest, Ardnamurchan, Western

Glen Hurich forest is a Forestry Commission owned forest (56°45'23"N, 5°33'60"W). The study site is composed of a mixture of coniferous plantations (25%), heather moorland/peatland mosaics (50%), patches of broadleaved forest, including the nationally important Sunart oak woods (5%) and rough grassland (10%) and areas of bog. The site is managed for deer, Local resident population around the study site is 117 (SCROL, 2011).

The last wildcat record within 5 km of the site was in 2005, no rabbit records exist for the area (Gateway, 2014a; Gateway, 2014b).

2.2.9. M – Strontian, Western

This site (56°42'05"N, 5°33'27"W) was located in the hills above the village of Strontian on the Ardnamurchan peninsula. Due to access restrictions, only four camera trap stations were set up here, all within the Forestry Commission land. Mainly pine plantation, the area is also coastal and supports large swathes of gorse and rhododendron as well as pockets of oak woodland and large areas of clearfell. The site borders pasture to the west which is grazed by sheep and Ariundle National Nature Reserve with its ancient oak woodlands to the north. Local resident population around the site is 219 (SCROL, 2011), the majority of which can be found in the village of Strontian, a popular tourist location.

Although the last recorded sighting in the area was in the 1970's (Gateway, 2014a), recent sightings of large "tabby" cats have been reported. Rabbits were last recorded in 2002 (Gateway, 2014b).

2.2.10. N – Lochaline, Western

The Lochaline site (56°33'21"N, 5°48'47"W) was predominantly located on the Forestry Commission land at Lochaline but some survey work was also carried out on the neighbouring Rahoy Hills Reserve, part of Ardtornish Estate and currently managed by the Scottish Wildlife Trust. Rahoy Hills Reserve supports a range of habitats primarily wet heath and bog on the upper slopes and broadleaved woodland on the lower slopes. The reserve is grazed by deer and livestock resulting in low heather cover and high grassland and tall herb cover. The cameras were located amongst the woodland covered slopes. The Forestry Commission land at Lochaline is heavily managed and undergoing extensive timber extraction at the time of the survey. The forest consists of a mosaic of mature forest, young growth and clearfell. Also within the site is a large cliff face on top of which is an area of open grassland and moorland. The site is managed for deer.

Last recorded wildcat sighting was in 2005 (Gateway, 2014a), although a cat with wildcat type pelage had recently been collected (2010) as a road traffic accident specimen. A local Scottish Wildlife Trust Ranger had reported wildcat sightings close to her home on the edge of the site. Rabbits were frequently seen on Rahoy Hills Reserve but the last records were in the 1980's (Gateway, 2014b) after which disease wiped out the population. They have not yet returned.

2.2.11. O - Inchnadamph Assynt/Vestey Estate, Highland

The Inchnadamph study site (58^{o}09'04"N, 4^{o}58'28"W) was based across the north eastern flank of the Assynt Estate and the western flank of the Inchnadamph Estate with a river dividing the two areas. This area is located in one of the few limestone valleys to be found in Scotland and has the most extensive underground cave network in the whole of Scotland. The bones caves on Inchnadamph estate are famous for not only human remains ~4500 years old but it is also the only site in Scotland where lynx bones have been found (~ 1700 years old). Along with Coigaich the Assynt region forms the North West Highlands Geopark.

Both estates are managed for deer although deer populations remain high in the area. The majority of the landscape is boggy moorland with small pockets of woodland, mainly native broadleaved and some areas of gorse. The Assynt estate is involved in replanting native tree species, primarily along the western edge of the estate. Inchnadamph village consists of only a few houses and a Youth Hostel which is popular in summer. Local resident population across the site is 79 (SCROL, 2011).

Inchnadamph estate has recently relinquished its status as a National Nature Reserve although the focus is still on trying to manage the estate in a wildlife friendly manner. Rabbits were previously abundant at Inchnadamph (A. Harrington pers comm., 2013) but were wiped out by myxomatosis a couple of years before the study commenced. The odd rabbit was seen during the study period. Last recorded wildcat sighting here was in 2003 (Gateway, 2014a).

2.2.12. P - Inverlael, Highland

The site at Inverlael (57°49'46''N, 5°02'25''W) was based partially within the Inverlael Forest owned and managed by the Forestry Commission and the remainder within the neighbouring Foich Estate. Some timber extraction was going on at the time of the survey. Foich Estate supports a large deer population and is composed of primarily open bog/heather moorland with rocky areas. Limited cover is found on Foich Estate. Local resident population is 95 (SCROL, 2011).

No recorded sightings for wildcat or rabbit exist (Gateway, 2014a; Gateway, 2014b) but the Forestry Commission have reported wildcat sightings from 2008 on the edges of Inverlael forest.

2.2.13. Q - Dundreggan Estate, Highland

Dundreggan (10 000 acres) is owned by Trees for Life (57°11'17"N, 4°46'37"W) and was purchased specifically in order to carry out reforestation projects. The estate contains substantial areas of ancient woodlands, including remnants of the original Caledonian Forest, superb birch-juniper woodlands and the largest expanse of dwarf birch in Scotland. The survey was carried out on both the Dundreggan Estate and Forestry Commission land to the east. Free-ranging wild boar can be found in the Forestry Commission land. Deer management is carried out across the site, and sheep graze the western edge of the Dundreggan estate. Local population estimate is 102 (SCROL, 2011).

No records of wildcats exist for Dundreggan although estate workers report recent local sightings of a “large tabby” cat. Rabbits were last recorded at Dundreggan in 1972 (Gateway, 2014b).

2.2.14. R - Sutherland Estate (Dunrobin), Highland

The site at Dunrobin (57°58’42”N, 4 °01’58”W) is part of the larger Sutherland Estates. Cameras were located in the area to the west of Dunrobin Castle. The site is composed of pockets of pine plantations which are managed for timber and deer and areas of farmland which are primarily grazed by sheep. The north of the site is mainly heather moorland which is managed for grouse and to the south and west exist large areas of gorse. Local population estimate is 84 (SCROL, 2011) which are located around the edges of the site.

The last recorded wildcat sighting within a couple of km of the site was in 2008 (Gateway, 2014a). A previous keeper states that wildcats were once plentiful on the hills across the site (A. Henderson, pers comm., 2012). Established rabbit populations are known to exist a few km away from the south western edge of the site, but most recent records close to the site are from 1975 (Gateway, 2014b).

2.2.15. S - Laggan, Highland

The site at Laggan (56°59'01"N, 4°20'50"W) lay to the north east of Loch Laggan in Forestry Commission land. Although predominantly pine plantation, habitat across the site was mixed with open patches of pasture/grassland, heather moorland and riverine habitat amongst the woodland patches. The land to the south east of the site is privately owned estate managed for deer and grouse. The Forestry Commission land itself is managed for deer and some timber extraction, although none at the time of the survey work. Local resident population is 91 (SCROL, 2011).

Wildcats were last recorded within 5km of the site as long ago as 1940 (Gateway, 2014a), although a local naturalist has reported hybrid/wildcat on camera trap on the edge of the site in 2012. Last rabbits recorded at Laggan in 1969 (Gateway, 2014b).

2.2.16. T - Achlibster Forest, Highland

Achlibster forest is located in the far north east of Scotland, Caithness. The forest itself is owned by the Forestry Commission and limited management occurs here. About 50% of the study area (58°25'51"N, 3°32'59"W) was located within the forest, the remainder on parts of the Thurso Estate to the east and south. To the east, the estate in managed by a tenant farmer, who grazes the land with sheep. To the south, the land is managed by the RSPB and is part of the Fornisard Fords, an area of threatened peatland protected for its summer resident species. Local resident population around the site is 101 (SCROL, 2011).

The last recorded wildcat sightings within a 5km radius of the site surveyed were in 2008 (Gateway, 2014a) and last rabbit sightings in 2009 (Gateway, 2014b).

2.2.17. U - Spinningdale, Highland

The Spinningdale site (57°53'08''N, 4°16'08''W) covered three properties; Creich Farm, a privately owned organic farm, Ledmore and Migdale woods owned by the Woodland Trust and Skibo Estate. The majority of the survey work was carried out on Creich farm and the Woodland Trust land. Creich farm lies on the north western edge of the Dornoch firth and grazes organic livestock. The south of the site is predominantly pasture with some rocky outcrops covered in gorse, the reminder of the site is a mixture of woodland and open rough grassland and bog. Ledmore and Migdale Woods encompass three Sites of Special Scientific Interest (SSSIs): Ledmore Oakwood (235 acres), Migdale Pinewood (356 acres) and Spinningdale Bog (71 acres). Habitats range from dense broadleaved deciduous woodland to conifer plantation; and open grasslands and marsh to the riparian environments of Spinningdale Burn and adjacent Dornoch Firth estuary. Deer management is carried out on the site. The northern end of the survey area encompassed parts of Skibo Estate, which is managed for deer and grouse shooting. The area is predominantly open heather moorland and bog. Predator control is carried out on this Estate. Local resident population around the site is 90 (SCROL, 2011).

The last wildcat recorded here was in 2002 (Gateway, 2014a) on the edge of Creich farm and the last rabbits were recorded at Spinningdale in 1999 (Gateway, 2014b). No rabbits were known to be in the area at the time of the survey.

2.2.18. V – Trossachs, Central

The site at Trossachs (56°09'59"N, 4°23'23"W) was located within the Queen Elizabeth Forest Park to the north and south of the village of Aberfoyle. The site also encompassed some of the farmland to the south east of the forest near Gartmoor. The Queen Elizabeth Forest Park is managed by the Forestry Commission and is a big tourist attraction. The site is primarily pine plantation in a mosaic of mature, young and clearfelled trees with mountainous areas covered in heather moorland. Deer are managed at this site. Local resident population around the site is 170 (SCROL, 2011).

Last wildcats records for the Queen Elizabeth Forest Park are from 1970 (Gateway, 2014a), although a cat with wildcat type pelage was recently trapped in the area. Rabbits were last recorded around Aberfoyle in 2012 (Gateway, 2014b).

2.2.19. W - Darnaway Forest, Highland

Darnaway Forest is part of the Moray estate **(**56°24'21"N, 5°19'05"W) and is located near Forres, Moray. Although much of the forest is spruce, a significant portion is ancient oak and beech woodland and is thought to be the oldest example of oak forest in Scotland (Phillips, 1988). The woodland has been actively managed for timber for the past 250 years and it was formerly a Royal hunting forest. Much of the land surrounding the woodland is now intensively farmed. Good populations of hare appear to exist here, but no rabbits have recently been recorded. Local human population is 114 individuals, the majority of which are found in the bordering farms (SCROL, 2011).

The last recorded wildcat sighting within 2-3 km of the site was in 2007 (Gateway, 2014a) and last recording of rabbits in Darnaway forest was in 1967 (Gateway, 2014b).

2.2.20. X - Glen Isla, Highland

Glen Isla is part of the Angus Glens, and sits on the north-west corner of the Angus Glens on the southern edge of the Grampian Mountains. In the north are heather moorlands which are managed for grouse, to the south pasture and arable land. The camera traps were located on the Forestry Commissioned owned land (56°46'11"N, 3°14'51"W), a mixture of mature pine plantations, clearfell and young replanted trees. The forested area is surround to the north, east and west by grousing estates, to the south is farmland used by sheep and cattle. The winter in the Angus Glens is severe with snow often lasting several months. During this study, heavy snowfall did not abate until May making survey work difficult. Local resident population is 73 (SCROL, 2011), which are predominantly found to the south of the study area.

Recent wildcat sightings have recently been reported by Forestry Commission staff and the Angus Glens in general are thought to support good wildcat numbers (e.g. Daniels, 1997). Rabbits are reported to be present at the southern end of the site in adjacent farmland.

2.2.21. Y - Hope Estate, Highland

Hope is a privately owned estate in the far north of Scotland. The estate is managed for pheasant and deer. The majority of the site (58°28'47"N, 4°36'08"W) is boggy moorland dotted with lochans and with small pockets of woodland, mainly native broadleaved with some small patches of pine plantation in the north. At the north of the site, there is a large area of coastal gorse with a high rabbit population and along the western edge of the site; along a river are areas of farmland and pasture, used for grazing sheep. The site is full of craggy rock faces and gorges offering potential den sites.

The last recorded wildcat sightings here were in 2001 (Gateway, 2014a).

2.2.22. Z - Fearnoch Forest, Central

The site at Fearnoch Forest (56°24'21"N, 5°19'05"W) lies to the north east of Oban. Some 40% of the site was located within Fearnoch forest itself, which is owned by the Forestry Commission and managed for timber, primarily Sitka spruce and deer. The remaining 60% of the site comprised the land to the south and south east of Fearnoch Forest, Dunach estate. A more open habitat, this area is currently managed by a tenant farmer and grazed by sheep. Wildcats have been seen in the past 10 years on an estate immediately to the west of this land (R. McGasgill, pers comm., 2012), but have disappeared recently owing to a crash in the local rabbit population due to RHV (R. McGasgill, pers comm., 2012). Local population estimate is 91 (SCROL, 2011), the majority of which are located in farms around the forest or on private estates.

The last recorded wildcat sighting within Fearnoch forest was in 1973 (Gateway, 2014a) and last rabbit sighting within 5 km of the study site was in 2010 (Gateway, 2014b).

2.2.23. AA - Tummel Bridge, Highlands

The Tummel Bridge site (56°43'45"N, 3°58'05"W) was located in Forest Commission land on the northern banks of Loch Tummel. The site is primarily managed for timber and deer and is primarily pine plantations of various ages with large open clear-felled patches. Farmland borders the site to the north, south and east and open mountainous moorland and bog to the west. Local resident population around the site is 106 (SCROL, 2011).

Wildcats were last recorded within 5km of the western edge of the site in 2008 (Gateway, 2014a) and the odd recent sighting of a tabby cat was reported by the forestry commission. Rabbits were last recorded on the edge of Loch Tummel in 1985 (Gateway, 2014b) and no recent sightings have been reported.

2.3. Methodology: data collection and analysis

Data on the presence of wildcats across different study sites was collected in a variety of different ways, described below. Specific analysis of data and the software used are described in the relevant chapters. All data were displayed in ArcMap 10.1 (Copyright © 1999-2012 Esri Inc.).

2.3.1. Camera trapping

Camera trapping was carried out using either pairs of Cuddeback ® Capture 3.0 megapixel camera traps or Reconyx ® HC500 models. Camera trapping was used in order to determine presence and generate density estimates of wildcats, hybrids and feral domestic cats within the specific study sites.

At each study site, 20-21 camera trap stations were set up in a grid with 2 camera traps placed at each station in order obtain photographs of both sides of an individual to assist with classification. Prior to the survey, a potential trapping grid was marked out on a map based on previous sightings data or local knowledge if it existed, but actual camera trap locations were chosen in the field. Radio-tracking studies have shown that a female wildcat has the smallest recorded home range of 172-175ha (Corbett, 1979; Daniels, 1997). Camera trap stations were therefore located at a distance of 1-1.5 km apart (diameter of a circle with an area of 172-175ha) in order to ensure all individuals have some chance of capture. At each potential station point, an area of approximately 500 x 500m around each point was surveyed for wildcat signs, these included foot prints, scats, den sites and scrape marks. If no cat signs were seen then stations were located in areas where there was either signs of pine marten (a species with very similar habitat and prey requirements to the Scottish wildcat e.g. Balharry, 1993; Birks *et al.*, 2005) or where there was high evidence of rabbit presence (e.g. burrows, actual sightings or latrine sites). The camera station location were established in such a way as to act as a funnel such that if the target species is nearby it will naturally walk past the camera traps because there are no obvious other routes. Animal trails were therefore used preferentially as these were already being used by one species or another, and if more than one route was present, these were blocked with vegetation or branches to ensure that the path past the camera traps offered the least resistance.

Camera traps were placed between 1.5 – 3m apart, on opposite sides of and perpendicular to the animal trail. Following Kilshaw and Macdonald (2011), camera stations were baited with either pheasant or partridge (to attract cats to the site both visually and by scent) and a scent based lure using a combination of Hawbakers ® Wildcat Lure #1 and #2. The bird bait was attached to a post/tree located between the two camera traps. The lure was spread onto squares of carpet attached to the post below the bait, within sniffing height for the cats. Location of each camera trap was checked by crawling or moving in front of the camera to take a photo and examining the photo on site using a Cuddeback photo viewer. Each camera trap was secured by a wire chain and padlock to reduce theft and labelled to indicate it was being used for a wildcat survey to minimise disturbance.

Camera traps were left on site for 2 months or ±60-80 days before being brought in (see Table 3.1, Chapter 3). Cameras were checked every 10-14 days, SD cards were swapped and batteries checked. Bait and lure were also refreshed every 10-14 days.

2.3.2. Wildcat identification

Cats were identified as wildcat, hybrid or feral domestic cat based on the pelage scoring system developed by Kitchener *et al.* (2005). This method is based on 7 different pelage markings which give cats a Seven Pelage Score (7PS). The pelage markings were scored as; 1 = domestic, 2 = hybrid, 3 = wildcat. Kitchener *et al.* (2005) suggested that any cat with a total score of 19 or more for the 7PS and with no scores of 1 should be regarded as a wildcat unless other data conflict with this (e.g. the cat has white paws). However, this definition could exclude many cats that may have a high proportion of wildcat genes that may usefully contribute to the restoration of the wildcat (Kitchener *et al.*, 2005). Therefore, a more relaxed field definition was also proposed whereby any cat that has a minimum 7PS of 14 and does not have a score of 1 for any of the seven pelage characteristics or for an additional eight pelage characters (white on chin, stripes on cheek, dark spots on underside, white on flank, white on back, colour of tail tip, stripes on hind leg and colour of the back of the ear) could be considered a wildcat (Kitchener *et al.*, 2005). These additional eight pelage characters are classified as 8PC hereafter (see Appendix 1a).

These pelage markings were used to give each cat a 7PS score as much as the photo enabled, in order to classify each individual as either wildcat, hybrid or feral cat based on the following criteria. Scores were also given for the 8PC to confirm the initial identification. Both the 7PS and 8PC were given a score of 1 = domestic; 2 = intermediate (hybrid); 3 = wildcat. Where the character could not be determined from the photograph, it was scored as unknown (U/K).

Based on the pelage scores each cat was classified as “wildcat”, “hybrid” or “domestic” using the following definitions; a strict definition (Strict ID), and a more relaxed definition (Field ID), described above as follows:

Strict ID

1. **Wildcat** = 7PS score of 19 or more, no scores of 1 for any of the 7PS characters and no scores of 1 for any of the 8PC.
2. **Hybrid** = scores 3 for one or more of the 7PS characters, but may also score 1 for one or more of these characters and may score 1 for one or more of the 8PC.
3. **Domestic** = no scores of 3 for any of the 7PS characteristics and scores of 1 or 2 in the other characteristics.

Field ID

Wildcat = 7PS score of 14 or more with no scores of 1 for any of the 7PS characters and no scores of 1 for any of the 8PC.

The scoring system used here means that under the Strict ID, no individuals identified as wildcats will display any domestic cat traits and no domestic cats will display any wildcat traits. Under the Field ID, wildcats will still have no domestic cat characteristics but may have some hybrid traits. Because of the low number of wildcats photographed, the Field ID was used for analysis purposes, but Strict ID is also reported for interest (Appendix 1b).

2.3.3. Scat surveys

Scats can provide a wealth of information on a species varying from information on abundance, distribution and sex ratios which can be obtained from DNA (e.g. Woods *et al.*, 1999; Mills *et al.*, 2000), dietary preferences (Stuart & Stuart, 2003) to the status of physiological health collected from hormonal data (e.g. Wasser *et al.*, 2000). Scat surveys were carried out across the study sites to a) establish the presence of wild-living cats, b) as a potential source of DNA.

Wildcats tend to leave single faeces exposed and use middens (scat accumulations) as scent-marking sites or along trails (Corbett, 1979). Although domestic/feral domestic cats generally bury their faeces, they may also leave them exposed at prominent sites to mark their territorial boundaries (Sharp & Saunders, 2004). It is, therefore, difficult to distinguish confidently between the scats of wildcats, feral domestic cats or hybrids without using DNA analysis. However, scat surveys can provide an indication of felid abundance and provide a useful indication of which areas wild-living cats are using. Scats were initially identified as cat based on the shape, size, smell, location and content. Wildcat faeces are short and cylindrical, measuring 40-80mm in length and about 15mm in diameter (Kitchener, 1995), they generally have hair remains such as rabbit and small mammal bones in them. However, because it is difficult to tell many carnivore scats apart, especially fox and cat, scats that were potentially not cat were also collected for genetic identification.

Because one of the aims of this thesis is to establish the most suitable monitoring protocol for future survey efforts of the wildcat, scat surveys were carried out in two different ways (Figure 2.2).

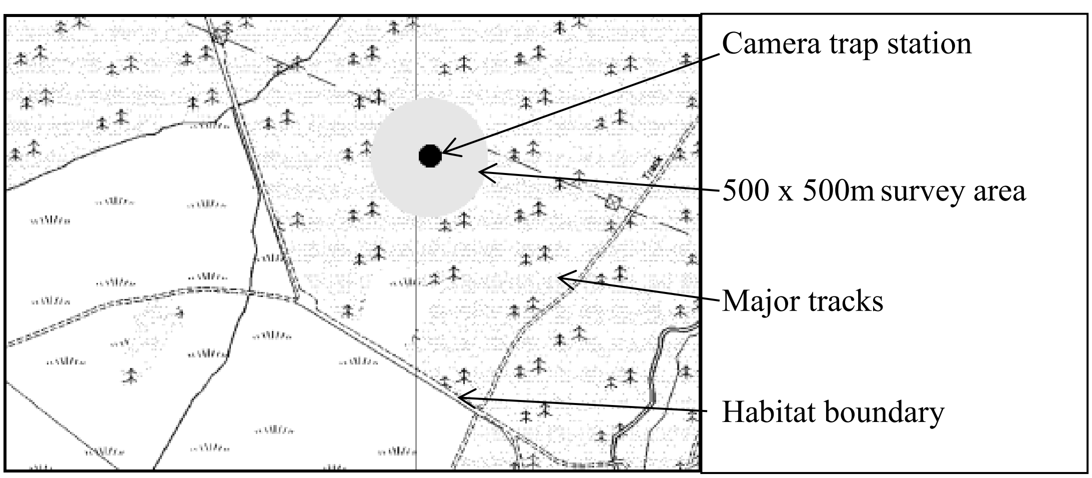
1. **Point surveys**

   Point surveys were carried out during the camera trap set up. In this case scats were searched for within 500m radius of each of the camera trap stations.

2. **Boundary edge and trail surveys**

   Wildcats, like many carnivores, are known to deposit scats along prominent land marks and linear features. During a pilot camera trapping study (Kilshaw & Macdonald, 2011), scats were often found along the edges of man-made tracks such as forestry tracks and along habitat boundaries such as between woodland and pasture. In order to assess whether scat surveys along these features would be more accurate than point surveys, the major habitat boundaries and tracks within each site were walked and scats looked for.

Figure 2.2 Example of the areas covered by the scat and sign surveys, 1) 500 x 500m survey area around each camera trap station, 2) boundaries between major habitat types and along main tracks.



2.3.4. DNA analysis

DNA analysis of scats was then carried out at the Wildgenes laboratory, RZSS, Edinburgh Zoo. DNA was extracted from scat samples using the Qiagen QIAamp R stool mini kit, following the standard protocol (Qiagen, Chatsworth, California, USA). Samples were then run through a rapid real-time PCR protocol designed to identify wildcat and domestic cat mtDNA (McEwing *et al.*, 2011). The original aim of DNA analysis of scats was to allow identification of individual cats using single nucleotide polymorphisms (SNP) and microsatellites on the nuclear DNA in order to 1) generate density estimates that were comparable with mark-recapture estimates from the camera trap surveys, 2) assess the level of hybridization in the local wild-living cat population. However, individual identification was not possible due to the low DNA yield of the samples.

2.3.5. Sign surveys

Sign surveys were carried out in the same way that scat surveys were. Looking for animals signs is often less expensive than other methods such as camera trapping and is often used to detect species presence and estimate abundance (e.g. Squires *et al.*, 2004; Sulkava, 2007), tracking animals by following footprints for example, is one of the most common and oldest methods used for identifying the presence of a mammal (Bider, 1968) but does depend on suitable field conditions (Burnham *et al.*, 1980). In Scotland, it is very difficult to see tracks of cats unless a light dusting of snow has fallen, they will generally not walk across muddy or wet areas if it can be avoided (per obs). Signs looked for included cat prints in the snow or appropriate substrate (e.g. thin layer of mud or sandy loam) along trails.

In addition, feeding remains, particularly of rabbits were also surveyed for. Wildcats generally consume their prey at the site of the kill and are unique in the way that they eat rabbits especially, because they often turn the skin “inside out” and generally leave the intestines and skull (of adults), which is often licked clean of meat. Meat from the bones is generally eaten first (Corbett, 1979). Rabbit carcasses are therefore often easy to find and can be identified as cat feeding remains. Rabbit remains were looked for primarily around areas of rabbit sightings or warrens recognized during the survey period and around the camera trap station locations.

2.3.6. Road Traffic Accident surveys (RTA)

RTA surveys have been used as a mechanism to collect data on “wild-living” cats in Scotland including wildcats and feral cats (Daniels, 1997; Balharry & Daniels, 1998). However, there are some concerns that this methodology may be biased towards domestic cats (A. Kitchener pers comm., 2011) as intuitively, domestic cats are found in greater concentrations near urbanized areas and are therefore more likely to suffer a RTA than a wildcat (BTO, 1999). Road traffic accident surveys were carried out for several reasons, 1) to detect the presence of a cat within an area, 2) to collect carcasses for genetic data and pelage assessment, 3) to determine whether RTAs are biased towards feral cats or hybrids in areas where wildcats are present based on camera trapping/live trapping data, 4) to examine in more detail the relationship between wild-living cats and habitat.

RTA surveys were carried out on the roads bisecting and surrounding each of the study sites when the cameras were checked every 10-14 days during the survey period. No carcasses were collected during the entire study.

Chapter 3

3.0 Predicting the distribution of the Scottish wildcat and mapping hybridisation risk: implications for future conservation management

3.1. Abstract

The Scottish wildcat is currently at risk of extinction because of hybridisation with feral domestic cats and hybrids. Conservation of the Scottish wildcat is hampered by limited information on the distribution of these three cat types and the spatial variation in hybridisation risk. From January 2010 to July 2013, I conducted widespread camera trapping surveys throughout Northern Scotland to document the distribution of these three cat types. Single-season occupancy models were fit to predict the probability of occupancy for feral domestic cats, hybrids, and wildcats across Scotland. Over 49 031 camera trapping days, I had 87 captures (photo of a cat at a camera trap station within a 24hr period) of wildcats, 145 captures of hybrids, and 193 captures of feral domestic cats. At over 48% of the camera trap stations where I detected wildcats, I also detected feral domestic cats or hybrids. Wildcat occupancy was predicted as a function of habitat covariates and feral domestic cats and hybrid occupancy probability. Wildcat occupancy probability was most affected by hybrid occupancy probability illustrating that wildcats tended to occur where hybrids also occurred. The probability of wildcat occupancy also increased in habitat with a higher proportion of mixed woodland habitat and decreased in habitat with more edge (the transition from closed to open habitats). This study not only identifies that wildcat distribution correlates to the distribution of hybrids illustrating considerable hybridisation risk throughout the range of the Scottish

wildcat, but also highlights where hybridisation risk is greatest. Furthermore, hybrids show a clear overlap in their distribution pattern with both feral domestic cats and wildcats, supporting recent suggestions that hybrids may pose a significant hybridisation threat by acting as a bridge between wildcats and feral domestic cats.

3.2. Introduction

Previously widespread across the UK, the Scottish wildcat (*Felis silvestris silvestris*) has suffered from heavy persecution and extensive habitat loss, and became restricted to parts of northern Scotland by the late 1800’s (Easterbee *et al.*, 1991; Balharry & Daniels, 1998; Davies & Gray, 2010). Via extrapolation of wild-living cat samples collected in the 1990’s, the population of Scottish wildcat was previously estimated to be roughly 400 (Macdonald *et al.*, 2004). However, this estimate is likely to be no longer accurate and Scottish wildcats, like European wildcats across their range, are primarily threatened by hybridisation with the feral domestic cat (*F.s.catus*) (Hubbard *et al.*, 1992; Nowell & Jackson, 1996; Macdonald *et al.*, 2004). Hybridisation with feral domestic cats threatens the genetic integrity and evolutionary persistence of wildcat populations (Randi *et al.*, 2001; Pierpaoli *et al.*, 2003). Because hybridisation has resulted in complications in surveying and monitoring for the wildcat across its range and particularly in Scotland, which has one of the highest levels of hybridisation (Oliveira *et al.*, 2008), limited data exists on both its distribution and the factors that might influence this (Macdonald *et al.*, 2004; O'Brien *et al.*, 2009). Understanding species distribution is an important component of conservation management and biodiversity conservation (Peterson *et al.*, 2011) but is often difficult to achieve, particularly for species which are challenging to survey or those for which limited information exists (Rushton *et al.*, 2004). Many carnivores fall into this category being both rare and reclusive, resulting in a lack of information on which to base management decisions. Paradoxically, these are the species that are so often highly threatened and in most need of urgent conservation action (Gittleman *et al.*, 2001). Given the risk of Scottish wildcat's extinction from hybridisation, conservation initiatives determining factors that promote spatial overlap between wildcats and their domestic relations, the domestic cat are essential.

Species Distribution Models (SDM's) are increasingly being used as a tool to comprehend animal-habitat relationships and to predict the distribution of a species of interest. SDM's relate species observations (such as presence, presence-absence, or count data) to environmental conditions (Graham *et al.*, 2004) and have been applied to mapping species invasions (Smolik *et al.*, 2010), examining adaption to climate change (Thomas *et al.*, 2004), or predicting the distribution of little-known carnivore species including the Andean cat (*Leopardus jacobita*) (Marino *et al.*, 2011); Flat-headed cat (*Prionailurus planiceps*) (Wilting *et al.*, 2010), and the Iberian wildcat (Monterroso *et al.*, 2009).

Recent developments in SDM's include likelihood-based occupancy modelling (Mackenzie *et al.*, 2002; Mackenzie, 2005; MacKenzie *et al.*, 2006), a robust analysis that uses presence/absence data to estimate the probability of occurrence (Ψ) by incorporating an additional parameter of detection probability ($\hat{p}$) as a function of habitat and survey and/or site-specific covariates. Likelihood-based occupancy modelling is used here in preference of other popular SDM's such as MaxENT (Phillips *et al.*, 2006) and Ecological Niche Factor Analysis (ENFA) (Hirtzel *et al.*, 2002) which use presence only data and generalized linear models (GLM's) (McCullagh & Nelder, 1989) which deal with presence and absence data because these alternative SDM's do not account for detectability. For example, both MaxENT and ENFA have been used to predict the distribution patterns of carnivore species from presence only data because they are able to deal with limited sample sizes or biased sampling often associated with wide ranging and difficult to detect species (e.g. radio tracking, Iberian wildcat; Monterroso *et al.*, 2009; scat samples, brown bear; Nawaz *et al.*, 2014). However, two key limitations of presence only data are that prevalence of the species (proportion of the landscape occupied) is not identifiable (Ward *et al.*, 2009) and that in general, sample selection bias (whereby some areas in the landscape are sampled more intensively than others) has a much stronger effect on presence-only models than on presence-absence models (Phillips *et al.*, 2009). For example, although MaxENT appears to be good at modelling sparse data sets robustly, studies have shown that it in prone to over fitting presence data (Peterson *et al.*, 2007) leading to omission errors or false absences whereas a limitation of ENFA is the occurrence of false positives (predicts occurrence where the species does not exist) in areas outside the range of the training data (Rebelo & Jones, 2010). Indeed Elith *et al.* (2011) state that where available, presence-absence data should be used in preference of presence only data. However, SDM's that deal with presence and absence data without accounting for detectability, rely on the generation of random 'pseudo-absence' data (where pseudo-absence points from the background data are chosen at random usually excluding known presence points) in grid cells without presence records (Ferrier & Watson, 1997) to overcome the problem that non-detection of a species at a site does not necessarily indicate a species is absent unless the probability of detection is 1 (MacKenzie *et al.*, 2006). One limitation of this method is that using pseudo-absence data may result in some absences being found in areas that are suitable for, and even inhabited by, the species (Graham *et al.*, 2004). False absences are therefore problematic for predictive modelling efforts, because they skew attempts towards under representing the area where a species is likely to occur (Tyre *et al.*, 2003).

Likelihood based occupancy modelling can be used to draw inferences about habitat use and selection and predict occurrence at multiple landscape scales (MacKenzie *et al.*, 2006). MacKenzie *et al.* (2006) state that "robust inferences about occupancy and the related dynamics can only be made by accounting for detection probability". For example, Comte and Grenouillet (2013) found that estimates of a species distribution were severely affected by whether or not imperfect detection was accounted for and the species detectability. Occupancy models provided better accuracy at predicting distribution for difficult to detect species than individual SDM's which do not account for detection bias (although this may not be the case for highly detectable species). Occupancy modelling has only recently been used to predict the distribution of difficult to detect species from camera trap data (O'Brien, 2008; Cove *et al.*, 2013). Camera trapping has been used to successfully survey for the Scottish wildcat (Kilshaw & Macdonald, 2011; Kilshaw *et al.*, 2015a) and wildcat populations in both Sicily and Portugal (Anile *et al.*, 2007; Anile *et al.*, 2009; Monterroso *et al.*, 2009). This method is likely to become more widely used across other parts of the wildcats range and it is therefore useful to examine the feasibility of using camera trap data to predict distribution patterns.

Between 2010 and 2013 I implemented camera trap surveys across northern Scotland to detect wildcats, feral domestic cats, and wildcat x domestic hybrids. Daniels (1997) previously produced a probability of occurrence map across Scotland based on the environmental variables associated with cats that had wildcat type characteristics. However, recent advances in both monitoring techniques and distribution models, identification of the wildcat using pelage characteristics (Kitchener *et al.*, 2005), changes in the Scottish landscape over the past 20 years and the possibility that the Scottish population may be classified as Critically Endangered if only a few genetically pure individuals are found to remain (Driscoll & Nowell, 2009) indicate the need of reassessing the potential distribution of this species.

The aims of this chapter are to; *i*) identify the habitat covariates associated with the occurrence of the three different cat types, *ii*) determine the degree of similarity between these animal-habitat relationships among different cat types, and *iii*) map the probability of occurrence for these cats throughout Scotland. These predictions serve two purposes; *i*) to identify the current distribution of the Scottish wildcat, *ii*) to identify the spatial configuration of hybridisation risk in the landscape.

3.3. Methodology

Camera trap data was collected as described in Chapter 2 and cats were identified as wildcat, hybrid or feral domestic cat based on pelage markings (Kitchener *et al.*, 2005) for all 23 sites surveyed. Additional data from five further surveys (one of which was carried out on the same site (A) as this study) were provided by the Royal Zoological Society of Scotland (RZSS) to increase the overall number of sites to 27. Two surveys over two consecutive years were carried out at each of these additional five sites. Occupancy models were developed to estimate wildcat occurrence (Mackenzie *et al.*, 2002). In order to maximize wildcat records, the field (relaxed) definition of a wildcat was used following Kitchener *et al.* (2005).

3.3.1. Modelling Design

Occupancy models were developed to estimate cat occurrence for feral domestic cats, hybrids, and wildcats. Using the camera trap data, occupancy matrices were created which depicted presence/absence of each cat type across the study period where every cell in the matrices was coded as 1 (presence), as 0 (absence), or as NA (where a survey was not conducted or the cameras were inactive due to either battery failure or snow cover) at a resolution of 1 trapping day. Data was binned into 7-day periods to improve computation and because of low detection of each cat type (see Ahumada *et al.* 2013). Thus, the final matrices consisted of 546 camera trap stations by 32 x 7-day sampling periods.

Single-species single-season site occupancy models (Mackenzie *et al.*, 2002) were fit to these matrices to predict the occupancy probability for each cat type using the UNMARKED package in R (R version 3.02.0, <www.cran.r-project.org>, accessed 1 May 2014 Fiske & Chandler, 2011). There are two important assumptions for this suite of models. Firstly, to separately estimate the probabilities of detection and occupancy, replicate surveys must be conducted among sites. Secondly, the state of species occupancy at a site is expected to remain constant throughout the study period. In this analysis, no one camera site was open for >6 months consecutively. Thus, here the system was assumed to be closed within the season. Dynamic multi-season occupancy models (Kéry *et al.*, 2013) were not fit to these data because the data collection efforts were temporally staggered across sites. The temporal staggering was due to the logistical constraints of maintaining numerous camera trap stations at various sites distributed across Northern Scotland (see Figure 1.1). Therefore, the temporal dimension of the dataset was not considered, which still permits modelling of the spatial variation in cat occurrence.

3.3.2. Observation process

The first component of the single season site occupancy model deals with the observation process and models the detection probability (P_{ij}) at the i^{th} site in the j^{th} replicate survey. This component of the process is where false-negative errors in the observation process are modelled to generate unbiased estimates of occupancy. This process is assumed to be a Bernoulli trial [$Y_{ij} \sim Bernoulli(z_i p_{ij})$] where the detection probability (P_{ij}) at the i^{th} site in the j^{th} replicate survey depends on species occurrence and the multiplication of z_{ij} and p_{ij} maintains that occurrence can be calculated only when z_{ij} = 1 (i.e., the cat type actually occurs).

3.3.3. Parameter Estimation

Here, the occupancy models enable the detection and state (occupancy) process to vary at the site-level (i^{th}; according to habitat covariates) and the survey-level (j^{th}; according to survey date). Model parameters are estimated via a generalized linear and quadratic function and a logit link. These models take the form $logit(\psi_{i1}) = \alpha + \beta x_i$, where the occupancy probability (ψ) depends on vectors of the fixed effects parameters βx_i or habitat covariates at the i^{th} site, and $logit(p_{ij}) = \alpha + \beta x_{ij}$, where x_{ij} represents the Julian date of the j^{th} survey at the i^{th} site (Kéry *et al.* 2013).

3.3.4. Habitat covariates

Habitat covariates represented biophysical, anthropogenic, land cover, and climatic conditions and all were depicted as continuous rasters. These covariates were depicted across the full extent of Scotland at a resolution of 500 x 500m (0.25 km^2). This resolution is based on the wildcats' core home range, the average size of the core area of its overall home range that a wildcat spends most of its time in (Corbett, 1979).

Variables were chosen that were expected to be important for Scottish wildcats, feral domestic cats and hybrids. Although limited data exists for the Scottish wildcat, the European wildcat shows similar requirements across its range, so data from these studies are also included if necessary. The variables considered are detailed below.

3.3.4.1. Landcover

The European wildcat in general has traditionally been considered to be a forest species reaching their highest densities in broad-leaved or mixed forests (Parent, 1975; Schauenberg, 1981; Stahl & Leger, 1992). However, more recent studies across Europe and in Scotland have indicated that this is not always the case (Langley & Yalden, 1977) and that wildcats use a wide variety of habitats ranging from Mediterranean scrubland (Ragni, 1981), riparian forest, to marsh boundaries and sea coastal habitat (Lozan & Korcmar, 1965; Heptner & Sludskii, 1972; Dimitrijevic & Habijan, 1977; Scott *et al.*, 1993) and display individual and seasonal variation in habitat selection (Wittmer, 2001). In general, wildcats appear to require areas with two basic habitat types; the first are areas that provide shelter and resting places, normally a closed structure habitat such as woodland. The second consists of open patches such as pastures or riparian areas for hunting (Corbett, 1979; Stahl *et al.*, 1988; Wittmer, 2001; Biro *et al.*, 2004a). Riparian areas within forest as well as edge habitats often provide a higher diversity and abundance of small prey mammals than interior forest (e.g. Doyle, 1990; Gomez & Anthony, 1998). In Scotland, wildcats are shown to use different habitat types based on prey availability but in general use a mixture of woodland (coniferous, mixed and broadleaved) and scrub for cover and riparian areas and rough pasture for prey (Corbett, 1979; Scott *et al.*, 1993; Daniels, 1997). Corbett (1979) study found that they moved across open heather moorland in the summer, whereas Daniels (1997) found they avoided heather moorland and areas of agriculture.

In comparison, studies on feral domestic cats show that they are mainly found close to human settlements with home-range size varying in relation to population density, food availability and distribution (Liberg & Sandell, 1988; Barratt, 1997). Farms in particular appear to be a priority environment for feral domestic cats (Corbett, 1979; Szemethy, 1993; Barratt, 1997; Daniels, 1997), with farm buildings themselves offering shelter, particularly over winter months (Germain *et al.*, 2008) and the area around farms the preferred land use of domestic cats (Ferreira *et al.*, 2011). Although they tend to use the edges of these habitats, avoiding open areas with little cover (Metsers *et al.*, 2010).

Very limited data exists for environmental factors affecting hybrid distribution but it is thought that they have similar habitat use as wildcats but utilize human resources unlike wildcats (Germain *et al.*, 2008). It is for this reason that hybrids are suspected to play a significant role in hybridisation as they straddle the landscapes that largely separate feral domestic cats and wildcats (Germain *et al.*, 2008).

Landcover data was extracted from the Land Cover Map 2007 (LCM2007; Under License LCM 2012-357vs2), a parcel-based classification of UK land cover (Morton *et al.*, 2011). LCM2007 uses 23 classes to map the UK at a resolution of 25m, which are based on the UK Biodiversity Action Plan (BAP) Broad Habitats. LCM2007 is created by classifying summer-winter composite images captured by satellite sensors with 20-30m pixels. LCM2007 uses a spatial framework based on generalised digital cartography (Ordnance Survey MasterMap topographic layer (OSMM), refined with image segments (see Morton *et al.*, 2011 for details) so that it is consequently constructed from polygons that clearly represent real-world objects, such as fields and blocks of woodland.

The proportion of 8 land cover types of interest were calculated at a resolution of 500m^2. These categories included deciduous woodland, mixed woodland, coniferous woodland, arable/horticultural areas, improved grasslands, semi-natural grassland, gorse and heather. Improved and semi-natural grasslands were then combined into a single category referred to as *grassland* and deciduous woodland and mixed woodland were combined into a category called *mixed woodland* giving a total number of 6 LCM 2007 habitat variables (see Table 3.2).

3.3.4.2. Elevation

Corbett's (1979) radio-tracking study found that wildcats moved to lower elevations (<1000m) during snowfall and Daniel's (1997) found that the median altitudinal range of his radio tracked wildcats was 320-383m and Easterbee *et al.* (1991) found wildcats at an altitude of 650m. Across Europe, the wildcat's range is thought to be up to 1300m (Dotterer & Bernhart, 1996; Mermod & Liberek, 2002). Elevation data (m) was extracted from Shuttle Radar Topography Mission data.

3.3.4.3. Human Population Density and potential disturbance

Easterbee *et al.* (1991) and Daniels (1997) found that wildcats preferred areas of low human density (<1/km^2). Studies in Europe found that human disturbance is an important factor for wildcat distribution (Klar *et al.*, 2008; Ferreira, 2010) with the probability of wildcat habitat use decreasing at distances less than 900m from villages and 200m from roads and single houses, although the exact critical distance is highly dependent on the habitat itself (Klar *et al.*, 2008).

As mentioned previously, studies on feral domestic cats show that they are mainly found close to human settlements (Liberg & Sandell, 1988; Barratt, 1997) and hybrids have also indicated a use of farm buildings in particular (R. Campbell unpublished data, 2015) suggesting proximity to urban areas may be an important variable for these two cat types.

Using data from the UK ordnance survey (1:250 000 scale) distance to the nearest urban/suburban area was calculated. Urban areas are typically towns and city centres while suburban areas are villages with a mix of housing and green spaces (e.g. parks, gardens).

3.3.4.4. Prey availability: rabbits and small mammals

Rabbits (*Oryctolagus cuniculus*) are one of the wildcats main prey species (Corbett, 1979; Hewson, 1983; Stahl & Leger, 1992; Daniels, 1997) and studies across Europe have indicated that distribution of the European wildcat is linked very closely with this species (e.g. Lozano *et al.*, 2006). Other important prey species include microtine and murinae spp. (Stahl *et al.*, 1992).

Because data describing the distribution of potential wildcat prey were not available at the extent of Scotland the effect of edge habitat was tested, presenting the transition from closed to open habitat types, as a proxy for wildcat hunting habitat. Edge was calculated based on the intersection of woodland habitat (deciduous, coniferous, and mixed) and open habitat (gorse, dwarf shrub, and semi-natural grasslands) known to be used by wildcat prey *(Silva et al*., 2013).

3.3.5. Model Selection

The model selection process initially compared a model with constant parameters to a model with a date-varying detection process. In this case the linear and quadratic effects of the camera trap survey date on the detection probability was modelled (*p*; Kéry *et al.* 2013) in order to examine whether time of year had any impact on detectability. Next, these models were compared with a model that included a date-varying detection process and the influence of habitat covariates on the occupancy process. The top-ranking model structure was retained as determined by AIC (see Appendix 2) and models from all-possible combinations of habitat covariates that are believed to affect the occupancy of feral domestic cats, hybrids, and wildcats (i.e., *a priori* rationale) were then evaluated. Thus, for feral domestic and hybrids, models of the occupancy process were fit based on elevation, amount of edge, distance to urban/suburban areas, and the proportion of conifer woodland, mixed woodland, grassland, arable, and gorse habitat. For wildcats, models of the occupancy process were fit based on elevation, amount of edge, and the proportion of conifer woodland, mixed woodland, grassland, gorse, and heather habitat.

All models with a cumulative weight of 0.95 were considered and parameter averaged across these models to produce final parameter estimates using the AICcmodavg package in R (Burnham & Anderson, 2002; Mazerolle, 2014). The relative importance of each habitat covariate was then assessed by calculating a summed AIC weight ($\Sigma AIC\omega$) across those models within a cumulative $AIC\omega$ of 0.95 (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). When the $\Sigma AIC\omega$ approximates 1, the habitat covariate is highly supported while a $\Sigma AIC\omega$ which tends towards 0 shows little support for that covariate.

These parameter estimates were then used to map the predicted probability of occurrence for each cat type. As in the case of the habitat covariates described above, these maps were rasters representing the predicted probability of cat occurrence (wildcat, hybrid, and feral domestic cat) across Scotland at a resolution of 500 m^2 (Figure 3.1). Studies have indicated, that for the European wildcat, the probability of wildcat habitat use decreases at distances less than 900 m from villages and 200 m single houses, although the exact critical distance is highly dependent on the habitat itself (Klar *et al.*, 2008). Further, areas of high elevation (>800 m) are also considered to be unsuitable habitat for these three cat types (e.g.Easterbee *et al.*, 1991; Daniels, 1997) and no areas above 802 m were surveyed during this study. Thus, habitat <900 m from villages, <200 m single houses, and >800 m in elevation were excluded from these predictions of cat occurrence. To assess uncertainty in occupancy probability for each cat type, a parametric bootstrapping procedure was used, based on a chi-square test statistic, with 500 replicate datasets. This test was computed for the best model, as determined by the AIC-ranking, describing the probability of occurrence of each cat type. In each replicate dataset the parameters and computed fit statistics were estimated. Model goodness-of fit was then examined by comparing the performance (i.e., chi-squared statistic) of the top-ranking model to an expected sampling distribution generated from a parametric bootstrapping process (Kéry *et al.*, 2005; Kéry *et al.*, 2013). This parametric bootstrapping procedure revealed no evident lack of fit in the best models describing the predicted probability of occurrence for feral domestic cats (P = 0.248), hybrids (P = 0.808), and wildcats (P = 0.926).

The next objective was to determine whether the predicted probability of occurrence for feral domestic cats and hybrids altered the predicted probability of occurrence for wildcats.

This was necessary to calculate the occurrence of wildcats given environmental covariates and feral domestic cats and hybrids in the system (i.e., to calculate spatial variation in hybridisation risk). Hybrids were included in this analysis because recent evidence has suggested they may increase rates of hybridization by acting as both wildcats and domestic feral cats (Germain *et al*., 2008). Therefore, the feral domestic cat prediction raster and the hybrid prediction raster were added to the list of environmental covariates. This increased the number of testable covariates from 7 to 9. Models built from all combinations of these covariates were then fit, tested for collinearity and any model with collinear covariates was removed from consideration. Model support was ranked using AIC and the parameter estimates were used to map the predicted probability of wildcat occurrence.

3.4. Results

3.4.1. Camera trapping

From January 2010 – July 2013 546 camera trap stations were deployed at 27 sites to detect wildcat, hybrids, and feral domestic cats across a total of 49 031camera trap days. During this period 87 camera trap events (number of captures per 24hr period) were recorded for wildcats, 145 for hybrids, and 193 for feral domestic cats across 86 different camera trap stations. Once the data was binned into 7 day periods this resulted in a total of 65, 94 and 132 captures for wildcats, hybrids and feral domestic cats respectively (Table 3.1). Wildcats were recorded at 7 of the 27 sites surveyed (across 25 different camera trap stations), hybrids at 13 different sites (across 47 camera trap stations), and feral domestic cats at 17 of the 27 sites (across different 47 camera trap stations) (Table 3.1). Although hybrids and feral domestic cats were found at all 7 of the survey sites that wildcats were captured at, I only recorded all three cat types at two of the same camera trap stations during the study period (2.3% of the camera trap stations where wild-living cats were documented). Wildcats and hybrids were both photographed at 8 different camera trap stations (12.7% of the camera trap stations where either was documented). Wildcats and feral domestic cats were both photographed at 5 camera trap stations (5.4% of the total camera trap stations either was documented at). On the other hand, feral domestic cats and hybrids were both recorded at 20 different camera trap stations (26.7% of those camera trap stations where either was documented).

Table 3.1 Summary statistics of trapping periods, number of traps, camera trap events, and habitat conditions at the sites surveyed.

Site	Sampling periods	No. of camera trap stations	Total camera days	No. captures/7 day-bin period			Elevation (m)	Amount of edge (km)	Distance to Urban (km)	Proportion of habitat cover/500m^2					
				Wildcat	Hybrid	Feral domestic cat				Arable	Grassland	Mixed woodland	Coniferous woodland	Heather	Gorse
A	Jan - May 2010, Nov 2011-Jan 2012	20, 20	1989, 1319	11	9	0	280-400	0.00-1.64	0.53-2.48	0-0.03	0-0.88	0-0.35	0-0.94	0-0.77	0-0.88
B	Jun - Dec 2010, Aug-Nov 2011	20, 20	3514, 1751	2	4	20	278-421	0.05-0.98	0.7-4.76	0-0.23	0.08-0.93	0-0.17	0-0.9	0-0.29	0.08-0.93
C	Nov 2010-Feb 2011, Nov 2011-Feb 2012	20, 20	1685, 1347	0	10	14	175-480	0.00-1.92	0.85-4.67	0-0.04	0-0.52	0-0.09	0-1	0-0.44	0-0.52
D	Feb-May 2011, Jan-April 2012	20, 20	1604, 1468	19	18	2	191-451	0.00-0.94	1.32-6.73	0-0.03	0-1	0-0.16	0-0.94	0-0.50	0-1
E	March-June 2011	20	1327	20	1	9	203-372	0.00-1.47	0.9-3.03	0-0.66	0-0.66	0-0.29	0-0.91	0-0.13	0-0.66
F	May-August 2011	20	1532	0	0	0	111-214	0.00-0.86	0.97-3.15	0-0.27	0-0.56	0	0.44-1	0-0.11	0-0.56
G	June-Oct 2011	20	2016	0	0	0	241-802	0.00-1.38	11.19-13.86	0-0.02	0-0.86	0-0.16	0-0.48	0-0.72	0-0.86
H	Sept - Nov 2011	20	1278	0	0	0	81-415	0.00-1.25	0.09-8.51	0	0-0.77	0-0.38	0-1	0-0.35	0-0.77
I	Feb-April 2011, Jan-March 2012	20, 20	1274, 1439	0	9	3	307-557	0.00-1.05	1.62-5.30	0	0-0.57	0-0.15	0-0.80	0-0.57	0-0.57
J	Nov 2011-Mar 2012	20	2162	3	5	1	180-431	0.00-1.24	1.64-5.03	0-0.17	0-0.81	0-0.37	0-1	0-0.35	0-0.81
K	Jan-April 2012	20	1914	0	0	10	7-613	0.00-1.38	0.01-6.93	0	0-0.62	0-0.53	0-0.45	0-1	0-0.62
L	March-June 2012	20	1478	0	0	12	3-369	0.00-1.78	0.07-3.80	0-0.05	0-0.88	0-0.37	0-0.96	0-0.30	0-0.88
M	May-June 2012	4	132	0	2	5	6-185	0.17-1.47	0.32-1.61	0-0.06	0.03-0.38	0-0.16	0.02-0.86	0.01-0.08	0.03-0.38
N	June-Sept 2012	21	1589	1	2	16	2-301	0.00-0.55	0.17-4.20	0-0.08	0-0.81	0-0.41	0-1	0-0.43	0-0.81
O	Oct 2012 - Jan 2013	20	1318	0	0	0	68-343	0.00-0.83	0.04-3.36	0	0-0.78	0-0.33	0-0.05	0-0.90	0-0.78
P	Oct-Dec 2012	20	1468	0	0	0	25-545	0.00-1.42	0.52-4.74	0-0.02	0-0.83	0-0.50	0-0.37	0-0.97	0-0.82
Q	Nov 2012-Jan 2013	20	1459	0	0	2	75-414	0.00-2.27	0.41-5.07	0-0.05	0-0.97	0-0.65	0-0.93	0-0.60	0-0.96
R	Nov 2012-Jan 2013	20	1285	0	0	0	39-357	0.00-1.31	0.19-2.53	0-0.21	0-0.69	0-0.06	0-0.98	0-0.99	0-0.69
S	Dec 2012-Feb 2013	20	1257	0	0	2	257-469	0.06-1.57	0.87-4.48	0	0-0.82	0-0.28	0.04-0.99	0-0.73	0-0.82
T	Dec 2012-Feb 2013	20	1514	0	0	5	62-122	0.00-0.56	0.82-4.51	0	0-0.85	0-0.06	0-1	0-0.14	0-0.85
U	Jan-April 2013	20	1410	0	6	4	20-301	0.00-1.61	0.16-3.05	0-0.53	0-0.42	0-0.47	0-0.93	0-0.90	0-0.42
V	Feb-April 2013	20	1342	0	7	2	17-299	0.00-1.51	0.16-2.75	0-0.21	0-0.80	0-0.58	0-1	0-0.47	0-0.80
W	Feb-April 2013	20	1440	0	0	2	29-190	0.00-2.08	0.09-2.83	0-0.72	0-0.81	0-0.24	0.12-1	0-0.02	0-0.81
X	Feb-May 2013	20	2013	9	20	23	271-610	0.00-1.76	0.91-5.26	0	0-0.62	0-0.12	0-1	0-0.52	0-0.62
Y	Feb - May 2013	20	1622	0	0	0	4-278	0.00-1.25	0.09-6.06	0	0-0.32	0-0.26	0-0.21	0-0.90	0-0.32
Z	Feb-May 2013	20	1376	0	1	0	59-314	0.00-0.62	2.56-6.32	0	0-0.88	0-0.3	0-1	0-0.95	0-0.88
AA	April-July 2013	21	1800	0	0	0	145-434	0.00-1.08	0.64-4.05	0-0.02	0-0.75	0-0.30	0.08-1	0-0.47	0-0.75
Total	**Jan 2010-July 2013**	**526***	**49 031**	**65**	**94**	**132**	**2-802**	**0.00-2.27**	**0.01-13.86**	**0-0.72**	**0-1**	**0-0.65**	**0-1**	**0-1**	**0-1**

3.4.2. Modelling

Results from the model selection process indicate that candidate models where the occupancy process varies as a function of habitat covariates and a time-varying detection process were superior to models with constant parameters for feral domestic cats, hybrids, and wildcats (see Appendix 2). Feral domestic cat occupancy was significantly influenced by the proportion of grassland habitat ($\Sigma AIC\omega =$ 0.92). In addition, distance to urban areas ($\Sigma AIC\omega$ = 0.80), proportion of arable habitat ($\Sigma AIC\omega$ = 0.65), proportion of coniferous woodland ($\Sigma AIC\omega$ = 0.59), and amount of edge habitat ($\Sigma AIC\omega$ = 0.51) also had a positive effect on occupancy. Occupancy for feral domestic cats was least affected by proportion of gorse (ΣAICω = 0.45) and proportion mixed woodland (ΣAICω = 0.31). Feral domestic cat occupancy increased in habitat with a higher proportion of arable and grassland habitat situated closer to urban areas (Table 3.2). Occupancy also increased in habitat with more coniferous woodlands and more edge habitat (Table 3.2).

Similar to feral domestic cats, hybrid occupancy was significantly influenced by the proportion of grassland ($\Sigma AIC\omega =$ 0.95) and was also significantly influenced by distance to urban areas ($\Sigma AIC\omega$ = 0.89). The amount of edge habitat ($\Sigma AIC\omega$ = 0.60) and proportion of coniferous woodland ($\Sigma AIC\omega$ = 0.47) and mixed woodland (ΣAICω = 0.93) also had a positive impact on occupancy. Occupancy was least affected by proportion of gorse ($\Sigma AIC\omega$ = 0.40) and proportion of arable habitat ($\Sigma AIC\omega$ = 0.31). Hybrid occupancy therefore, increased in habitat with a higher proportion of grassland habitat situated closer to urban areas (Table 3.2). As with feral domestic cats, hybrid occupancy also increased in habitat with more coniferous woodlands and more edge habitat but as with wildcats, also increased in habitat with more mixed woodland (Table 3.2).

Wildcat occupancy was significantly influenced by the proportion of mixed woodland ($\Sigma AIC\omega = 0.85$). The proportion of grassland ($\Sigma AIC\omega = 0.62$) and proportion of coniferous woodland ($\Sigma AIC\omega = 0.50$) also had a positive impact on occupancy but occupancy decreased in areas with a higher proportion of gorse ($\Sigma AIC\omega = 0.66$). Occupancy was least affected by heather ($\Sigma AIC\omega = 0.42$) and amount of edge habitat ($\Sigma AIC\omega = 0.25$). Wildcat occupancy increased in habitat with more mixed woodland (Table 3.2). As with feral domestic cats and hybrids, wildcat occupancy also increased in habitat with more grassland and coniferous woodland but decreased in areas with more gorse habitat (Table 3.2).

When including occupancy rates of feral domestic cat and hybrids the order of covariate importance changed. When the wildcat model included both habitat covariates and the feral domestic and hybrid occupancy rates, wildcat occupancy was most influenced by hybrid occupancy probability ($\Sigma AIC\omega = 0.82$). Comparatively, the occupancy probability of feral domestic cats ($\Sigma AIC\omega = 0.39$) was not nearly as strong a predictor as the occupancy probability of hybrids. The proportion of mixed woodland ($\Sigma AIC\omega = 0.76$) continued to be influential. Wildcat occupancy probability was positively related to proportion of mixed woodlands and hybrid occupancy probability (Table 3.2).

Table 3.2 Model averaged occupancy model parameters with beta coefficients (β) and standard errors (SE) for each habitat covariate in the models depicting feral domestic cat, hybrid, and wildcat occupancy based on camera trap data collected throughout Scotland between 2010 and 2013. The 95% unconditional confidence intervals of the estimates are also shown. Those represented in bold type face indicate where the confidence interval estimate does not overlap zero.

Occupancy parameter (Ψ)	Feral domestic cats			Hybrids			Wildcats			Wildcats with feral domestic and hybrids		
	B	**SE**	**95% CI**	**β**	**SE**	**95% CI**	**β**	**SE**	**95% CI**	**β**	**SE**	**95% CI**
Arable	3.83	1.96	(-0.02, 7.68)	2.57	3	(-3.32, 8.45)	---	---	---	---	---	---
Mixed woodland	-1.94	2.77	(-7.36, 3.48)	1.95	2.31	(-2.58, 6.48)	**5.98**	**2.54**	**(1.00, 10.97)**	5.09	2.61	(-0.03, 10.21)
Coniferous woodland	1.49	0.95	(-0.36, 3.34)	1.21	0.92	(-0.59, 3.02)	1.65	1.55	(-1.38, 4.69)	0.36	0.67	(-0.96, 1.67)
Edge	0.81	0.53	(-0.24, 1.85)	0.76	0.44	(-0.09, 1.62)	0.02	0.58	(-1.11, 1.15)	---	---	---
Elevation	0.00	0.00	(-0.01, 0.00)	0.01	0.00	(0.00, 0.01)	0.01	0.00	(0.00, 0.01)	0.00	0.00	(-0.01, 0.01)
Gorse	-2.8	2.62	(-7.94, 2.33)	-1.65	1.67	(-4.93, 1.63)	-3.57	2.32	(-8.11, 0.98)	-2.22	2.14	(-6.42, 1.98)
Grassland	**2.67**	**1.13**	**(0.45, 4.89)**	**3.00**	**0.95**	**(1.14, 4.85)**	2.42	1.57	(-0.66, 5.50)	0.41	1.37	(-2.27, 3.09)
Heather	---	---	---	---	---	---	-2.51	2.68	(-7.76, 2.74)	-0.23	1.78	(-3.73, 3.26)
Urban	-0.34	0.18	(-0.69, 0.02)	**-0.30**	**0.15**	**(-0.59, -0.01)**	---	---	---	---	---	---
Feral domestic cats	---	---	---	---	---	---	---	---	---	4.24	3.8	(-3.20, 11.68)
Hybrids	---	---	---	---	---	---	---	---	---	**4.19**	**1.31**	**(1.62 , 6.75)**

Predicting the occupancy probability of each cat type across Scotland revealed that habitat with a high predicted occupancy probability for feral domestic cats was primarily concentrated in the east of Scotland or in areas with a higher proportion of arable farmland and urban areas (Figure 3.1a). Hybrid occupancy was more broadly distributed throughout Scotland, showing a similar distribution to wildcats, but overlapping the predicted distribution of feral domestic cats in the east and south of Scotland (Figure 3.1b). Habitat with a high predicted occupancy probability for wildcats was greatest in the central Highlands (Figure 3.1c). When the predicted occupancy probability of feral domestic cats and the predicted occupancy probability of hybrids were included as parameters in the wildcat model, the subsequent prediction showed that the wildcat occupancy probability in Scotland (Figure 3.2) showed a positive relationship to hybrid occurrence in the landscape.

Figure 3.1 Predicted occupancy probabilities (0-1) for; a) feral domestic cats, b) hybrids, and c) wildcats based on camera trapping surveys conducted throughout Scotland from 2010-2013. Urban areas are masked in black and habitat > 800 m in elevation (unsuitable habitat for all cat types) is represented in white.

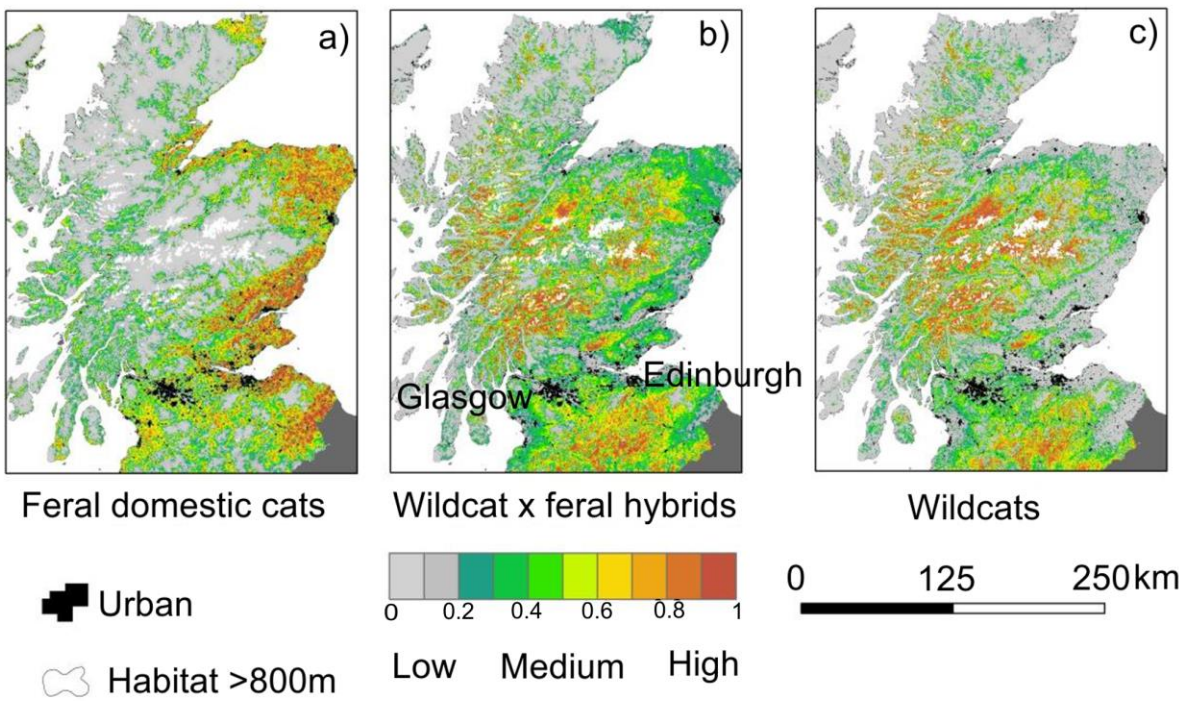
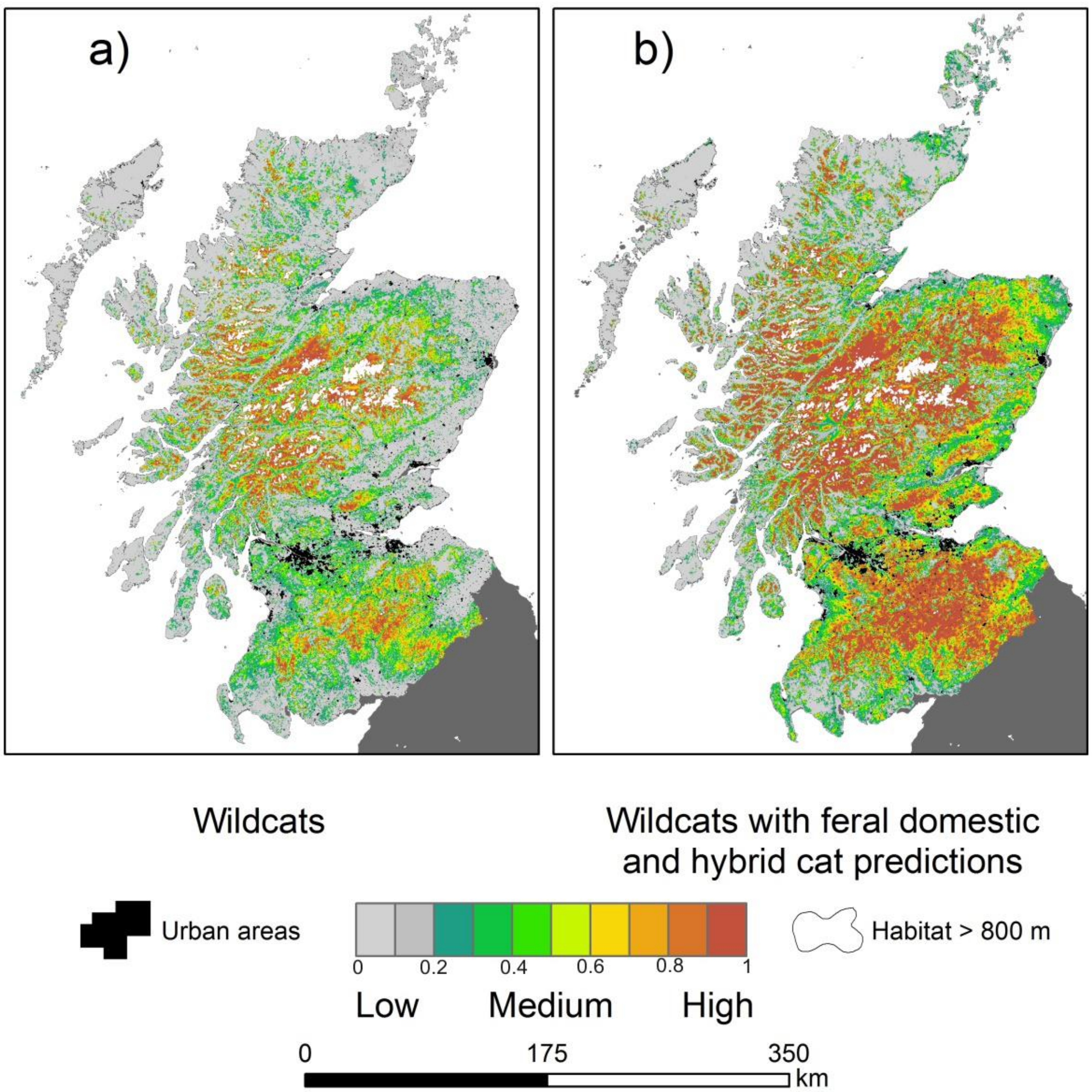


Figure 3.2 Predicted occupancy probability (0-1) for wildcats from models built a) without feral domestic and hybrid predictor, and b) from models that incorporate the predicted probability of feral domestic and hybrid occurrence based on camera trapping surveys conducted throughout Scotland from 2010-2013. Urban areas are masked in black and habitat > 800 m in elevation (unsuitable habitat for all cat types) is represented in white.



3.5. Discussion

Camera trapping efforts revealed that feral domestic cats and hybrids are widespread throughout the Scottish wildcat's potential range in Northern Scotland. Feral domestic cats and/or hybrids were present at all 7 of the sites wildcats were detected, with wildcats sharing 48% of all camera trap stations they were captured at with either a hybrid or feral domestic cat. Specifically, hybrids occupied >12% of those camera trap stations where I recorded wildcats, whereas domestic cats and wildcats only shared 5% of the camera trap stations. In comparison, hybrids and feral domestic cats co-occurred at >25% of the camera trap stations. Thus, from the raw capture data, the degree of spatial overlap for feral domestic and hybrids is greater than the overlap documented for feral domestic/hybrids and wildcats. These findings are consistent with other surveys carried out on both Scottish wildcats and European wildcats which have found that hybrids share their ranges with both wildcats and feral domestic cats (Corbett, 1979; Daniels, 1997) with reduced overlap among wildcats and feral domestic cats (e.g. Germain *et al.*, 2008). This result is seen more evidently in Figure 3.1 where predicted hybrid occupancy clearly overlaps that of both feral domestic cats and wildcats suggesting they could form a bridge for introgressive hybridisation to occur. Only two sites in the study area were completely free of feral domestic cats (A and D; Figure 2.1), although additional surveys at these sites went on to photograph feral domestic cats in both these areas as well (Hetherington & Campbell, 2012; Littlewood *et al.*, 2014).

Wildcat occupancy predictions support other studies on both the Scottish and European wildcat that suggest wildcats require habitat that provides shelter and resting places (such as woodland) and more open patches for hunting (such as open fields or riparian areas) (Corbett, 1979; Stahl *et al.*, 1988; Wittmer, 2001; Biro *et al.*, 2004a). For example, the European wildcat in general tends to be associated with forests, reaching their highest densities in broadleaved or mixed forests (Parent, 1975; Schauenberg, 1981; Stahl & Leger, 1992) although they appear to avoid large and homogenous coniferous forests (Castells & Mayo, 1993) likely due to the lack of prey diversity and/or abundance within these stands (Easterbee *et al.*, 1991). In Mediterranean habitats, wildcats select broadleaved and mixed woodland and avoided *Erica spp.* scrubland (Sarmento *et al.*, 2006). In Scotland, studies have shown that wildcats select habitat mosaics consisting of open fields and reforested patches (Easterbee *et al.*, 1991) and tend use woodland and stream edges while avoiding heather moorland (Daniels, 1997), although Daniels' (1997) study also noted they avoided open pasture, in contrast to Easterbee's (1991) study. Corbett's (1979) study, also in the north-east of Scotland, found that Scottish wildcats used forested habitat but avoided mature pine forests, and Scott's *et al.* (1993) study in the west of Scotland reported that wildcats showed a preference for woodland and gorse habitat in relation to its availability within their home ranges. It is important to note however, that with the exception of the recent national survey, the pelage classification was not available for previous surveys and as a result, it is difficult to draw inferences from these surveys because they may not have been able to differentiate between wildcats/hybrids and hybrids/tabby feral domestic cats.

Factors that might influence feral domestic cat or hybrid occurrence have been largely unstudied in Scotland although a positive association with feral domestic cats and farm buildings has been documented in winter and spring (Daniels, 1997). This may connect with observations of cats scavenging around farms during times of year when rabbits are less available (Corbett, 1979). In Scotland, arable farmland is frequently interspersed with patches of woodland and grassland providing a mosaic of cover including edge habitat and suitable prey for cats. Farm buildings, especially in winter provide suitable cover for feral domestic cats and prey opportunities (Germain *et al.*, 2008). These results support observations of feral domestic cats tending to remain near (<3 km) human habitation and that most feral domestic cat colonies are found around farmlands (e.g. Biro *et al.*, 2004b; Germain *et al.*, 2008) with proportion of grassland, arable and proximity to urban areas being the most important predictors of occupancy. Indeed, the ability of feral domestic cats to exist in resource-poor areas outside of close human habitation where they would be competing with wildcats is unknown (Balharry *et al.*, 1994). Interestingly, feral domestic cats were negatively associated with mixed woodland habitat, the habitat showing the highest occupancy probability for wildcats.

Previous studies have found some evidence that hybrids act like both wildcat and domestic cats, sharing many of the same habitat features but utilizing human resources more readily than wildcats (see Germain *et al.*, 2008) such as using farm buildings within their home ranges regularly (R. Campbell, unpublished radio tracking data, 2015). This analysis supports this contention as higher hybrid occupancy probabilities were predicted in areas between that of feral domestic cats and wildcats (Figure 3.1). In addition, although hybrid occupancy is driven by many of the same factors that influence the occupancy of feral domestic cats in particular, proportion of grassland and proximity to urban areas (Table 3.2), Figure 3.1 also indicates the extent to which hybrid occupancy overlaps that of wildcats, supporting the general view that by utilizing many of the same habitats as wildcats and feral domestic cats, hybrids play an important role in hybridisation.

As anticipated, predicted feral domestic cat occupancy probability increased in the east of Scotland where a higher proportion of arable farmland and urban areas was present (Figure 3.1a). Predicted feral domestic cat occupancy decreased in the north and north-west of Scotland (Figure 3.1a), areas that are both less inhabited (average human population ~8 - 15 people/km2, north – west; SCROL, 2011) and with far less arable habitat (MLURI, 1993).

Thus, these parts of Scotland likely provide habitat that is not highly suitable for feral domestic cats. In comparison, predicted hybrid occupancy, although also quite high in the east (Figure 3.1b), was predominately greater in the central Highlands and parts of the west than feral domestic cats. These areas of Scotland tend to provide a greater mosaic of woodland and grassland habitats and less arable farmland. The probability of occupancy for hybrids was predictably less in areas where the probability of wildcat occurrence was also low. The prediction of wildcat occurrence as a function of habitat variables alone (Figure 3.1c) indicates that potential occupancy probability is greatest in eastern Scotland (although not in the far east with areas of extensive arable farmland), the edges of the Cairngorms national park, western edges of the Black Isle and in suitable habitat along the coastal regions of western Scotland including parts of Morvern and Ardnamurchan peninsulas, areas of Argyll and Lochaber as well as small pockets of Sutherland and Caithness in the far north (Figures 3.1c and 3.2). These findings are consistent with previous surveys (Easterbee *et al.*, 1991; Balharry & Daniels, 1998; Davies & Gray, 2010).

The previous survey of Scottish wildcats found the wildcat to be less widely distributed than any surveys formerly conducted (Davies & Gray, 2010). For example, a survey in the 1980’s (Easterbee *et al.*, 1991) indicated that wildcats were widespread across Scotland north of the Central Belt (although the survey did not account for levels of hybridisation) but a subsequent survey in the 1990’s (Balharry & Daniels, 1998) suggested that wildcats had become predominantly restricted to the eastern part of Scotland. The most recent survey by Davies and Gray (2010) shows a similar pattern of distribution to the Balharry and Daniels (1998) survey with wildcat strongholds in the East, parts of the Highlands and the Ardnamurchan and Morvern peninsulas. They also noted however, fewer records from the far north. This study shows a similar pattern to the two previous studies with wildcats appearing to be predominant in eastern Scotland and the Cairngorms National park, but notably missing records from Ardnamurchan, the Black Isle and sites in the north that have previous recorded wildcats, even at low numbers. These findings are supported by a reduction in sightings reported to the National Biodiversity Network (www.NBN.org.uk) over the past 5-10 years, suggesting a potential decrease in wildcat numbers. In addition to hybridisation risk, the range of the Scottish wildcat might also be constrained by wild prey abundance and availability. Scotland has recently experienced a dramatic reduction in rabbit populations as a result of either disease and/or three successive hard winters with heavy snowfall between 2009-2012 (K. Kilshaw pers obs.). This reduction in rabbits, a favoured prey species of Scottish wildcat (Delahay *et al.*, 1998), may be one explanation for the reduced distribution, particularly in the far north of Scotland where pockets of suitable habitat exist surrounded by less hospitable heather moorland and bog habitat. The Black Isle in particular, once teeming with rabbits (R. Scott pers comm., 2011) and a known wildcat stronghold from all previous surveys, suffered from a huge rabbit population crash in early 2009 due to disease and bad weather and rabbits are now only found in low numbers to the western edge of the Black Isle, where some recent reports of wildcats have occurred. It is likely that wildcat occupancy in less favourable habitats is highly dependent on a suitable prey base and becomes restricted to more suitable, productive habitat during periods of low prey availability. Fluctuations in wildcat populations have been observed in Europe in relation to rodent density dynamics and climatic factors such as cold winters (Heptner & Sludskii, 1972). As the rabbit populations re-establish themselves, we could expect to see a corresponding increase in wildcat occurrence.

This decrease in wildcat distribution is also supported by the observation that wildcat occupancy probability appears to increase when hybrids are added to the model. Hybrids would not exist without the presence of wildcats; the most obvious explanation for this observation therefore is that the hybrid-wildcat model shows where wildcats have historically (perhaps even very recently) had high occupancy probabilities whereas the wildcat distribution map is based on the current wildcat data available. The wildcat occupancy probability map when hybrids are included as a variable therefore highlights areas that may either still be suitable for wildcat occupancy for example, potential areas of re-introduction, or areas that are particularly problematic for wildcats either in terms of high levels of hybridization or other factors. For example, extensive trophic niche overlap has been noted between these three cat types in European studies with hybrids and wildcats overlapping by 88% and feral domestic cats and wildcats by 80% (Biro *et al.*, 2005) suggesting the potential for competition over resources. In particular, the use of grassland habitat, often providing high abundance of rabbits (Corbett, 1979), has been shown to be used by all three cat types (Germain, 2007) and in this study the probability of occurrence of all three cat types increased in relation to the proportion of grassland habitat, most importantly for feral domestic cats and hybrids. Hybrids in particular may have a competitive advantage over wildcats by overlapping habitat use with wildcats and feral cats, allowing them to outcompete wildcats by utilizing human based resources but also by directly competing with them for resources. Certain combinations of environmental factors may therefore increase the chances of hybrids displacing wildcats.

Scottish wildcats are at risk from hybridisation across much of their current distribution from feral domestic cats and/or hybrids. Based on this study, hybrids may present a greater hybridisation risk than feral domestic cats, having an increased probability of occupying much of the same habitat as wildcats. Indeed, hybrids were the most significant predictor of wildcat occupancy, indicating the importance of controlling their impact on wildcat populations. Interpretation of the results of this assessment can also be used to focus conservation action on habitats with the highest probability of wildcat occurrence and to prioritize future wildcat surveys. In addition, the distribution maps highlight areas of high predicted occupancy for all three cat types which could be used to help direct and prioritize further survey work. In 1995, Kitchener raised the possibility of captive breeding and reintroduction or reinforcement of the Scottish wildcat as a potential conservation method (Kitchener, 1995). Although the Scottish captive population is currently not in a position to provide cats for translocation purposes (RZSS pers comm., 2014), studies such as this can indicate potentially suitable areas for translocation or release in the future provided suitable measures have been put into place to reduce the local feral domestic cat/hybrid populations.

Chapter 4

4.0 The current population status of the Scottish wildcat

4.1. Abstract

Estimating population sizes and density of species is an important part of effective conservation efforts but difficult to achieve for species that are difficult to survey for. Here, I use camera trap data collected between January 2010-July 2013 from sites across Northern Scotland and Spatially Explicit Capture Recapture analysis in SECR to produce estimates of density/100 km^2 and home range size of wildcats, hybrids and feral domestic cats. These estimates were then used to calculate an overall population size of the Scottish wildcat.

Mean density estimates of 3.5 (SD = 7) wildcats/100 km^2 were comparable to other studies in Scotland using different survey methods. Wildcats had larger home range sizes ($\bar{x}$ = 96.81 km^2; SD = 99.12 km^2; range = 26.72-166.90 km^2) than hybrids (44.99 km^2) and feral domestic cats ($\bar{x}$ = 8.02 km^2; SD = 6.98 km^2; range = 1.44-15.35 km^2). Capture rates and densities of total wild-living cats significantly varied between different sites, likely in relation to prey availability and habitat quality. Realistic estimates for an overall population size of the Scottish wildcat ranged between 115-314 individuals depending on local densities and home range size. Based on these data, the Scottish wildcat should have its current status of Least Concern reviewed.

4.2. Introduction

Establishing reliable estimates of population size is one of the central questions for ecological studies (Krebs, 1998). The effectiveness of conservation efforts is clearly difficult to evaluate without them. However, basic baseline data is lacking for many species that are difficult to survey. Without basic data, conservation planning and management are impossible (Weber & Rabinowitz, 1996). Knowledge of population size is particularly important for rare or threatened species that may be at increased risk of extinction from natural or anthropogenic causes.

Once a species falls below a critical level, often termed the Minimum Viable Population size (e.g. Shaffer, 1983), it is doomed to extinction unless radical conservation action is taken. Habitat loss and degradation, over-harvesting such as from persecution or hunting are frequently implicated as factors which can reduce population sizes towards this threshold value (Gilpin & Soule, 1986; Soulé *et al.*, 1986). This is the predicament facing many wide-ranging carnivores, where habitat loss and fragmentation, and persecution can have a particularly detrimental effect (Noss *et al.*, 1996; Woodroffe, 1998). In the absence of basic knowledge, conservationists do not know how close to critical the status of a population is. The Scottish wildcat (*Felis silvestris silvestris*) is one such species.

The Scottish wildcat is Britain's only surviving native felid (Macdonald *et al.*, 2004) and while currently classified as Least Concern (Driscoll & Nowell, 2009), its status is not healthy by historical standards. Previously widespread across the UK, the Scottish wildcat is now thought to be limited to the north of Scotland (Balharry & Daniels, 1998; Davies & Gray, 2010). The decline of the wildcat has been attributed to habitat loss, in particular loss of forested areas, and to hunting for its fur and persecution as a predator on livestock and game animals (Kitchener, 1995). The development of sporting estates in Scotland from the mid-19th

Century increased the rate of decline (Langley & Yalden, 1977; Tapper, 1992). The current threats are thought to be mainly hybridisation with, and disease transfer from, domestic/feral cats (*F.s.catus*), habitat loss and human persecution (McOrist *et al.*, 1991; Hubbard *et al.*, 1992; Nowell & Jackson, 1996). The most recent and widely cited, population estimate of 400 individuals was extrapolated from museum data collected in the 1990s (Macdonald *et al.*, 2004) and is therefore likely to be out of date. If the effect of hybridisation has been severe and only a few genetically pure individuals are found to remain, then the Scottish wildcat could be reclassified as Critically Endangered under the IUCN guidelines (Driscoll & Nowell, 2009) there is, therefore, an urgent need to reassess the current population size of the Scottish wildcat.

Recent density estimates existing for the Scottish wildcat are few. These are 1 individuals/100 km^2 in the west of Scotland (Scott *et al.*, 1993) estimated using radio tracking, 30 individuals/100 km^2 in the east of Scotland (Corbett, 1979) estimated using radio tracking and scat surveys and more recently, estimates from camera trapping ranging from 68 (SE=9, CI=50-80) individuals/100 km^2 in the north-eastern Cairngorms National Park (Kilshaw *et al.*, 2015a) to 2 (SE=1, CI=1-6) individuals/100 km^2 on the Morvern peninsula on the western coast of Scotland (Littlewood *et al.*, 2014) for wildcats and hybrids combined. Similarly, limited data exist for home range sizes, for example Corbett (1979) found males and females to have home range sizes of approximately 1.75 km^2 in eastern Scotland, and Daniels (1997) found mean home range size varied from 1.72 km^2 for females to 6.06 km^2 for males also in the east of Scotland, whereas Scott *et al.* (1993) found home range sizes of wildcats in the west of Scotland varied from 8 km^2 for females to 18 km^2 for males. Recent GPS radio tracking studies have found female wildcats to have a mean home range size of 6.94 km^2 (R. Campbell unpublished data, 2015).

Recent studies on both the European wildcat and the Scottish wildcat have indicated that camera trapping can be useful to some extent for determining the presence and abundance of this species (Anile *et al.*, 2007; Anile *et al.*, 2009; Monterroso *et al.*, 2009; Anile *et al.*, 2012; Kilshaw *et al.*, 2015a). Camera trapping has been widely used to monitor rare and elusive species such as carnivores (e.g. Griffiths & Van Schaick, 1993; Jones & Raphael, 1993; Karanth & Nichols, 1998a; Carbone *et al*., 2001; Tobler *et al*., 2013) and can be used to generate population density estimates (Karanth & Nichols, 1998b). In this chapter, I explore the potential for camera trapping to estimate densities and population sizes of the Scottish wildcat northern Scotland. These estimates are also used to generate a total population size estimate for the Scottish wildcat.

4.3. Methodology

Camera trap surveys were carried out across the 23 sites as described in Chapter 2

4.3.1. Analysis of camera trapping data

Data from the camera traps was managed in the program Camera Base (© 2007 Mathias Tobler; http://www.atrium-biodiversity.org/tools/camerabase/). As well as many other features, Camera Base allows the user to manage multiple surveys in one database. Data were displayed in ArcGIS 10.1 and statistical analysis was carried out using Rcmdr in R version 3.1.2 (© 2004. The R Foundation for Statistical computing).

Trap nights (TN)

Trap nights were calculated as the total number of days/nights or in this case, 24hr periods, for which all camera trap stations were active.

Capture events

A capture event was defined as the capture of an individual at a camera trap station within a 24hr period. If more than one photograph of the same individual was taken within the 24hr period, it was considered one capture event. If the animal was not individually identifiable, or difficult to identify, and captured within a short time period (for this study an arbitrary 30-minute interval was chosen) (Kilshaw *et al.*, 2015a), then this was assumed to be the same individual and it was not counted as a multiple capture event.

Capture frequency

Capture frequencies of wildcats, hybrids or feral domestic cats were calculated as the total number of capture events/100 trap nights (Lynam, 2001). Because the capture frequency takes into account the number of trap nights each survey is carried out for, capture frequencies of wildcats from different surveys carried out over varying periods of time can still be compared.

4.3.2. Density estimates using Spatially Explicit Capture Recapture (SECR)

Density estimates for the different cat types were calculated for each of the sites where possible (see Table 4.1) using SECR 2.9.4, an R package designed for spatially explicit capture recapture analysis (Efford, 2015). SECR models use the spatial information of capture-recapture data from a variety of different detectors (in this case camera traps) to estimate the distribution of animals in space and their density. SECR models have advantages over classic capture-recapture models, particularly in estimating density because they address the uncertain edge effects and spatially heterogeneous detection probability caused by movement in conventional animal trapping (Otis *et al.,* 1978; Efford *et al.,* 2004; Efford *et al.,* 2007; Borchers & Efford, 2008; Efford & Fewster, 2013). SECR models can be parameterized both within a maximum likelihood (Borchers & Efford, 2008; Efford *et al.,* 2009) as well as a Bayesian framework (Royle *et al.,* 2009; Royle & Gardner, 2011). SECR models assume that home ranges are approximately circular and remain stable for the duration of the survey period and that the detection probability (g0) decrease with increasing distance from the activity centre (Efford, 2015).

4.3.2.1. Data input

The primary data for SECR models are; 1) detections of known individuals on one or more sampling occasions (i.e. their detection histories) and 2) the locations of the detectors. In addition, SECR combines a state model and an observation model. The state model describes the distribution of animal home ranges in the landscape, and the observation model (a spatial detection model) relates the probability of detecting an individual at a particular detector to the distance of the detector from a central point in each animal's home range. The state model is described by a 'habitat mask' which is constructed by placing a buffer around the camera traps and generating points within this buffer. Each point represents a grid cell of potentially occupied habitat and the SECR likelihood is evaluated by summing values at points on the mask. The habitat masks can exclude known non-habitat. Habitat masks can be automatically generated or user specific.

1. **Animal capture data file:** each unique individual captured during the camera trapping surveys was given a unique identification number ranging from 1 to X (Maximum No. individuals captured at the specific study site). Each camera trap location was also given a unique ID ranging from 1 to 20/21 and each sampling occasion was given a unique ID ranging from 1 – X (Maximum No. days each survey was run for). An

animal capture file was then created with a location ID column, an animal ID column and a sampling occasion ID column. Each row represents a capture event for an individual showing its ID, what trap station it was caught at and what sampling occasion it was captured on.

2. **Detector layout file:** provides information on usage (the dates on which each camera trap station is active), and so provides the programme with useful information on any trap night losses (as a result of snow or theft for example). Each camera trap station is given a trap ID from 1-20/21 and a value of "1" or "0" for active or non-active camera traps for each trapping occasion for the duration of the survey. The X co-ordinates and Y co-ordinates of each trapping station are also incorporated into this file.

3. **Habitat mask:**

   Here the habitat mask was generated in ArcGIS 10.1 by first generating a "Minimum Area Rectangle" by connecting the outermost camera trap stations. A buffer was then created around this Minimum Area Rectangle which was large enough to ensure that no individual outside of the buffered area has any probability of being camera trapped. In this case, a buffer was established at a distance of 3km from the Minimum Area Rectangle (double the diameter of the minimum known home range of a female wildcat) (Kilshaw *et al.*, 2015a). A grid of points 250m apart was then generated within this buffer area.

Homogenous density model

The habitat at each point was classified as suitable "1" or unsuitable "0" for the homogenous model. Unsuitable habitats in this case were water bodies, roads and urban areas and elevation above 800m. The home range centres file consist of the X and Y co-ordinates of each point and the suitability of the habitat at each point.

InHomogenous density model

Each point in the habitat mask was given a probability of occupancy (ψ) for a wildcat, hybrid or feral domestic cat based on the proportion of landcover at each point, elevation (m), amount of edge (km) and/or distance to the nearest sub-urban/urban area (km) using the Beta (β) coefficient and intercept values obtained in Chapter 3 (see Table 3.2). Probability was calculated for each cat type and for wildcats with hybrid and feral cat occupancy included in the occupancy model (Kilshaw *et al.*, 2015b) by using the following equations:

1. $PREDICTION_{Feral/Hybrid} = Int + (\beta_{Arable} * _{Arable}) + (\beta_{Cwoodland} * _{Cwoodland}) + (\beta_{Grassland*Grassland}) + \beta_{Gorse} _{*Gorse}) + \beta_{Woodland*Mixed\ woodland}) + (\beta_{Edge*\ Edge}) + (\beta_{Elevation*Elevation}) + (\beta_{Urban*\ Urban})$

2. $PREDICTION_{Wildcat} = Int + (\beta_{Cwoodland} * _{Cwoodland}) + (\beta_{Grassland*Grassland}) + \beta_{Gorse\ *Gorse}) + \beta_{Woodland*Mixed\ woodland}) + (\beta_{Edge*\ Edge}) + (\beta_{Heather*Heather}) + (\beta_{Elevation*Elevation})$

3. $PREDICTION_{Wildcat\ with\ hybrid\ and\ feral\ occupancy\ =} Int + (\beta_{Cwoodland} * _{Cwoodland}) + (\beta_{Grassland*Grassland}) + \beta_{Gorse\ *Gorse}) + \beta_{Woodland*Mixed\ woodland}) + (\beta_{Heather*Heather}) + (\beta_{Elevation*Elevation}) + (\beta_{Feral*Feral}) + (\beta_{Hybrid*Hybrid})$

4. The Prediction values were then converted into an estimate of occupancy probability using the Inverse-Logit link:

   $\psi_{Feral/Hybrid/Wildcat/Wildcat\ with\ hybrid\ and\ feral\ occupancy} = EXP(PREDICTION)/(1+EXP(PREDICTION)$

4.3.2.2. SECR models run

Two different basic models were used to analyse the camera trap data:

1. **Homogenous density model**

Under this model, two real parameters, the probability of detection ‘g0’ (or ‘λ0’) and the spatial scale movement parameter ‘sigma’ (σ) are estimated directly when the SECR model is fitted by maximising the conditional likelihood (CL=TRUE). Density ‘D’ is then derived from the model. Density is considered to be consistent across the entire area included in the mask.

2. **Inhomogenous density model**

Under this model, three real parameters are estimated; ‘g0’, ‘σ’ and ‘D’ and SECR models are fit by maximising the numerical (full) conditional likelihood (CL=FALSE). The SECR log likelihood is evaluated by summing values at points on the habitat mask. Each point in a habitat mask represents a grid cell of potentially occupied and/or unoccupied habitat (their combined area may be almost any shape). Here the effect of a continuous variable, ‘*Occupancy*’ on ‘D’ was examined. Density may vary across the habitat mask dependent on ‘*Occupancy*’.

All models were run using the ‘Nelder-Mead’ algorithm following initial runs which indicated the default; ‘Newton-Raphson’ algorithm was leading to maximization errors. The Nelder-Mead method is more robust than the default method (Efford, 2015). A half-normal detection function was used which describes the decline in detection probability with distance (d) from the home range centre using the equation: g(d) = g0 exp(-d^2 /(2 σ^2)). The specific SECR models run are shown below (Table 4.1).

In some cases, density estimates of specific cat types were not obtained directly using the SECR models because of low recaptures, in which case, a density estimate was calculated from the total cat density based on the proportion of that cat type in the overall population. For example, if a total of 6 cats was captured, and only two of these were wildcats, then the proportion of wildcats in the overall cat population was calculated as 2/6 (0.33) and the overall cat density estimate from the SECR output was multiplied by this proportion to get an approximate estimate of wildcat density at that site. These estimates are provided for interest as opposed to estimates generated directly by SECR.

Table 4.1 Specific models run under both the Homogenous Basic model and InHomogenous Basic model, describing how detection probability (g0) and/or density/ha (D) vary under different models, the movement parameter (σ) remains constant (σ ~1) in all models.

MODEL	MODEL NAME	MODEL DESCRIPTION
	Homogenous Density Models	
g0~1	BASE model	g0 is constant across animals, occasions and detectors
g0~b	Trap happy/shy model	learned response affects g0
g0~B	Transient response model	g0 depends on detection at preceding occasion (Markovian response)
g0~K	Site response model	site effectiveness depends on preceding occasion
g0~bk	Site learned response model	site-specific step change affects g0
go~Bk	Site transient model	site-specific step change affects g0
g0~T	Time model	linear trend over occasions on link scale
	InHomogenous Density Models	
D~Occupancy, g0~1	BASE model	D varies with 'Occupancy', g0 is constant across animals, occasions and detectors
D~Occupancy, g0~b	Trap happy/shy model	D varies with 'Occupancy', learned response affects g0
D~Occupancy, g0~B	Transient response model	D varies with 'Occupancy', g0 depends on detection at preceding occasion (Markovian response)
D~Occupancy, g0~K	Site response model	D varies with 'Occupancy', site effectiveness depends on preceding occasion which affects g0
D~Occupancy, g0~bk	Site learned response model	D varies with 'Occupancy', site-specific step change affects g0
D~Occupancy, go~Bk	Site transient model	D varies with 'Occupancy', site-specific step change affects g0
D~Occupancy, g0~T	Time model	D varies with 'Occupancy', linear trend over occasions on link scale

4.3.2.3. Data output

Data output from the SECR models includes density (D) as the number of animals/ha which was converted to animals/100 km^2, σ (presented in metres) and g0. The SEs and 95% Confidence Intervals are also shown. Under the bivariate normal model for animal movement, σ was converted to provide an estimate of 99% home range area using the formula: $A = \pi(2.25 * \sigma)^2$.

4.3.2.4. Assessment of models

Models were assessed used AIC criteria corrected for small sample sizes (AICc). The model with the lowest AICc value and the highest AICc weight was considered the best model for the data. AICc values of models run using different conditional likelihood methods (e.g. CL=TRUE or FALSE) cannot be compared directly (Efford, 2015). Therefore AICc values for inhomogenous and homogenous density models were examined separately.

4.3.3. Northern Scotland wildcat population size estimate

The occupancy probability estimates produced in Chapter 3 for wildcats (with hybrid and feral cat occupancy included as covariates; see Figure 3.2) was used here to quantify the available habitat for the wildcat. Habitat with an occupancy probability of ≥ 0.8 was included in the overall area estimate following an initial assessment where models were run with occupancy probability varying between 0.6-0.9. The 0.8 cut-off point most realistically represented the naïve data points across the landscape and was therefore considered the most suitable to use in the modelling. As detailed in Chapter 3, this occupancy probability also excluded areas around houses and settlements that not considered to be optimal habitat (Klar *et al.*, 2008) using a 200m radius buffer around single house settlements and 900m buffer around urban areas.

Littlewood *et al.* (2014) suggested an area of 4000 ha of suitable habitat within a matrix of other habitats would be required to support a viable population of 20 female wildcats. Green (1991) also noted a dispersal distance of 4km for wildcats. Here I presume that habitat with ≥ 0.8 probability of occupancy but <2km^2 and >4km away from other suitable habitat would not provide sufficient habitat to support a viable local wildcat population. This is to exclude very small patches of suitable habitat within a matrix of unsuitable habitat from the overall area estimate. Patch sizes that were large enough to support individual females and 20 females based on minimum home range sizes were then estimated to account for the variation in home ranges associated with prey and habitat differences (e.g. Corbett, 1979; Scott *et al.*, 1993; Daniels, 1997). Two home range size estimates exist for female wildcats; these estimates are comparable to other European wildcat populations (Appendix 3) and are used here to generate overall population size estimates. These area estimates were then multiplied by the density/100 km^2 estimates derived (see Figure 4.2) to get wildcat population estimates.

1. Minimum home range size of a female = 1.72-1.75km^2 (North-east Scotland; Corbett, 1979; Daniels, 1997). All suitable habitat <2km^2 was excluded from final area estimates.
2. Minimum home range size of a female = 8km^2 (West of Scotland; Scott *et al.*, 1993). All suitable habitat <8km^2 excluded from final area estimates.
3. Area required to support a viable population of 20 females with MHR 2km^2 = 40km^2 Suitable habitat <40 km^2 excluded from final area estimates.
4. Area required to support a viable population of 20 females MHR 8km^2 = 160km^2. Suitable habitat <160km^2 excluded from final area estimates.

5. Minimum and maximum home range sizes from this study were also included but estimates were calculated from male and female wildcats so are likely to be larger than female only estimates (see Table 4.5).

4.4. Results

4.4.1. Summary data

Cats were caught at 15 of the 23 sites surveyed and wildcats were photographed at 5 of these sites (Table 4.2).

Table 4.2 No. of different individuals caught, no. of capture events for the different cat types and the no. of different trap stations cats were caught at across the study sites. Estimates of the Minimum Number Alive are also shown.

Site	Study	Total captures & recaptures	Wildcat capture events	Hybrid capture events	Feral cat capture events	No. different individuals	No. ind wildcats	No. ind hybrids	No. ind ferals	No different stations
Seafield and Strathspey	A	9	1	7	1	3	1	1	1	3
Gartley	E	34	22	1	11	7	3	1	3	11
Fetteresso	J	19	9	8	2	4	1	2	1	3
Letterewe	K	30	0	0	30	4	0	0	4	1
Glen hurich	L	20	0	0	20	5	0	0	5	4
Strontian	M	11	0	3	8	5	0	2	3	3
Lochaline	N	22	1	2	19	7	1	1	5	6
Dundreggan	Q	3	0	0	3	1	0	0	1	1
Laggan	S	3	0	0	3	2	0	0	2	2
Achlibster	T	5	0	0	5	1	0	0	1	1
Spinningdale	U	35	0	17	18	2	0	1	1	2
Trossachs	V	17	0	15	2	3	0	1	2	2
Darnaway	W	2	0	0	2	2	0	0	2	2
Glen Isla	X	72	11	28	33	12	4	4	4	12
Fearnoch*	Z	2	0	1	1	2	0	1	1	1
TOTAL		**284**	**360**	**278**	**120**	**60**	**10**	**14**	**36**	**54**

*Seen but not captured

The total number of trap nights each site was active for varied from 132-2162 ($\bar{x}$ = 1480, SD = 394) resulting in overall capture rates ranging from 0 – 8.33 captures/100TN ($\bar{x}$ = 1.20, SD = 1.87), captures rates for wildcats ranged from 0-1.66 captures/100TN ($\bar{x}$ = 0.17, SD = 0.36), hybrids ranged from 0-2.27 ($\bar{x}$ = 0.45, SD = 0.60) and feral domestic cats ranged from 0-6.06 ($\bar{x}$ = 0.95, SD = 1.31) (Table 4.3). Capture rates did not vary significantly between cat types (One-Way ANOVA; F =2.36, df = 2, p = 0.10) but varied significantly between sites (T-test; t =2.80, df = 22, p = 0.01).

Table 4.3 Trap nights and capture frequencies at each site (No. captures/100TN) for each cat type. Sites for which there were sufficient recaptures to carry out SECR analyses are highlighted in grey.

Site	**Site ID**	**Trap nights**	**Captures/100 TN**			
			Total	**Wildcats**	**Hybrids**	**Ferals**
Seafield and Strathspey	A	1319	0.68	0.08	0.53	0.08
Gartley	E	1327	2.56	1.66	0.08	0.83
Black Isle	F	1532	0	0	0	0
South Glen Affric	G	2016	0	0	0	0
North Glen Affric	H	1278	0	0	0	0
Fetteresso	J	2162	0.88	0.42	0.37	0.09
Letterewe	K	1914	1.57	0	0	1.57
Glen hurich, Ardnamurchan	L	1478	1.35	0	0	1.35
Strontian, Ardnamurchan	M	132	8.33	0	2.27	6.06
Lochaline	N	1589	1.38	0.06	0.13	1.20
Inchnadamph	O	1318	0	0	0	0
Inverlael	P	1468	0	0	0	0
Dundreggan	Q	1459	0.21	0	0	0.21
Dunrobin, Golspie	R	1285	0	0	0	0
Laggan	S	1257	0.24	0	0	0.24
Achlibster	T	1514	0.33	0	0	0.33
Spinningdale	U	1410	2.48	0	1.21	1.28
Trossachs	V	1342	1.27	0	1.12	0.15
Darnaway	W	1440	0.14	0	0.00	0.14
Glen Isla	X	2013	3.58	0.55	1.39	1.64
Hope	Y	1622	0	0	0	0
Fearnoch Forest	Z	1376	0.15	0	0.07	0.07
Tummel Bridge	AA	1800	0	0	0	0

Overall, 6 sites were analysed using SECR (see Table 4.3). Both the homogenous and inhomogenous models produced comparable results for density, sigma and home range estimates, therefore the results from the inhomogenous models are detailed below.

4.4.2. Density estimates

Across all sites, the trap happy/shy model or site learned response models were the favoured models for estimating wildcat densities where detection probability on subsequent trap occasions was affected by an individual's response to the camera trap and/or location of the camera trap. In comparison, hybrid and feral domestic cat densities were estimated using the BASE models where detection probability was constant across all animals, occasions and detectors.

Densities for total number of wild-living cats across the six sites ranged from 8-28 cats/100 km^2 ($\bar{x}$ = 17, SD = 7) and differed significantly between sites (T-test; $t = 5.78$, $df = 5$, $p = 0.002$) but did not differ significantly between different cat types (One Way ANOVA; $F = 0.97$, $df = 3$, $p = 0.45$).

Densities estimates for wildcats were obtained from two sites and did not differ significantly from one another (T-test; Wildcats - $t = 7$, $df = 1$, $p = 0.09$) giving a mean estimate of 3.5 wildcats/100 km^2 (SD = 0.7). Only one density estimate was obtained for hybrids of 6/100 km^2 using SECR. Feral domestic cat estimates ranged from 3-20 individuals/100 km^2 ($\bar{x}$ = 10, SD = 7) but did not differ significantly between sites (T-test; - $t = 2.89$, $df = 3$, $p = 0.06$) (Table 4.4). Guestimate values calculated from the proportion of each cat type in relation to the overall cat density estimate for that site are also shown in Table 4.4 for interest.

Table 4.4 Density/100 km^2 estimates for each of the six sites and different cat types generated using SECR under the inhomogenous model. Estimates highlighted in grey are calculated from the total cat population density based on the proportion of each cat type and are shown for interest only and not included in the analysis

Site	All cat	Wildcat	Hybrid	Feral
Gartley	8	4	1	9
Fetteresso	28	18	9	6
Glen hurich, Ardnamurchan	20	0*	0*	20
Lochaline	14	4	4	9
Trossachs	22	0*	15	15
Glen Isla	12	3	6	3

*No photographs taken of these cat types therefore density estimates not generated

4.4.3 Movement parameter Sigma and Home range size estimates

Overall, estimates of sigma varied significantly across sites for all cat types (T-test; t = 3.22*, df* = 5*, p* = 0.02) ranged from 147.35-2830.92m ($\bar{x}$ = 1233.94, SD = 1078.84). Estimates of home range size for all cats/km^2 however, did not differ significantly between sites (T-test; t = 1.91, *df* = 5, *p* = 0.11) and ranged from 0.35-127.39 km^2 ($\bar{x}$ = 39.62, SD = 50.82).

For the sites that σ and home range size could be calculated for, mean wildcat σ and home range sizes were greater than hybrids and feral cats but not significantly (One Way Anova; *F* = 1.43, *df* = 2, *p*= 0.36; *F* = 2.30, *df* = 2, *p*= 0.25 for σ and home range size respectively) (Table 4.5).

Table 4.5 Variation in mean σ and home range estimates between the different cat types under the inhomogenous model. Shows the SD and estimate ranges.

	σ (m)				Home range estimate (km^2)			
	Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Wildcats	2268.40	1374.46	1296.51	3240.3	96.81	99.12	26.72	166.90
Hybrids*	1682.28	-	-	-	44.99	-	-	-
Feral domestic cats	653.61	341.30	301.29	982.70	8.02	6.98	1.44	15.35

*Only one value for hybrids estimates

4.4.4. Detection probability (g0)

Detection probabilities for all cats ranged from 0.0025-1 ($\bar{x}$ = 0.22, SD = 0.40) but did not differ significantly between sites (T-test; t = 1.36, df = 5, p = 0.23).

For the sites that detection probability could be calculated, mean wildcat g0 was greater than hybrids and feral domestic cats but not significantly (One Way ANOVA; F = 0.57, df = 2, p = 0.61) (Table 4.6).

Table 4.6 Variation in mean detection probability (g0) estimates under the inhomogenous model between the different cat types. Shows the SD and estimate ranges.

	g0			
	Mean	**SD**	**Min**	**Max**
Wildcats	0.29	0.41	0.0007	0.59
Hybrids*	0.004	-	-	-
Feral domestic cats	0.11	0.17	0.001	0.36

*Only one value for hybrids estimates

4.4.3. Northern Scotland wildcat population estimate

Population estimates varied from 115-467 individuals depending on uncertainty in home range sizes (Table 4.6) and were based on the mean density estimates for wildcats obtained using the SECR Inhomogenous models. There was insufficient habitat to support a population of 20 breeding females if the largest home range size (168 km^2) estimated from this study was used.

Table 4.6 Total population estimates for wildcats in Scotland dependent on known minimum home range size of female wildcats of 2 and 8 km^2 and estimated the overall population size if habitat patches large enough to support 20 female wildcats are considered. Minimum and maximum home range sizes calculated from this study are also used to estimate population sizes using the mean density obtained in this study of 3.5 wildcats/100 km^2.

	Available area (km^2)	**Density**/100 km^2	**Pop size (N)**
All available habitat (≥ 0.8 occupancy)	1 3 349	3.5	467
Minimum home range size (km^2)			
2	12 058	3.5	422
8	10 934	3.5	383
28	9174	3.5	321
168	5892	3.5	206
Area required to support 20 females (km^2)			
40	8978	3.5	314
160	5892	3.5	206
560	3300	3.5	115
3360	NA	NA	NA

4.5. Discussion

The density estimates observed here fell between those from other studies in Scotland but lower than those estimated across Europe, for example, 28 wildcats/100 km^2 in Sicily (Anile *et al.*, 2012), 10-13/100 km^2 in the Polish Carpathians (Okarma *et al.*, 2002), 35 wildcats/100 km^2 in Switzerland

(Weber *et al.*, 2008) and 11/100 km^2 in Hungary (Heltai *et al.*, 2006). Here, mean wildcat densities were 3.5 wildcats/100 km^2, and using guestimates, they also varied slightly across different sites. This pattern has been observed in other studies in Scotland with wildcats in the east showing higher densities than the west (Corbett, 1979; Scott *et al.*, 1993; Littlewood *et al.*, 2014). These observations are thought to result from lower prey densities and poorer habitat in the west compared to the east of Scotland.

Observations here that wildcats had larger home range sizes than hybrids and feral domestic cats are supported by other studies (e.g. Corbett, 1979; Szemethy, 1993; Biro *et al.*, 2004b; Germain *et al.*, 2008). Typically it is suggested that this difference is primarily because feral domestic cats in particular do not need large home ranges because they use food and shelter from human settlements (Liberg & Sandell, 1988), whereas wildcats need to account for seasonal variations in prey abundance and prey availability (Corbett, 1979; Liberek, 1999). Studies have also shown that hybrids share many of the same habitat features as both wildcats and feral/domestic cats but also utilize human resources more readily than wildcats (Germain *et al*., 2008; R. Campbell, unpublished radio tracking data, 2015; Chapter 3), we would therefore expect their home range sizes to fall somewhere between wildcats and feral domestic cats.

Home range sizes of wildcats also varied between sites, an observation supported by other studies on *F. s. silvestris* where home range sizes may vary between sexes and seasons and in relation to prey availability (Corbett, 1979; Stahl *et al.*, 1988; Scott *et al.*, 1993; Liberek, 1999). Here, the mean wildcat home range size in Gartly (166 km^2) was almost five times greater than that of wildcats in Glen Isla (27 km^2). Both sites have rabbits and were camera trapped across a similar season but the difference in home range size may indicate the area is more resource rich in terms of prey availability and therefore wildcats do not need such large home ranges to meet all their needs.

Interestingly, the SECR models indicated that some degree of trap awareness was occurring for wildcats, with either the trap happy/shy model or site learned response model showing the most support for the data. Kilshaw *et al.* (2015a) noted an increase in capture rates of wildcats when bait was used, indicating some positive association with camera traps and bait. Anile *et al.* (2012) also noted that wildcats did not appear to be adversely affected by the presence of camera traps. Although wildcat capture rates were comparable to those of other studies (e.g. Kilshaw *et al.*, 2015a), they were lower than hybrids and feral domestic cats, although not significantly. Hybrids and feral domestic cats did not appear to be trap happy or shy and had relatively high capture rates (0.45-0.95). In comparison, detection probabilities of wildcats were higher than hybrids and feral domestic cats. One explanation for these observations are that because wildcats have larger home range sizes, they are more likely to come into contact with more camera traps because they have a wider area over which they roam which would account for the slightly higher detection probabilities but because of their lower densities, capture rates are lower. Increasing the overall size of the survey area could increase capture rates of wildcats to account for this.

Recent total wildcat population estimates range from 400 (Macdonald *et al.*, 2004) to as low as 35 (www.wildcathaven.co.uk), although a large part of this variation is due to both the difficulties in identifying wildcats and the methods used for the estimates. The estimates obtained here fall between just above these values and vary depending on the home range sizes used for the estimate. As stated above, densities of wildcats vary across different sites. This has important implications for an overall population estimate. Here, based on the availability of habitat with a high probability of wildcat occurrence and using the mean density estimate of 3.5 wildcats/100 km^2 obtained here, the highest potential population size for wildcats is 467 individuals. However, this is an unrealistically high estimate because it includes all isolated small patches of habitat (0.25 km^2) which are not large enough to support one female wildcat with a minimum home range size of 2 km^2, particularly if that patch falls within highly unsuitable habitat and is not within easy commutable distance for a wildcat. The more realistic population estimate based on home range sizes of between 2-168 km^2 suggest a total wildcat population of between 206-422 individuals. However this estimate falls even further when we examine how much directly connected habitat of high occupancy probability is available to support a minimum population of 20 breeding females to 115-314 wildcats. Much of the available habitat is also highly fragmented and the remaining population is likely to be found in isolated or partially isolated sub-populations. In addition, much of these areas may have lower/higher wildcat densities than those used here. Traditionally, in order to preserve genetic integrity of a population a minimum viable population size of 50-500 breeding individuals is considered sufficient (Shaffer, 1981), although more recent studies suggest several thousand are required for the long-term survival of most vertebrate populations (Reed *et al.*, 2003; Traill *et al.*, 2007). Clearly, here the Scottish wildcat population falls below the recommended threshold for vertebrates and is therefore likely to become extinct in the near future unless steps are taken urgently. For example, increasing the amount of habitat with a high probability of occupancy either through habitat restoration or connection of smaller habitat patches and reducing the numbers of feral domestic cats and hybrids in high quality wildcat habitat could all help increase wildcat numbers in the long-term. Currently *F.s. silvestris* is classified as Least Concern by the IUCN (Driscoll & Nowell, 2009), but based on the IUCN's criteria, these estimates provide support for the Scottish wildcat population to have its status reconsidered.

Chapter 5

5.0 Comparing the use of camera trap surveys, scat surveys, sign surveys and road traffic accident surveys for detecting the Scottish wildcat and recommendations for future monitoring practices.

5.1. Abstract

Detection of rare species such as the Scottish wildcat for conservation management purposes is essential but difficult to achieve. Many different methods exist for monitoring species presence/suspected absence, but methods vary in both their detectability and the amount of effort that goes into utilising them. Here, four different methods used for surveying "wild-living" cats (scat surveys, road traffic accident surveys, sign surveys and camera trap surveys) were carried out at various field sites across Northern Scotland between January 2010-July 2013. Insufficient data was collected from road traffic accident surveys (0 detections) and sign surveys (11 detections) and therefore, the detectability of camera trap surveys and scat surveys only were compared.

Camera trapping was more expensive and time consuming than scat surveys (£30 000 vs £14 000 and 621 days vs 237 days for camera traps and scat surveys respectively). However, under the multi-method model, camera trapping had a higher detection probability than scat surveys ($p = 0.25$, 0.10 for camera trapping and scat surveys respectively) and survey output was greater for camera traps (0.49 captures/day of survey effort) compared to scat surveys (0.14 scats/day of survey effort). Overall detectability was greatest if both survey methods were used ($p = 0.4$).

Detection by camera traps significantly increased when cats had been detected in prior surveys ($p = 0.25$ without recaptures, $p = 0.78$ with recaptures). Detection by scat surveys also increased if a

previous detection had occurred, but not significantly ($p = 0.10$ without recaptures, $p = 0.21$ with recaptures).

Overall, the findings from the multi-method and single-season analysis suggest that camera trapping is the most appropriate method to use out of those examined to detect wild-living cats, but detection can be further increased by using more than one survey method. Detection of wild-living cats can be improved by carrying out the surveys in habitats expected to have a higher occupancy probability including habitat with a higher proportion of grassland and arable farmland, by utilizing linear features such as fence lines and tracks in the survey site and by maximizing the chances of recaptures occurring (e.g. through baiting camera traps or by improving scat survey techniques).

5.2. Introduction

Monitoring is frequently essential for effective conservation management (e.g. Barlow *et al.*, 2008; Balme *et al.*, 2010; Karanth *et al.*, 2011), particularly for species like the wildcat (*Felis silvestris silvestris*) that are vulnerable to local extirpation. The Scottish wildcat is Britain's only surviving native felid (Macdonald *et al.*, 2004), and is currently at risk of extinction and is likely to be classified as Critically Endangered if evidence emerges that the current population is less than the most recent estimate of c400 (Driscoll & Nowell, 2009). Previously widespread across the UK, the Scottish wildcat is now thought to be limited to the north of Scotland (Balharry & Daniels, 1998; Davies & Gray, 2010). The decline of the Scottish wildcat has been attributed partially to habitat loss, in particular loss of forested areas, and partially to hunting for its fur and persecution (Kitchener, 1995). The development of sporting estates in Scotland from the mid-19th Century increased the rate of decline (Langley & Yalden, 1977; Tapper, 1992). Current threats are thought to be hybridisation with, and disease transfer from, domestic/feral cats (*F.s.catus*) and human persecution (McOrist *et al.*, 1991; Hubbard *et al.*, 1992; McOrist & Kitchener, 1994b; Nowell & Jackson, 1996; Macdonald *et al.*, 2004). As a species vulnerable to extinction, regular monitoring with sufficient sensitivity to detect changes in population size is highly desirable.

Many methods exist for monitoring species (e.g. Wilson *et al.*, 1996). To date, a combination of road traffic accident (RTA) surveys, live trapping, radio tracking, scat surveys and interviews and questionnaires have been used to collect data on "wild-living" cats in Scotland including wildcats and feral domestic cats (Corbett, 1979; Easterbee *et al.*, 1991; Scott *et al.*, 1993; Daniels, 1997; Balharry & Daniels, 1998; Davies & Gray, 2010). More recently, Kilshaw *et al.* (2015a) found that camera trapping can also be used to survey for the Scottish wildcat. Although these methods can generate a variety of useful data, each has its limitations. For example, although RTA surveys can be a suitable technique for monitoring large-scale changes in populations (Rolley & Lehman, 1992; Gehrt, 2002), RTA surveys may not be suitable for measuring abundance of low-density populations (Hein & Andelt, 1995) such as wildcats, suggesting that there may be a minimum population density, below which this technique is not capable of detecting small changes in abundance (Gehrt, 2002). RTA surveys may also be affected by traffic volume, traffic speed, season and weather (Case, 1978). In addition, RTAs are thought to be biased towards hybrids and feral domestic cats as domestic cats are likely to be concentrated near urban areas (A. Kitchener pers comm., 2008), and are therefore more likely to suffer a RTA than a wildcat (BTO, 1999).

Many species can be identified from their tracks and signs (Edwards *et al.*, 2000; Wilson & Delahay, 2001; Triggs, 2002; Funston *et al.*, 2010; Karanth *et al.*, 2011) and scat surveys can provide a wealth of information on a species varying from information on abundance, distribution and sex ratios which can be obtained from DNA (Woods *et al.*, 1999; Mills *et al.*, 2000), dietary preferences (Stuart *et al.*, 2003) to the status of physiological health collected from hormonal data (e.g. Wasser *et al.*, 2000). However, although some studies have separated wildcat scats from feral domestic cat scats on the basis of size (e.g. Lozano *et al.*, 2003), it is difficult to distinguish easily between scats of wildcats and feral domestic cats in the field. It is therefore likely to be difficult to use this methodology to determine whether wildcats or feral domestic cats are present in a study area without genetic analysis, and even then, successful identification to species or individuals rather than just "cat" will depend on how fresh the scat collected is. In addition, the low density of wildcats makes their scats difficult to find (BTO, 1999). Some studies have also suggested that trail scat surveys are not as efficient as camera trapping or track plates for detecting cats in general (Gompper *et al.*, 2006) and the main factor limiting the use of scat surveys is that the relationship of scat survey estimates to absolute population densities has not yet been validated (Sadlier *et al.*, 2004). Similarly, live trapping of wild-living cats is time consuming and requires both licensing and experience, although a recent survey found that using camera traps prior to setting live traps greatly improved capture success (Littlewood *et al.*, 2014). Questionnaires and interviews based on sightings data are less expensive than trapping and equivalent to scat surveys, but data may be biased because they may reflect the distribution of interviewees rather than species distribution and are also dependent on how visible the species was to the viewer at the time (Davies & Gray, 2010). Main issues with this methodology include misidentification of wildcats, in particular, in view of the difficulties in easily identifying the wildcat in the field (Kitchener *et al.*, 2005), low response levels to the questionnaire, and bias of animal sightings along roads or near human habitation (Gese, 2001).

Although one survey method may be better at detecting the species in question than another, it is also important to factor in the cost effectiveness of the different methods available which can vary widely (Schauster *et al.*, 2002; Balme *et al.*, 2010). For example, methods such as scat collection may easily be carried out by trained volunteers but may require genetic analysis for identification purposes which can be expensive but may still be more effective than live trapping (Solberg *et al.*, 2006) which is not only very time consuming but requires either specialist training or veterinary support. Camera trapping involves an initially expensive outlay to purchase equipment and training of scat dogs is even more expensive (Long *et al.*, 2007). Different methods are more suited to different types of terrain and weather and it's important to consider the practicalities associated with carrying out the survey work as well. In addition, as recently noted by Gopalaswamy *et al.* (2015), care needs to be taken when extrapolating abundance estimates from index-calibration methods (where intensively measuring animals numbers on a small scale using one method (e.g. camera trapping) and are related to a wider scale survey method (e.g. scat surveys or questionnaires) using calibration) because unless specific assumptions can be met, these methods are likely to result in wasted resources and be of little value.

No matter what method is used to survey for the presence of a species, there is nearly always a risk that even if a species is present at a site, it may not be detected by surveyors; this gives rise to "false absences", which may be particularly problematic for species that exist at low densities and may already be difficult to detect (Mackenzie *et al.*, 2002). The problems associated with species that have imperfect detection have led to the development of occupancy models. This methodology estimates the probability of detecting at least one individual of the species during a sampling occasion when the species is present, which is incorporated into occupancy models (Mackenzie *et al.*, 2002; Tyre *et al.*, 2003; Stauffer *et al.*, 2004). As discussed in Chapter 3, failure to do so is more likely to produce biased estimates of prevalence, and to lead to misinformed conservation management decisions (MacKenzie *et al.*, 2006).

As far as I am aware no comparison of the ability of the methods currently used to detect wildcat/wild-living cat occurrence in Scotland have been made. The aims of this chapter are therefore to; *i*) compare the ability of different survey methods to detect the presence of wild-living cats, *ii*) to examine what factors influence the detectability of wild-living cats with the methods used. These aims are designed to *i*) to help identify the most effective method for identifying wild-living cats in the field, *ii*) to ascertain ways in which detectability could be improved for future monitoring efforts, *iii*) to determine if using a combination of different methods improves detection rates.

5.3. Methodology

Twenty-three survey areas (see Figure 2.1, Chapter 2) were surveyed for wild-living cats using a combination of camera traps, scats surveys, RTA surveys and signs surveys which were carried out as described in Chapter 2. Because of the difficulties in distinguishing between signs and scats of wildcats, hybrids or feral domestic cats, the ability of these methods to detect "wild-living" cats in general is estimated. No RTAs were collected over the period of the entire survey and only a few signs were observed in the field (Table 5.1) so only camera trap data and scat data were analysed here. Here, camera trap data was analysed in terms of capture events, where a "capture" was defined as the capture of an individual at a camera trap station within a 24hr period (see Chapter 4 for more details).

I used the Single-Season Multi-Method Occupancy Model (Nichols *et al.*, 2008) to compare the detectability of wild-living cats using camera trap surveys and scat surveys. Not all sites had scats collected at the same time as camera trapping; therefore these sites were excluded from the multi-method analysis but included in the single season occupancy analysis, in addition, sites with <2 camera trap captures (No. individuals photographed/4 week period) were also excluded from the analysis to improve model performance. Overall, 12 of the 23 sites surveyed were included in the Single-Season, Multi-Method Model (Table 5.1).

I then used the Single-Species Single-Season Occupancy Method (Mackenzie *et al.*, 2002) to examine factors affecting the ability of camera traps to detect wild-living cats in more detail.

Both sets of models were run using the programme PRESENCE v6.4 (Hines, 2006) (Proteus Wildlife Research Consultants, New Zealand; http://www.proteus.co.nz) which employs maximum likelihood estimation for generalized linear models.

5.3.1. Single-Season Multi-Method Model

The single season model (Mackenzie *et al.*, 2002) allows estimation of the probability that a site (*i*) will be occupied (ψ) by the target species in situations where it is not certain to be detected even when present. Under this basic model, p[*j*] is the probability of detecting the species in the j^{th} survey, given it is present at the site. The Single-Season-Multi-Method Model adds to this basic model by allowing detection probabilities to be different for different methods of observation. This allows the computation of an additional parameter, θ which is the probability that individuals are available for detection at the site, given that they are present. The parameter θ is estimated to account for the varying and often reduced availability probabilities across secondary sampling units (site) given presence of the species at the scale of the primary sampling unit (survey area). Under this model the parameters estimated are; ψ (probability that the area is occupied by the species), θ_t (probability that individuals are available for detection at survey *t*, given presence), p^{s}_{t} (probability of detecting species at survey *t* using method *s*).

This model has several advantages over the basic occupancy models because it *i*) deals with the lack of independence among detections by different methods at the same sampling site induced by animal(s) presence at the local sample site, *ii*) the method makes efficient use of data from the different methods both for estimating occupancy and for comparing detection probabilities associated with the different methods.

To depict a site *i,* a 500m radius buffer was placed around each camera trap station and the area within this buffer represented a *site*. Only scats collected within each of these *sites* were considered in the analysis in order to compare the two methods. Each survey area was sampled for 60-80 days (this restricts the chances of occupation changing during the sampling period so that the population can be assumed to be closed (e.g. Otis *et al.,* 1978). Camera traps were checked every 10-15 days, and scat surveys were also carried out during the checking period and at the start of each survey during the setting up period.

Occupancy matrices were created using the camera trap data which depicted presence/absence of wild-living cats across the study period. Every cell in the matrices was coded as 1 (detected), as 0 (not detected), or as NA (where a survey was not conducted or the cameras were inactive due to either battery failure or snow cover) at a resolution of 1 trapping day. Data were binned into 4-week periods to improve computation and because of low detection of wild-living cats (see Ahumada *et al.*, 2013) to give three-four survey occasions *(t)* for each site. Occupancy matrices were also created for the scat data so that scat surveys carried out during the 4-week survey period *(t)* at site *i* were coded as 1 (scat detected), 0 (scat not detected) or NA (scat survey not carried out). The final matrices for the Single-Season Multi-Method analysis consisted of 225 sites (*i*) x 4 survey occasions (*t*) x 2 methods (*s*).

Table 5.1 Detection history summary (1= detected, 0=not detected, “-“ = not surveyed) for all 23 sites across three/four survey periods (S1-S4) using camera traps (CT), scat surveys (SS), sign surveys (SI) and road traffic accident surveys (RT). Sites highlighted in grey are included in the occupancy modelling. The total number of wild-living cat capture events (see methods, chapter 4 for more detail), total number of cat scats collected and cat signs observed and then the respective numbers for CT, SS and SI when data was collapsed into 4 week periods are shown.

Site	Name	S1				S2				S3				S4				Total No. Captures			Captures/4 week period		
		CT	SS	SI	RT	CT	SS	SI	RT	CT	SS	SI	RT	CT	SS	SI	RT	CT	SS	SI	CT	SS	SI
A	Seafield	1	-	1	0	1	-	0	0	1	-	0	0	-	-	-	-	28	0	8	6	0	5
E	Gartley	1	1	0	0	1	1	0	0	1	0	0	0	-	-	-	-	34	7	0	16	6	0
F	Black Isle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G	South Glen Affric	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H	North Glen Affric	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
K	Fetteresso	1	1	1	0	1	1	0	0	1	1	0	0	1	1	0	0	19	12	3	8	7	2
J	Inverewe	1	0	0	0	1	0	0	0	1	0	0	0	-	-	-	-	30	0	0	3	0	0
L	Glen hurich	1	0	0	0	1	0	0	0	1	0	0	0	-	-	-	-	20	0	0	9	0	0
M	Strontian	1	0	0	0	1	1	0	0	0	0	0	0	-	-	-	-	11	2	0	5	1	0
N	Lochaline	1	0	0	0	1	0	0	0	1	0	0	0	-	-	-	-	22	0	0	12	0	0
O	Inchnadamph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	Inverlael	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Q	Dundreggan	1	0	0	0	1	0	0	0	1	0	0	0	-	-	-	-	3	0	0	3	0	0
R	Dunrobin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S	Laggan	1	0	1	0	1	0	0	0	0	0	1	0	-	-	-	-	3	0	2	1	0	2
T	Achlibster	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5	0	0	2	0	0
U	Spinningdale	0	0	0	0	1	0	0	0	1	0	0	0	-	-	-	-	35	0	0	5	0	0
V	Trossachs	1	0	0	0	1	0	0	0	1	0	0	0	-	-	-	-	17	0	0	4	0	0
W	Darnaway	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	-	2	0	0	2	0	0
X	Glen Isla	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	72	13	2	28	8	1
Y	Hope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Z	Fearnoch	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	1
AA	Tummel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

5.3.2. Habitat covariates – Single-Season Multi-Method

The habitat covariates used in the Single-Season Multi-Method model were chosen based on their importance as identified in Chapter 3. Habitat covariates were depicted as continuous rasters at a resolution of 500m x 500m. The habitat variables identified as important by Kilshaw *et al.* (2015b) (see Chapter 3) for occupancy of all three different cat types were primarily 'grassland' and 'mixed and broadleaved woodland' (*mwoodland*), but 'arable', 'coniferous woodland' (*cwoodland*), and the amount of 'edge' habitat also had a positive influence on occupancy and were therefore included in the analysis. A total of 5 *site* covariates were used including *i*) proportion of 'arable', 'coniferous woodland', 'mixed and broadleaved woodland' (*mwoodland*) and 'grassland' within each *site*; *ii*) the amount of edge habitat (*edge*). Habitat proportions were calculated from the UK Land Cover Map (LCM) 2007 (Under Licence LCM 2012-357vs2) which portrays land cover type at a resolution of 25 m. Because the LCM data was produced in 2007, the proportion of habitat was ground-truthed using field knowledge and aerial photography (www.gridreferencefinder.com). The amount of edge, representing the transition from closed to open habitat types, as a proxy for wildcat hunting habitat (see Klar *et al.*, 2008; Jerosch *et al.*, 2010), was calculated based on the intersection of woodland habitat (deciduous, coniferous, and mixed) and open habitat (gorse, dwarf shrub, and grassland) which are known to be used by wildcat prey (Silva *et al.*, 2013). Three *survey* covariates were also included in the model; *i*) *Recaptures,* based on whether any recaptures (photos or scats) had occurred in surveys 2-4. If a capture or recapture had occurred in any prior survey it was classified with a "1" and if no previous captures or recaptures had occurred it was given a "0". This was to ask if a detection of a wild-living cat affected subsequent detectability, *ii) Julian Date + Julian Date*^{2} to examine if the time of year the survey was carried out in had an impact on detectability. The Julian date was based on the start of each of the 4 survey periods for each site and also accounted for year of survey.

5.3.3. Model Selection

Initially a null model was run where occupancy (ψ), theta (θ) and detection (p) were kept constant ($\psi(.),\theta(.),p(.)$). Two sets of candidate models were then produced in order to compare the detectability of the two surveys methods; 1) Method model where ψ and θ were held constant and p varied according to method ($\psi(.),\theta(.)$, p(m)) and 2) Habitat model where ψ varied in relation to various habitat variables. Following initial analyses using various combinations of the different habitat variables identified as important in Chapter 3, grassland and mixed woodland were used here and p varied according to method (ψ(gr+mw),$\theta(.)$, p(m)). Keeping the Method model and Habitat model as basic units, the effect of different combinations of site and survey covariates on detectability (p) was then examined.

The best models were selected based on Akaike Information Criterion corrected for small sample size (AICc) and Akaike weights (*wi*). Although AICc is normally applied to small sample sizes, the use of AICc, rather than AIC is recommended by Burnham and Anderson (2002) regardless of sample size (*n*) or the number of parameters (*k*) because AICc converges to AIC as *n* gets large. To evaluate model fit, a Pearson Chi-Square goodness-of-fit test was carried out on the global model (the model with the most parameters) by performing 1000 simulated parametric bootstraps to determine how well the models represented the data (Mackenzie & Bailey, 2004). This method uses observed and expected numbers of observations and calculates a test statistic from parametric bootstrapping and also provides an estimate of the over dispersion parameter ĉ ($\hat{c} = X^2_{\mathrm{Obs}} / X^2_{B}$).

Values of ĉ >1 indicate that the data are not a good fit and are over dispersed, in which case standard errors are inflated by a factor of √ĉ and quasi-corrected AIC_c ($QAIC_c$) values are used for model selection instead (Burnham & Anderson, 2002). In this case ĉ can be adjusted in PRESENCE and 1 added to *K* parameters to generate QAIC estimates. QAICc can then be calculated from these QAIC estimates using the formula; $-2\log$ Likelihood/ $\hat{c} + 2K + 2K(K + 1)/(n - K - 1)$ where n is the sample size (in this case 225). Values of ĉ *>4* indicate that the model structure is unacceptable and over dispersion may not be the only factor affecting the results (Burnham & Anderson, 2002).

Initial results found that the models run using the Habitat model did not reach numerical convergence and were a poor fit to the data (ĉ >4). These models were therefore discarded.

A total of 40 different models were then compared using the Method model (Appendix 4) where ĉ = 2.30 for the global model. Models that did not reach numerical convergence were discarded then QAICc values were calculated for all remaining models to identify the one that best fit the data with the lowest values indicating the best fitting model. QAICc weights for each model were calculated using the expression: $wi = \mathrm{Exp}(-0.5*\Delta)/ \Sigma\, \mathrm{Exp}(-0.5*\Delta)$, where the relative difference in QAICc (Δ) was calculated using the formula $\Delta_i = QAICc_i - {}_{min}QAICc$.

All models contributing to a cumulative weight of 0.95 were considered (Table 5.3) and unconditional parameter estimates were calculated using standard model averaging procedures. Each model parameter (*β* value) was multiplied by the weight of that model and then summed across all models to provide a model average (Burnham and Anderson, 2002). The relative importance of each covariate was assessed by calculating a summed QAICc weight (ΣQAICcω) across all models with a cumulative QAICcω of 0.95 containing the respective covariate (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). Where $\Sigma QAICc\omega$ approximates 1, the covariate is highly supported while a $\Sigma QAICc\omega$ closer to 0 shows little support for that covariate.

5.3.4. Single-Season Single-Species Model

Single-species single-season models were fit to the camera trapping matrices to examine in more detail how the placement of camera traps affects detectability. As noted above, the single season model (Mackenzie *et al.*, 2002) allows estimation of the probability (ψ) that a site (i) will be occupied by the target species in situations where it is not guaranteed to be detected when present. Under this basic model, p[j] is the probability of detecting the species in the j^{th} survey, given it is present at the site. See Chapter 3 for a more detailed discussion of single-season models.

5.3.5. Habitat covariates – Single-Season Single-Species

The habitat covariates used in the Single-Season Single-Species model were chosen based on a combination of factors: a) their importance as identified in Chapter 3, b) their importance based on the multi-method analysis, and *a priori* selection of variables thought to impact detectability.

In addition to the habitat variables used in the multi-method model, the *cwoodland* category was further divided into *coniferous woodland* and *felled.* Recent radio-tracking surveys have shown that areas of felled woodland can provide important denning sites for wildcats (R. Campbell, unpublished data 2015) and Daniels *et al.* (2001) noted that wild-living cats use clearfell in proportion to its availability. The recent radio-tracking work has also identified gorse as an important habitat for wildcats. A total of 14 site covariates were examined (see Table 5.2) and the survey covariate *Recaptures* was also included.

Table 5.2 Site and Survey covariates used in the Single-Species Single Season models

Site Covariate
Proportion of habitat within 500m radius of camera trap
Arable
Mixed woodland
Coniferous woodland
Felled
Grassland
Gorse
Amount of edge (km)
Distance from nearest track or trail >1m (km)
Distance from Suburban and urban (km)
Edge habitat = Suitable (Woodland, gorse, felled, grassland, arable, dwarf shrub heath) yes/no
Camera trap location
Suitable habitat (Woodland, gorse, felled, grassland, arable, dwarf shrub heath) yes/no
On Fence (Located adjacent or within 50m of a fence/wall) yes/no
On Track (Located across a track such as a forestry track or obvious animal trail >1m) yes/no
In Edge (Located within a habitat that is <150m from a different habitat) yes/no
Survey Covariate
Recaptures = Has a cat been detected in any prior surveys yes/no

5.3.6. Model Selection

A total of 31 different models were examined (Appendix 5). A goodness of fit test on the global model found it to be over-dispersed ($\hat{c}$ = 3.34), therefore QAICc values were used to select the best models.

5.4. Results

Once the data had been collapsed into 4 week periods, we obtained a total of 99 capture events of wild-living cats on camera, and 22 scat occurrences across all 12 sites (Table 5.1). Camera trapping and scat surveys appeared to be more effective at detecting wild-living cats in the field than sign surveys and road traffic accident surveys (Table 5.1). As a result only camera trapping and scat data were used for the analysis. A rough breakdown of costs and efforts for all methods to include equipment costs, genetic analysis and days of effort to carry out field work and analyse photographs and scats indicate that camera trap surveys are more expensive and require more man hours than other methods (Table 5.3). Using the raw data (No. capture events and number of cat scats), the survey output (results/day of survey effort) was greater for camera trap surveys (0.49 captures/day) than scat surveys (0.14 scats/day) (Table 5.4).

Table 5.3 Shows the number of man hours (days) each method required across all 23 sites surveyed and equipment costs for each specific method. Miscellaneous costs such as vehicle, petrol, field accommodation and field assistant expenses are not shown because they would have been the same for all methods used (in this case at approximately £40,000 over 2.5 years of survey work).

	Camera trapping	**Scat Surveys**	**RTA's**	**Sign Surveys**
Man hours (days)				
Initial set up pre site visit	46	0	0	0
Start of survey work	115	23	23	23
Per check (3 checks per survey)	276	69	69	69
End of survey period	69	23	23	23
Additional survey work	0	92	0	0
Data Analysis	115	30	0	1
TOTAL	**621**	**237**	**115**	**116**
Equipment				
Batteries	£5,068.89	-	-	-
Cameras and import costs	£28,237.09	-	-	-
Security	£1,572.69	-	-	-
Bait and lure	£536.25	-	-	-
SD cards	£588.51	-	-	-
Miscellaneous	£68.61	-	-	-
tubes and bags	-	£80.10	-	-
Freezer	-	£100.00	-	-
DNA extraction £15/sample	-	£6,300.00	-	-
Lab technician	-	£7,500.00	-	-
Miscellaneous	-	£29.96	-	-
TOTAL	**£36,072.04**	**£14,010.06**	**£0.00**	**£0.00**

Table 5.4 Shows the raw data for the different survey methods and the survey output based on the data obtained per day of survey effort.

	Camera trapping	Scat Surveys	RTA's	Sign Surv
No. Cat captures	302	-	-	-
No. Scats	-	34	-	-
No. RTA's	-	-	0	
No. Signs	-	-	-	16
Survey output (result/day)	0.49	0.14	0.00	0.14

The results of the different analyses in PRESENCE carried out are detailed below.

5.4.1. Single-Season Multi-Method occupancy modelling

Camera trapping had a slightly higher detection probability than scat surveys ($p = 0.25, 0.10$ for camera trapping and scat surveys respectively). However, overall detectability using both methods (ψ (.), p (.)) was higher ($p = 0.4$). Overall occupancy was estimated as $\psi = 0.5$.

No single model appeared to be strongly supported therefore model averaging was carried out as described previously (Table 5.5).

Table 5.5 Shows the top-11 ranking models (models with summed QAICc weight of 0.95) for the multi-method single-season model for both methods, number of parameters (*n*Pars), QAICc score, weight of each model (QAICc$\boldsymbol{\omega}$) and the difference between each model and the top-ranking model (ΔQAICc). Occupancy (ψ) and theta (θ) are held constant across all models and detectability (p(method)) (i.e. detection using either camera traps or scat surveys) varies according to the proportion of grassland (gr), mixed woodland (mw), coniferous woodland (cw), arable (a), amount of edge habitat (e), date of survey (dd+dd^2) and recaptures (r).

Model	***n*Pars**	**QAICc**	**ΔQAICc**	**QAICcω**
ψ(.),θ(.),p(m+r+gr)	7	206.28	0.00	0.33
ψ(.),θ(.),p(m+r)	5	207.24	0.96	0.21
ψ(.),θ(.),p(m+r+a)	7	208.74	2.47	0.10
ψ(.),θ(.),p(m+gr)	5	209.05	2.77	0.08
ψ(.),θ(.),p(m+r+e)	7	209.82	3.54	0.06
ψ(.),θ(.),p(m)	3	210.06	3.78	0.05
ψ(.),θ(.),p(m+r+mw+gr)	9	210.41	4.13	0.04
ψ(.),θ(.),p(m+dd+dd^2+g)	9	211.41	5.14	0.03
ψ(.),θ(.),p(m+r+cw)	7	211.42	5.14	0.03
ψ(.),θ(.),p(m+r+a+gr+e)	11	211.85	5.57	0.02
ψ(.),θ(.),p(m+r+dd+dd^2+g)	11	212.35	6.07	0.02
ΣQAICcω				**0.95**

Overall, detectability was most positively influenced by whether or not previous recaptures had occurred (ΣQAICcω $= 0.8$) and was greater in areas with a higher proportion of grassland (ΣQAICcω $=$ 0.52). There was weak support that detection increased using either method when the proportion of arable ($\Sigma QAICc\omega = 0.012$), and edge habitat ($\Sigma QAICc\omega =$ 0.10) increased (Table 5.6).

Detection of wild-living cats increased significantly (95% confidence intervals did not overlap 0) using camera trap surveys when previous survey/s had detected a wild-living cat using this method (p = 0.25 without recaptures, p = 0.78 with recaptures) (Figure 5.1). Detection using camera traps also increased in areas with a higher proportion of grassland (p = 0.96) and to a lesser extent as the proportion of arable increased (p = 0.55) (Table 5.6).

Detectability using scat surveys also increased when previous surveys had detected a cat scat, but not significantly (p = 0.10 without recaptures, p = 0.21 with recaptures) (Figure 5.1) and to a lesser degree as the proportion of grassland (p = 0.17) and arable (p = 0.21) increased. Detection probability using scat surveys was negatively associated to an increase in the proportion of mixed woodland (Table 5.6).

Figure 5.1 Detection probabilities for wild-living cats using camera trap surveys and scat surveys with and without recaptures in one or more of the prior survey periods.

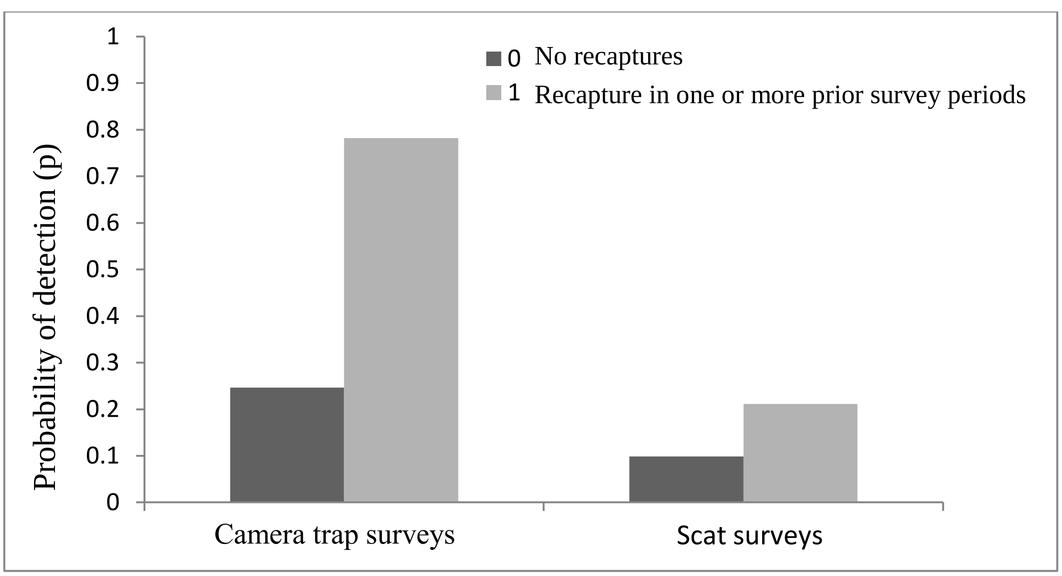


Table 5.6 Model averaged parameters with beta coefficients (β) and standard errors (SE) (corrected for over-dispersion) and summed QAICc weights ($\Sigma QAICc\omega$) for each of the model covariates for the different survey methods (P_{CT} = camera trapping, P_{SS} = scat surveys) based on survey data collected throughout Scotland between 2010 and 2013. The 95% unconditional confidence intervals of the estimates are also presented. Those represented in bold type face indicate where the estimate does not overlap zero.

	β	SE	Upper 95% CI	Lower 95% CI	$\Sigma QAICc\omega$
$P_{CTINTERCEPT}$	-1.12	0.69	-2.48	0.24	-
$P_{SSINTERCEPT}$	-2.21	0.64	-3.46	-0.96	-
$P_{CTRecaptures}$	**2.40**	**1.11**	**0.22**	**4.58**	**0.80**
$P_{SSRecaptures}$	0.89	0.93	-0.92	2.71	0.80
$P_{CTGrassland}$	4.30	4.11	-3.76	12.35	0.52
$P_{SSGrassland}$	0.60	1.74	-2.82	4.01	0.52
$P_{CTArable}$	1.33	9.06	-16.42	19.09	0.12
$P_{SSArable}$	0.89	5.14	-9.17	10.96	0.12
P_{CTEdge}	0.03	0.26	-0.48	0.54	0.10
P_{SSEdge}	0.01	0.25	-0.47	0.49	0.10
$P_{CTConiferous\ Woodland}$	0.01	1.29	-2.52	2.54	0.03
$P_{SSConiferous\ Woodland}$	0.01	1.39	-2.72	2.73	0.03
$P_{CTMixed\ Woodland}$	0.10	5.87	-11.40	11.61	0.04
$P_{SSMixed\ Woodland}$	-0.02	4.55	-8.94	8.89	0.04
P_{CTdd}	0.21	2.45	-4.59	5.02	0.04
P_{SSdd}	0.00	1.50	-2.95	2.94	0.04
P_{CTdd2}	-0.22	2.40	-4.92	4.49	0.04
P_{SSdd2}	0.01	1.48	-2.90	2.92	0.04

5.4.2. Single-Season Single-Species occupancy modelling: Camera trap surveys

No single model appeared to be strongly supported therefore model averaging was carried out as described previously (Table 5.7).

Table 5.7 The top-18 ranking models for the single-species single-season model, the number of parameters (nPars), QAICc score, weight of each model (QAICs$\boldsymbol{\omega}$) and difference between each model and the top-ranking model (ΔQAICc). Occupancy (ψ) is held constant and detectability (p) varies according to the proportion of arable (a), coniferous woodland (cw), felled (f), grassland (gr), mixed woodland (mw), and gorse (g), the amount of edge habitat (e), whether the camera trap is located on a fence/wall (OF), on a track (OT), within cover (CC), if the edge habitat was cover (EC), in relation to distance from the nearest track (DT), suburban (SU) or Urban (U) areas and if any recaptures have occurred in prior surveys (r).

Model	***n*Pars**	**QAICc**	**ΔQAICc**	**QAICcω**
ψ(.),p(r+a+mw+cw+f+gr+g+e+OF)	11	176.60	0.87	0.08
ψ(.),p(r+OF)	4	176.60	0.88	0.08
ψ(.),p(OF+OT)	4	176.77	1.05	0.07
ψ(.), p(.)	2	176.94	1.22	0.07
ψ(.),p(DT)	3	177.23	1.50	0.06
ψ(.),p(SU+U)	4	177.52	1.79	0.05
ψ(.),p(r+OF+OT+OE)	6	177.54	1.81	0.05
ψ(.),p(r+DT)	4	177.62	1.89	0.05
ψ(.),p(r+OF+OT)	5	177.67	1.95	0.05
ψ(.),p(EC)	3	177.82	2.10	0.04
ψ(.),p(OT)	3	177.96	2.24	0.04
ψ(.),p(CC)	3	178.00	2.27	0.04
ψ(.),p(r+SU+U)	5	178.39	2.67	0.03
ψ(.),p(r+EC)	4	178.53	2.80	0.03
ψ(.),p(OF+OT+OE+DT)	6	178.56	2.83	0.03
ψ(.),p(r+a+mw+cw+f+gr+g+e+OE+OF+OT)	13	179.03	3.31	0.02
ψ(.),p(a+mw+cw+gr+e)	7	179.17	3.45	0.02
ψ(.),p(a+mw+cw+f+gr+g+e)	9	179.41	3.68	0.02
ψ(.),p(r+a+mw+cw+f+gr+g+e+OF)	11	176.60	0.87	0.08
ΣQAICcω				**0.95**

Model averaged detectability was high (p = 0.67). Overall occupancy was estimated as $\psi = 0.3$. Placing a camera trap along a fence line/wall had the strongest positive influence on detection probability ($\Sigma QAICc\omega = 0.55$) although the effect was still weak (p = 0.65) (Table 5.6). Detectability also increased slightly if previous recaptures had occurred ($\Sigma QAICc\omega = 0.4$) and was weakly positively influenced if the camera was placed on a track ($\Sigma QAICc\omega = 0.3$). The remaining variables did not appear to have any effect on detection (Table 5.8).

Table 5.8 Model averaged parameters with beta coefficients (β) and standard errors (SE) (corrected for over-dispersion) and summed QAICc weight ($\boldsymbol{\Sigma QAICc\omega}$) for each of the model covariates. The 95% unconditional confidence intervals of the estimates are also presented.

	β	**SE**	**Lower 95%CI**	**Upper 95%CI**	$\boldsymbol{\Sigma QAICc\omega}$
ψ	-1.06	0.32	-1.69	-0.42	-
$P_{INTERCEPT}$	0.72	0.9	-1.05	2.49	-
$P_{OnFence}$	0.56	0.73	-0.87	1.98	0.55
$P_{Recapture}$	0.04	0.75	-1.5	1.42	0.44
$P_{OnTrack}$	0.01	0.86	-1.67	1.7	0.30
$P_{Mwoodland}$	0.01	3.88	-7.6	7.61	0.14
$P_{Grassland}$	0.64	2.09	-3.46	4.74	0.14
$P_{Coniferous}$	0.31	1.79	-3.2	3.83	0.14
P_{Arable}	0.78	4.66	-8.36	9.91	0.14
P_{Dtrack}	0.08	1.47	-2.8	2.96	0.13
P_{Gorse}	2.27	21.71	-40.27	44.82	0.12
P_{Felled}	0.79	2.93	-4.95	6.52	0.12
P_{Urban}	0.01	0.32	-0.61	0.63	0.08
$P_{Suburban}$	-0.03	0.35	-0.71	0.65	0.08
$P_{EdgeCover}$	-0.02	0.56	-1.12	1.08	0.07
$P_{CamCover}$	0	0.91	-1.78	1.78	0.04
P_{Edge}	0.02	0.21	-0.4	0.44	0.01
P_{OnEdge}	0.02	1.42	-2.76	2.81	0.01

5.5. Discussion

Scat surveys and camera trapping may be more effective at detecting wild-living cat presence than sign surveys or road traffic accident surveys. Camera trapping is however initially more expensive and time consuming than scat surveys which may be a consideration when using this method. The advantage of camera trapping over scat surveys combined with genetic analysis however is that once the initial outlay for the equipment has been accounted for, provided they are maintained in a good condition, camera traps can be used for several years with only running costs then required. For example, after the first survey costs have been covered, subsequent surveys using camera traps would only incur battery and bait costs and the running costs associated with fieldwork (petrol, vehicle maintenance, accommodation and field assistant), so dependent on the number of scats being genetically analysed, would be comparable or even cheaper than scat surveys. In the long-term therefore, camera traps might be more economical than scat surveys.

5.5.1 Single-Season Multi-Method

Under the multi-method model, detection using camera trap surveys was more than twice as great as using scat surveys. However, overall detection was greatest when data from both methods were combined, similarly occupancy probability was greater when both methods were used rather than camera trapping alone, in both cases, this is because scat surveys detected wild-living cats in some sites that camera traps did not. Studies on several carnivores have shown that combining different survey methods can greatly improve detection and in some cases decrease survey duration and costs (Campbell *et al.*, 2008). Indeed, during this study, at some of the sites, scat surveys detected wild-living cats where camera traps did not;

suggesting using a combination of these survey methods would improve overall detection of wild-living cats. This has been observed in other cat species as well, for example studies on tigers (*Panthera tigris*) (Gopalaswamy *et al.*, 2012) and jaguars (*P.onca*) (Sollmann *et al.*, 2013) found that combining data from camera trapping and scat surveys improved the accuracy of overall density estimates.

Detection by camera traps significantly increased when cats had been detected in prior surveys. Evidence from recent camera trapping surveys (Kilshaw *et al.*, 2015a; Chapter 4 this thesis) indicate that a positive trap response is present using camera traps, likely because of the use of baited and scented camera trap stations, therefore we would anticipate that wild-living cats would revisit the camera traps and hence increase the probability of detection over the duration of the survey period. The use of bait at camera stations has been shown to increase detection probability of other species including carnivores (e.g. Thorn *et al.*, 2008; Paull *et al.*, 2011; du Preez *et al.*, 2014) and the use of scent lures has increased detection probability of some wildcat populations using hair lure stations (e.g. Hintermann & Weber, 2008). The observed increase in detection over the survey period as a result of previous recaptures also supports Kilshaw *et al.* (2015a) study on the Scottish wildcat that suggested camera trap surveys should be carried out for 60-80 days in order to maximise the chances of detecting a wild-living cat on camera.

Although detection by scat surveys was lower than camera trapping, detectability could be improved by changing the survey method slightly. Here the scat surveys were carried out at the start and end of each survey period and every two weeks when the camera traps were checked and re-baited. As a result, many of the scats collected were not fresh and could therefore not be confidently identified as cat using DNA analysis. Out of 310 scats collected, DNA could either not be extracted or amplified in 177 samples (>50% failure rate). Carrying out scat surveys daily for a shorter period of time would allow the collection of fresher scats and improve DNA extraction, thus maximising the chances of identifying the scats correctly. Similarly extending the survey period would increase potential recaptures, for example, Piñeiro and Barja (2012) carried out monthly scat survey transects for wildcats over a 10 month period. Another technique to improve the detection of scats is the use of scat dogs, domestic dogs trained to detect scats of one or more species. These have become an increasingly popular tool for scat surveys, particularly in remote areas (Wasser *et al.*, 2004; Smith *et al.*, 2005; Long *et al.*, 2007). Studies have indicated that scat dogs are three times more effective at detecting species than camera trapping or hair traps (Long *et al.*, 2007). Scat dogs have also been more successful for locating scats than researchers (Smith *et al.*, 2001). Although scat dogs have not yet been trialled on the Scottish wildcat, this is something that could be developed as a potential method for future wildcat surveys.

The increase in detectability by camera trapping and to a lesser degree by scat surveys in areas with a higher proportion of grassland and arable farmland is supported by the findings in Chapter 3. Here, occupancy of all three cat types increased in relation to the proportion of grassland habitat, in particular for feral domestic cats and hybrids. Grassland is used by all three cat types, especially in areas with high rabbit abundance (Corbett, 1979; Biro, 2005). It is therefore unsurprising that detection increased in areas with a higher proportion of grassland where wild-living cats were more likely to have a higher occupancy probability.

5.5.2. Single-Species Single-Season

The detection of wild-living cats increased if camera traps were placed on or near a fence line or wall. Use of fence lines and or other linear features such as trails, either for traversing (e.g. badgers, *Meles meles* (Delahay *et al.*, 2000), jaguars and pumas, *Puma concolor* (Harmsen *et al.*, 2009) or to increase hunting success has been recorded in other carnivores (e.g. African wild dogs, *Lycaeon pictus* (Rhodes & Rhodes, 2004)). Many of the fence lines and walls in the study areas followed the division between covered habitat such as woodland or scrub and more open habitat such as grassland or arable farmland and it is possible that wild-living cats utilise these features as both cover and a hunting aid. A similar technique has been observed in feral ferrets (*Mustela furo*) which appears to use the cover associated with fences such as gorse and broom and hunt in the adjacent pastoral habitat (Ragg & Moller, 2000).

Similarly, the slight increase observed in detection when camera traps were placed on tracks is supported by other studies that show carnivores often use trails to traverse along (e.g. jaguars and pumas (Harmsen, 2006; Harmsen *et al.*, 2009) or to scent mark along e.g. Iberian wolves, *Canis lupus* (Vila *et al.*, 1994). Studies on the European wildcat have shown that they regularly leave scats on trails and prominent tufts of grass (e.g. Schauenberg, 1981; Barja *et al.*, 2005; Piñeiro & Barja, 2012; Lozano *et al.*, 2013). Detection by camera traps along trails could therefore be increased by placing them where cat scats are also found.

As with the multi-method analysis, when recaptures were included as a survey covariate, detection probability increased, although not statistically significantly in the single season analysis. As mentioned above, this observation is likely to be as a result of a combination of a trap response to baiting and as a result of the length of the overall survey period increasing the overall probability of detecting a wild-living cat in the area.

Surprisingly, the distance of the camera trap from the nearest rural/urban area had no impact on detection probability. The outcome for the rural covariate was unexpected because studies have shown that feral domestic cats and hybrids are positively associated with farm buildings (Corbett, 1979; Daniels, 1997) and use human resources such as those found around farms regularly (Germain *et al.*, 2008). We would have expected detection of wild-living cats, in particular feral domestic cats to increase at camera trap sites located closer to rural areas.

Overall, the findings from the multi-method and single-season analysis suggest that camera trapping is the most appropriate method to use out of those examined to detect wild-living cats, but detection can be further increased by using more than one survey method. Detectability can be improved by carrying out the surveys in habitats expected to have a higher occupancy probability, for example in this study, camera traps and surveys were carried out across a wide range of habitats to ensure comprehensive coverage of the available habitat types but detection rates could have been increased by focusing efforts on habitat more likely to be utilised by wild-living cats. In addition, utilizing linear features such as fence lines and tracks in the survey site and maximizing the chances of recaptures occurring (e.g. through baiting camera traps or by improving scat survey techniques) can also improve detection rates.

Chapter 6

6.0 Population Viability Analysis of the Scottish wildcat; management implications

6.1. Abstract

The Scottish wildcat is currently threatened by a range of different factors including hybridisation with domestic feral cats and hybrids, habitat loss, road traffic accidents and persecution. As a result, the current population is estimated to be <400 individuals, which are thought to be constrained to Northern Scotland and likely exist in various sub-populations which may or may not be able to mix easily with one another. Here, I use population viability analysis (PVA) in the programme VORTEX to examine the probability of the Scottish wildcat's long-term (~100 years) survival under various scenarios.

The baseline model indicated that the metapopulation was not viable and is likely to go extinct within the next 50 years (Mean TE = 48.2 years (SD = 9.39) years and the probability of survival at 100 years was 0 (SE = 0) unless specific management efforts to reduce mortality rates of female wildcats in particular and/or long-term supplementation of the population with at least 1 male and 1 female every 1-9 years from captive bred individuals is carried out.

The models were sensitive to the initial population size estimates, which were based on reported wildcat densities/100 km^2 in Scotland. At the lower density estimate of 1 wildcats/100 km^2, mean TE = 23.1 years (SD = 5.64). In comparison, at the higher density estimate of 30 wildcats/100 km^2, the mean TE = 92.6 years (SD = 6.22) and a mean probability of survival at 100 years of 0.88, SE = 0.01).

Larger litter sizes resulted in increased mean TE. The sex ratio of kittens born was also influential, with a skewed ratio towards males resulting in a drastic decrease in mean TE. The ideal ratio of male: female kittens was 20:80 which resulted in mean TE of 73.28 years (SD = 14.11). The percentage of females breeding annually had a large impact on population viability, with the mean TE falling as the percentage of breeding females decreased. The models also demonstrated how population viability was sensitive to variation in the percentage of individuals dispersing and of those, surviving each year, but even with only 1% of the population dispersing, the probability of metapopulation survival at year 100 was still zero (SE = 0). Overall, the modelling highlighted the importance of having detailed data on various demographic and environmental parameters that could affect how viable the population is in the long-term.

6.2. Introduction

Conservation planning and wildlife management increasingly concern the viability of populations of threatened species (Akçakaya & Sjögren-Gulve, 2000). Quantifying risk of extinction is therefore central. Population viability analysis (PVA) aims to estimate that risk and to suggest which management strategies may most benefit threatened populations or metapopulations (Shaffer, 1981; Boyce, 1992; Slotta-Bachmayr *et al.*, 2004). In PVAs, the dynamics of a species are modelled in response to a range of deterministic and stochastic processes (i.e. density-dependence, reproduction, litter size) (Beissinger & Westphal, 1998; Possingham *et al.*, 2002). PVA has been used extensively as a tool for informing the management of endangered or rare species, including carnivores (e.g. ocelots, *Leopardus pardalis* (Haines *et al.*, 2006), tigers, *Panthera tigris* (Linkie *et al.*, 2006), grizzly bears, *Ursus arctos horribilis* (Proctor, 2004)). PVA is also useful for identifying the variables that are most important for successful species reintroduction (e.g. Lubow, 1996; Bustamante, 1998; Salz, 1998) as well as a useful tool for assessing and managing 'at risk' species (Beissinger, 2002; Morris & Doak, 2002; Reed *et al.*, 2002). Although some authors have noted that the results of PVA modelling may be limited because validity of the models depends on both model structure and data quality (Reed *et al.*, 2002). Coulson *et al.* (2001) also noted that PVA's may only be accurate if sufficient, reliable data is included.

Several software packages now exist for carrying out spatially explicit PVAs, including RAMAS® Metapop (Akçakaya, 1997) and VORTEX (Lacy & Pollak, 2014). These models incorporate a diversity of demographic and spatial attributes such as distance-dependent migration, allee effects, social population structure, habitat quality and spatial arrangement, and genetic variability. Although some studies have indicated that different programmes give different predictions of extinction risk, for example, in response to stochastic variation in breeding structure (Mills *et al.*, 1996; Brook *et al.*, 1999), other studies show that this need not be the case provided that the parameters used are chosen with care (e.g. Brook *et al.*, 2000).

The Scottish wildcat population (*Felis silvestris silvestris*) was thought by Macdonald *et al.* (2004) to be around 400 individuals in size, but may be even lower. While currently considered to be Least Concern by the IUCN, if only a few genetically pure individuals remain then the Scottish population is likely to be reclassified as Critically Endangered (Driscoll & Nowell, 2009). The main threats are currently habitat loss and fragmentation, persecution and incidental deaths such as through road traffic accidents and accidental poisonings and hybridisation with and disease transmission from the domestic cat (*F.s.catus*) (Langley & Yalden, 1977; McOrist *et al.*, 1991; Hubbard *et al.*, 1992; McOrist & Kitchener, 1994b; Kitchener, 1995; Beaumont *et al.*, 2001; Macdonald *et al.*, 2004). Although evidence suggests that the current stronghold for the Scottish wildcat is northern Scotland (Easterbee *et al.*, 1991; Balharry & Daniels, 1998; Davies & Gray, 2010), it is likely that due to the landscape of this area, the population may be fragmented into a series of smaller populations, some of which may have limited ability to disperse and breed with the wider metapopulation. To date, limited analysis has been carried out examining the population viability of this species and how different management options benefit the species in the long-term (Kilshaw & Macdonald, 2009; Littlewood *et al.*, 2014).

In this chapter, the data collected on population densities (Chapter 4) and the information from the occupancy modelling on the current probable distribution of the species (Chapter 3) will be used to carry out an individual-based population viability analysis using the programme VORTEX (Ver. 10.0; Lacy & Pollak, 2014). The main objectives are to determine *i*) the long-term population viability of the Scottish wildcat, *ii*) to establish if there would be a significant benefit from supplementing the population with individuals from the captive breeding stocks, and if so, how many need to be supplemented and how often, *iii*) if habitat restoration to increase carrying capacity improves long-term viability, *iv*) if methods to reduce mortality rates such as through a reduction in road traffic accidents or persecution could be applied to reduce the extinction risk.

6.3. Methodology

6.3.1 Habitat network and sub-population estimates

Due to the fragmentation of suitable habitat across Scotland, it is likely that the remaining wildcat population exists as a series of sub-populations, some very small. Using ArcGIS 10.1, I calculated the number of habitat patches available with a high probability of wildcat occurrence ($\psi \geq 0.8$) that could support a minimum population of 10 individuals (Klar *et al.*, 2012) and were no more than 10km away from each other using the following steps:

1. Initially any patches of habitat with occupancy probability ($\psi \geq 0.8$) but smaller than 200ha (mean minimum home range size of a female wildcat) and ≥10km away from another patch were excluded. This was to remove any patches of available habitat that would support no more than one wildcat.
2. Following Klar *et al.* (2012), I assumed that occupancy probability would influence the way wildcats moved across the landscape and dictate where sub-populations would be most likely to exist. All habitat patches with $\psi \geq 0.8$ and capable of supporting 20 female wildcats with a minimum home range size of 200ha were included (e.g. patches ≥ 4000ha). Any individual patches surrounded by habitat with a low probability of occupancy ($\psi \leq 0.4$) and ≥ 4km away (suspected typical dispersal distance of the Scottish wildcat (Green, 1991)) from another patch were removed. As discussed in Chapter 3, habitat with $\psi \geq 0.8$ also excluded habitat falling within 200m of settlements and 900m of urban areas because wildcats avoid these areas (Klar *et al.*, 2008) and areas over 800m a.s.l which are considered unfavourable.
3. The remaining available habitat was then divided into sub-populations with major rivers and lochs acting as barriers and motorways/dual carriageways acting as significant limiting factors on movement between different areas (Klar *et al.*, 2010; Klar *et al.*, 2012) (Figure 6.1a).
4. The overall area of high probability of occupancy habitat for each sub-population was then calculated (km^2) and this value was multiplied by the mean wildcat density estimate obtained in Chapter 4 (3.5 wildcats/100 km^2) to get an estimate of the number of individuals that could be supported by each sub-population (see Table 6.2).

5. Any sub-populations that were both smaller than 10 individuals and more than 10km away from another sub-population were then excluded from the PVA analysis (Figure 6.1b).

6.3.2. Population Viability Analysis using VORTEX

The programme VORTEX (ver 10.0; Lacy & Pollak, 2014) was used to simulate the survival of the Scottish wildcat population under different scenarios. VORTEX models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation (EV) in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. VORTEX also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations (Lacy *et al.*, 2015).

Input parameters were taken primarily from Kilshaw and Macdonald (2009) and from data collected during this study and from studies carried out on both the Scottish wildcat or from the European wildcat if no data existed for the Scottish wildcat. Parameters are described in detail below and summarized in Table 6.1.

6.3.2.1. Reproductive ecology of the wildcat

Although wildcats reach maturity by the age of 1 year (9-10 months for male wildcats and 12 months for female wildcats), limited data exist on the first age of reproduction in the wild; I assumed it to be 2 years following Kilshaw and Macdonald (2009). Under favourable conditions in the wild, studies in Scotland have indicated that female wildcats can live up to a maximum of 10 years and males to 8 years old (Daniels *et al.*, 1998). The maximum age of reproduction was therefore estimated to be 10 years. Estimated sex ratio at birth was 50:50 (K. Hupe pers comm., 2011) but because the sex ratio in the wild is unknown, the impact it has on population viability was modelled by varying the ratio. Data from studies in the wild have indicated that the mean litter size (n=10) is greater than that seen in captivity (Macdonald & Barrett, 1993; Daniels, 1997) and recent radio-tracking data (R. Campbell unpublished data, 2015) indicates a mean litter size of 3 kittens in the wild (n=4). A mean value of 4.3 (Daniels, 1997) was used here. The model was run at various litter sizes to determine how sensitive the population viability was to this parameter. A maximum of 1 litter per year, a minimum litter size of 1 and a maximum litter size of 6 kittens (Daniels, 1997), were used as these values are similar to those observed in the European wildcat (e.g. Muntyanu *et al.*, 1992).

Limited data exists for the age at which Scottish wildcats will breed in the wild, but I assumed the age of first reproduction would be from 1-2 years old. Although wildcats often form monogamous pairs in captivity, in the wild, home ranges of males overlap home ranges of several females (Daniels, 1997); therefore, wildcats were modelled as polygamous.

6.3.2.2. Carrying capacity and initial population size

The baseline model was run with a population density of 3.5 wildcats/100 km^2 based on the density of wildcats obtained from the camera trapping survey work in this study (See Chapter 4), with initial population sizes estimated using this value and the amount of habitat with a high probability (≥0.8) of wildcat occurrence. However, reported population densities for the Scottish wildcat range from 1-30 individuals/100 km^2 (Corbett, 1979; Scott *et al.*, 1993) so the effect of initial population size on overall viability was also examined.

Following Littlewood *et al.* (2014) (where initial population size was estimated at 80% of a theoretical carrying capacity), carrying capacity (K) was estimated at 120% of the initial population size. It is important to note however that without detailed survey work of local sub-populations and the prey availability within them, this estimate of carrying capacity is at best guess a minimum estimate.

6.3.2.3. Sub populations

Sub-populations were calculated as described in 6.2.1.

6.3.2.4. Mortality rates of the population

Information on survival of Scottish wildcats is scarce. Most of the data used for this parameter in the model was derived from studies on the European wildcat. Based on an extensive radio tracking study carried out in Germany (K. Hupe pers comm., 2008), an estimated 20% of juveniles (<12 months) were assumed to survive annually, and 60% of sub-adults (<24 months) and 80% adults (>36 months). Hence annual mortality rates are 80% for juveniles, 40% for sub-adults and 20% for adults.

6.3.2.5. Inbreeding depression

Inbreeding depression was incorporated into the PVA; because no data exists on the number of recessive alleles or lethal equivalents in the Scottish wildcat population, the lethal equivalents and the percent of lethal equivalents attributed to recessive alleles were set at 3.14% and 50% respectively following other studies on felids (e.g. Haines *et al.*, 2005).

6.3.2.6. Dispersal

VORTEX allows users to model the age of the dispersers, what percentage of each sub-population disperses each year and between which sub-populations dispersal is allowed to occur.

Almost no information exists on dispersal of wildcats, although in captivity adult males become intolerant of young males once they get past the age of 1 year, unless they are clearly subordinate (Harmann, 2005), I therefore assumed that males would disperse at the age of 1. Female dispersal is likely to occur at a later age as female wildcats often have overlapping home ranges and are thought to stay in the natal territory for longer than males (e.g. Daniels, 1997). I therefore considered that females would not disperse until they were 2 years old or would establish territories within or close to the natal home range. In addition, the percentage of males dispersing was considered to be twice that of females as they are more likely to travel out of the natal range. Dispersal between sub-populations was prevented if carrying capacity had been reached and individuals will move to a different population instead (if there is an unsaturated one available to receive immigrants) (Lacy *et al.*, 2015).

Whether individuals could disperse between sub-populations was based on the presence of potential barriers including large water bodies (lochs) and major rivers, major roads such as motorways and distances greater than 10km. For example, individuals from sub-population Q are unlikely to be able to easily move between any other sub-populations except sub-population P because it is surrounded on two sides by major rivers that would present a substantial barrier to any movement (Figure 6.1). Therefore, dispersal from sub-population Q was only allowed to sub-population P.

In addition, the impact of survival of dispersers was also modelled.

6.3.2.7. Reducing mortality

A 75%, 50% and 25% reduction in the mortality rates of sub-adults and adults was simulated. This was visualised as being brought about by mitigation activities such as awareness campaigns and education to reduce persecution and the introduction of wildlife passages across roads identified as high risk. For example, Klar *et al.* (2005) and Grilo *et al.* (2008) showed that the use of correctly placed culverts, overpasses and fences decreased wildcat mortality.

I assumed that it would be difficult to reduce the mortality rates of juveniles through any intervention because some studies in Europe have shown that wildcat young mortality is most commonly attributed to predation by other carnivores (K.Hupe pers comm 2008) which would be difficult to reduce, so these remained constant. It was also assumed that a reduction in mortality rates would affect females and males equally.

Four sub-populations were identified as having a high risk of RTAs due to the large number of main roads and urban areas bordering their edges (Figure 6.4). The effect of reducing mortality rates of female and male wildcats in these areas only on the overall metapopulation survival was also modelled.

6.3.2.8. Increasing carrying capacity

Habitat restoration, in particular of riverine habitats and through afforestation may aid recovery of the wildcat populations into areas they previously inhabited and is listed on many of the local Scottish Biodiversity Action Plans (BAPs) (e.g. Sutherland Biodiversity Group, 2003; Ross & Cromarty (East) Biodiversity Group, 2004; Wester Ross Biodiversity Group, 2004). In addition, sub-populations to the west in particular have a lower proportion of high quality habitat in them (see Table 6.2). Areas of suitable habitat may exist in some cases outside of the sub-populations but either were considered too small (<200ha) or too far away (>10km) to be included. Steps to increase the amount of high quality habitat could be taken;

the development of habitat corridors between habitat patches, for example. Carrying capacity could also be increased through a reduction in hybrid and feral cat densities, which would potentially allow local wildcat populations to increase through reduced competition. The model was run at various carrying capacities to determine how sensitive it was to an increase in the estimated carrying capacity.

6.3.2.9. Catastrophe

Monthly and daily rainfall greater than average, particularly periods of intense heavy rain, has been shown to reduce rabbit (*Oryctolagus cuniculus*) densities five-fold (Palomares, 2003). As one of the most important prey species for the Scottish wildcat, reduction in rabbit densities could have an impact on the population viability. For example, data from the UK's Met Office indicates that extreme rainfall resulting in flooding has occurred in the Highlands area in 1989 and in 2002 (Met Office, 2012). I therefore predicted that rainfall heavy enough to have a significantly negative effect on rabbit populations would occur approximately every 15 years. To test the sensitivity of the model to heavy rainfall resulting in a reduction in rabbit densities, a corresponding reduction in reproduction rates by 10-90% was modelled; in addition a reduction in survival rates by 10-90% and a reduction in both reproduction and survival by 10-90% were also modelled.

Not all of the sub-populations have local rabbit populations, so the impact of increased rainfall was included only for eastern sub-populations J-S and sub-population E in the west.

6.3.2.10. Supplementation

Currently the captive Scottish wildcat population contains low numbers of wildcats considered suitable for breeding from. However, the captive population is currently being managed with the long-term aim of a sufficiently robust population being established (N. Buck pers comm., 2009; R. Ogden, pers comm., 2014). Therefore, the impacts of supplementation of individuals into the population are examined. In particular the impact of supplementing female wildcats following Blundell *et al*. (2002). Under the recommendation of these authors, females are reintroduced when dispersal is low or when extirpated populations need to be established. In theory, one immigrant per generation is sufficient to prevent genetic drift (Wright, 1969) but in practice up to 10 immigrants per generation is recommended and augmentation needs to be more frequent for small than large populations (Lacy, 1987; Mills & Allendorf, 1996; Vucetich & Waite, 2000) . Kilshaw and Macdonald (2009) found that supplementation of both males and females were required in order to have an impact on population viability. I therefore simulated supplementation of different numbers (1, 5 and 10) of males and females aged 1yr, at different intervals (1-10 years) and over a period of 10-100 years.

Table 6.1 Summary of input parameters for population PVA, values in italics represent baseline values.

Parameter	Values modelled
Reproductive System	Polygamous
Age of first offspring (yrs.) ♀, ♂	1, *2*, 3, 4
Maximum age of reproduction (yrs.)	*10*
Maximum number of litters per year	*1*
Maximum no. of kittens per litter	*6*
Sex ratio at birth M:F	90:10, 80:20, 70:30, 60:40, *50:50*, 40:60, 30:70, 20:80, 10:90
% Adult ♀ breeding	15,25,50,75, *100*
Mean litter size	1, 2, 2.3, 3, 3.5, 4, *4.3*, 5, 6
Environmental Variation in mean litter size	0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, *1.0*, 1.1, 1.2, 1.3, 1.4, 1.5, 1.6, 1.7, 1.8, 1.9, 2.0
Annual mortality rates	
♀ mortality 0-1	*0.8 (EV = 5%)*
♀ mortality 1-2	*0.4 (EV = 5%)*
♀ mortality >2	*0.2 (EV = 7%)*
♂ mortality 0-1	*0.8 (EV = 5%)*
♂ mortality 1-2	*0.4 (EV = 5%)*
♂ mortality >2	*0.2 (EV = 7%)*
% reduction in mortality rates of ♀ and ♂ > 1yr	*0*, 25, 50, 75
Dispersal	
Age of ♀	*2*
Age of ♂	*1*
% population dispersing	1, 2, 3, 4, *5*, 10, 15, 20, 25
% dispersers surviving	15, *25*, 50, 75, *100*
Initial population size	
Density x amount (km) of high probability habitat (>0.8) in each sub-population	1, 2.5, *3.5*, 4, 5, 10, 20, 30 ind/100 km^2
Carrying capacity (*K*)	
Size	120% of initial population sizes
Total % increase/decrease over 100 yrs.	± 10, 20, 30, 40, 50, 60%
Supplementation	
♂ + ♀ (No. ind)	*1* , 5 , 10
Supplementation intervals (yrs.)	*1*, 2, 3, 4, 5, 6, 7, 8, 9, 10
Supplementation period (yrs.)	10, 20, 30, 40, 50, 60, 70, 80, 90, *100*
Catastrophe	
% Reduction in reproduction rates	*0*, 10, 20, 30, 40, 50, 60, 70, 80, 90
% Reduction in survival rates	*0*, 10, 20, 30, 40, 50, 60, 70, 80, 90
% Reduction in reproduction and survival rates	*0*, 10, 20, 30, 40, 50, 60, 70, 80, 90

6.4. Results

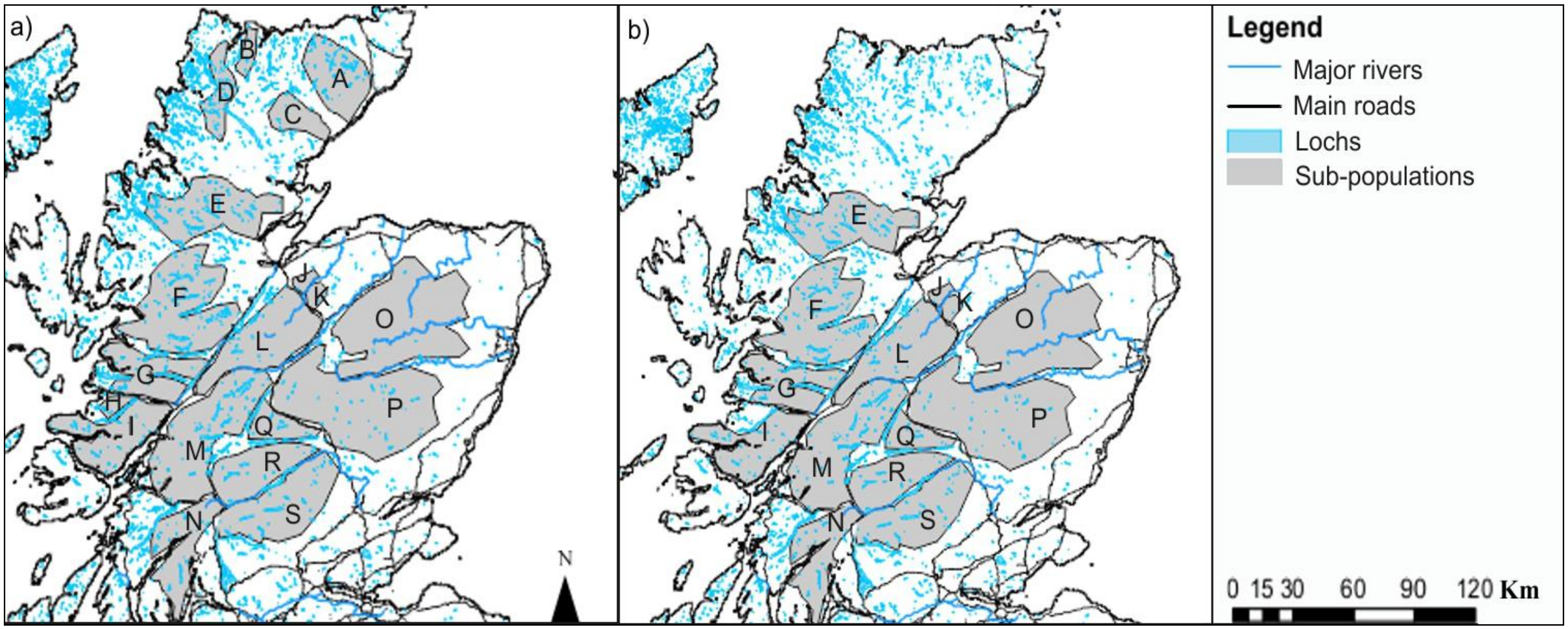
6.4.1. Habitat analysis and sub-populations

Habitat analysis indicated that, out of a potential 19 sub-populations (Figure 6.1a; total potential population size N = 381), 12 of these were large enough to support a minimum of 10 individuals based on the amount of habitat with a high probability of wildcat occurrence ($\psi \geq 0.8$) within each sub-population (Figure 6.1b; total potential population size N = 348). A further two areas (J and K) were very small but within range (≤4km) of larger sub-populations and were therefore included within the PVA analysis (Figure 6.1.b). The number of wildcats each sub-population could support and the percentage of high quality habitat within each sub-population vary considerably (Table 6.2).

Table 6.2 Sub-populations A-S, showing the total area (ha), amount of habitat with a high probability of wildcat occurrence within each area ($\psi \geq 0.8$) (% of total area) and total wildcat population (N).

Sub-Population	Total Area (ha)	Amount of high quality habitat ($\psi \geq 0.8$)	Population size (N)
A	96 250	43 925 (45.6%)	15
B	15 900	7175 (45.1%)	3
C	43 550	16 000 (36.7%)	6
D	47 825	20 250 (42.3%)	7
E	141 025	58 875 (41.7%)	21
F	192 475	105 550 (54.8%)	37
G	87 775	51 825 (59%)	18
H	11 850	7800 (65.8%)	3
I	99 450	34 025 (34.3%)	12
J	8525	4250 (49.9%)	1
K	10 575	6625 (62.6%)	2
L	134 425	106 325 (79.1%)	37
M	183 600	12 0150 (65.4%)	42
N	89 700	50 200 (56%)	18
O	219 000	122 950 (56.1%)	43
P	255 350	158 700 (61.2%)	56
Q	39 375	23 250 (59%)	8
R	86 450	67 225 (77.8%)	24
S	131 450	84 525 (64.3%)	30

Figure 6.1a and b Figure a shows the total number of potential wildcat sub-populations based on the amount of habitat with a high probability of wildcat occurrence (ψ≥0.8). Figure b shows the sub-populations that can support at least 10 individuals at a density of 3.5 wildcats/100 km^2 and <4km apart from another sub-population.



6.4.2. Long-term population viability of the Scottish wildcat

Under the baseline model, the mean time to extinction for the metapopulation was 48.2 (SD = 9.39) years and the probability of survival at 100 years was 0 (SE = 0). Models were then run to see if various scenarios could improve this prediction.

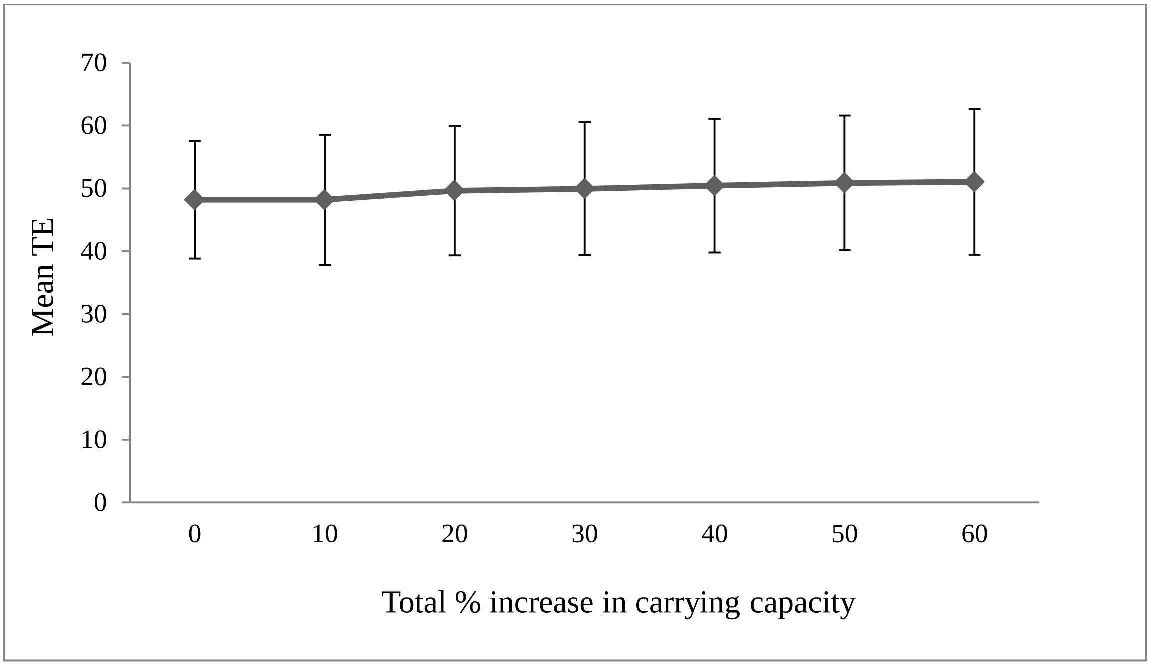
6.4.2.1. Initial population size

Modelling a range of different initial population sizes (with carrying capacity K = 120% of each current estimated population size) had a large impact on the probability of extinction with the metapopulation going extinct after a mean of 23.1 (SD = 5.64) years with no probability of survival at 100 years (SE = 0) at the lowest density of 1 wildcats/100 km^2 and after 92.6 (SD = 6.22) years at the highest density of 30 wildcats/100 km^2 (Probability of survival at 100 years = 0.88, SE = 0.01).

6.4.2.2. Carrying capacity

Increasing the carrying capacity of each sub-population by up to 60% over a period of 5 years resulted in only a very slight increase in the mean time to extinction from 48.2 (SD = 9.39) years with no increase in K to 51.04 (SD = 11.11.62) years if K had been increased by 60% (Figure 6.2) but probability of survival at year 100 was zero (SE = 0) under all scenarios.

Figure 6.2 Variation in the mean time to metapopulation extinction (TE) when carrying capacity was increased over a period of 5 years. Error bars show the standard deviation of the mean TE.



6.4.2.3. Reproduction

The mean time to extinction decreased as the age of first reproduction increased from 48.2 (SD = 9.39) years when reproduction first occurred at age 2 to 29.86 (SD = 5.02) years when age of first reproduction was 4. Probability of survival at year 100 was zero (SE = 0) under all scenarios.

The sex ratio of litters born had a large impact on the mean time it took for the metapopulation to become extinct, with a reduced TE as the proportion of males in each litter increased (Table 6.3)

Table 6.3 Variation in the mean time to metapopulation extinction (Mean TE ± SD) and the probability of survival (PS ± SE) at year 100 when the litter sex ratio differs. The baseline model = 50:50.

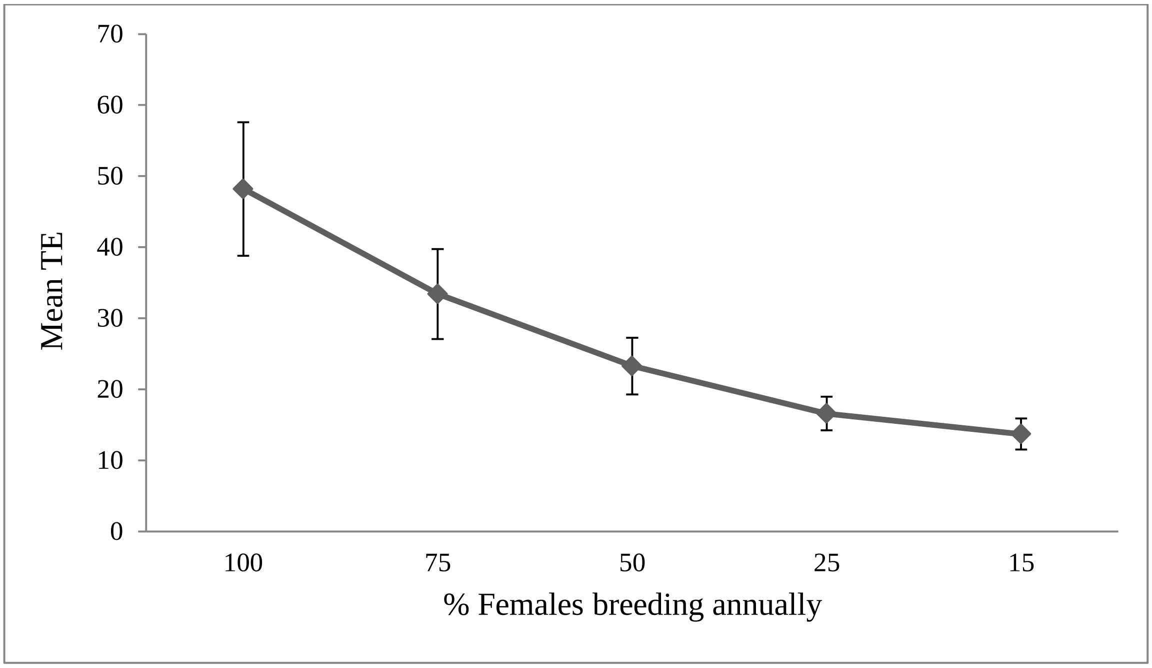
Sex ratio M:F	Mean TE	SD	PS	SE
90:10	12.79	3.11	0	0
80:20	19.11	3.80	0	0
70:30	26.01	4.92	0	0
60:40	35.25	6.91	0	0
50:50	48.20	9.39	0	0
40:60	61.90	13.02	0.01	0.01
30:70	72.98	14.12	0.12	0.02
20:80	73.28	14.11	0.13	0.02
10:90	48.19	13.81	0	0

Population viability was sensitive to mean litter size, with the mean time to extinction increasing from 21.8 (SD = 3.01) years at a mean litter size of 2 to 61.8 (SD = 12.39) years at a mean litter size of 5, but after 100 years the meta-population was extinct under all scenarios with a probability of survival of zero (SE = 0) at a mean litter size of 2 and probability of survival of 0.004 (SE = 0.003) when mean litter size was 5.

Population viability was not sensitive to variations in the standard deviation of the mean litter size: probability of survival to year 100 was zero under all scenarios (SE = 0). In all cases, extinction occurred after 45.8 – 48.2 years ($\bar{x}$ = 47.28, SD = 0.62).

A reduction in the percentage of females breeding annually resulted in a large reduction on the overall mean time to extinction of the metapopulation (Figure 6.3). Probability of survival to year 100 was zero under all scenarios (SE = 0).

Figure 6.3 Reduction in the mean time to extinction (Mean TE) of the metapopulation as the percentage of females breeding is reduced. Error bars show the standard deviation of the mean TE. Baseline model = 100% of females breeding annually.



6.4.2.4. Decreasing female and male mortality >1yr

Population viability was assured by reducing male and female adult mortality rates by ≥50% with a probability of survival of 1 (SE = 0) after 100 years and reducing adult male and female mortality rates by 25% almost doubled the time it took for the metapopulation to become extinct to 84.17 years (SD = 10.75) with a probability of survival of 0.5 (SE = 0.02) at year 100. However, even a reduction in male mortality by 75% did not result in long-term population viability, with the metapopulation going extinct after 49.59 (SD = 9.82) years (Probability of survival = 0, SE =0). Similarly, reducing female mortality rates by 75%

resulted in the metapopulation becoming extinct after 46.83 (SD = 8.98) years, with a probability of survival of zero (SE = 0) after 100 years.

Reducing female and male mortality by only 25% in 4 of the sub-populations most likely to be at a high risk from road traffic accidents (Figure 6.4) resulted in a mean TE of 95.5 years (SD = 3.54) and a probability of survival of 0.99 (SE = 0.003) of the metapopulation at year 100 (Figure 6.5) and a reduction of 50% resulted in metapopulation viability (Probability of survival = 1, SE = 0 at year 100). However, at the lowest density estimate of 1 individual/100 km^2, in order to achieve survival of the metapopulation for at least 100 years (Probability of survival = 1, SE = 0) then in addition to a reduction in female and male mortality rates by 75%, carrying capacity of these four sub-populations would need to be doubled (K x 2) (Figure 6.5).

Figure 6.4 Map showing the four sub-populations (N, O, P and S) most likely affected by high road and human population densities.

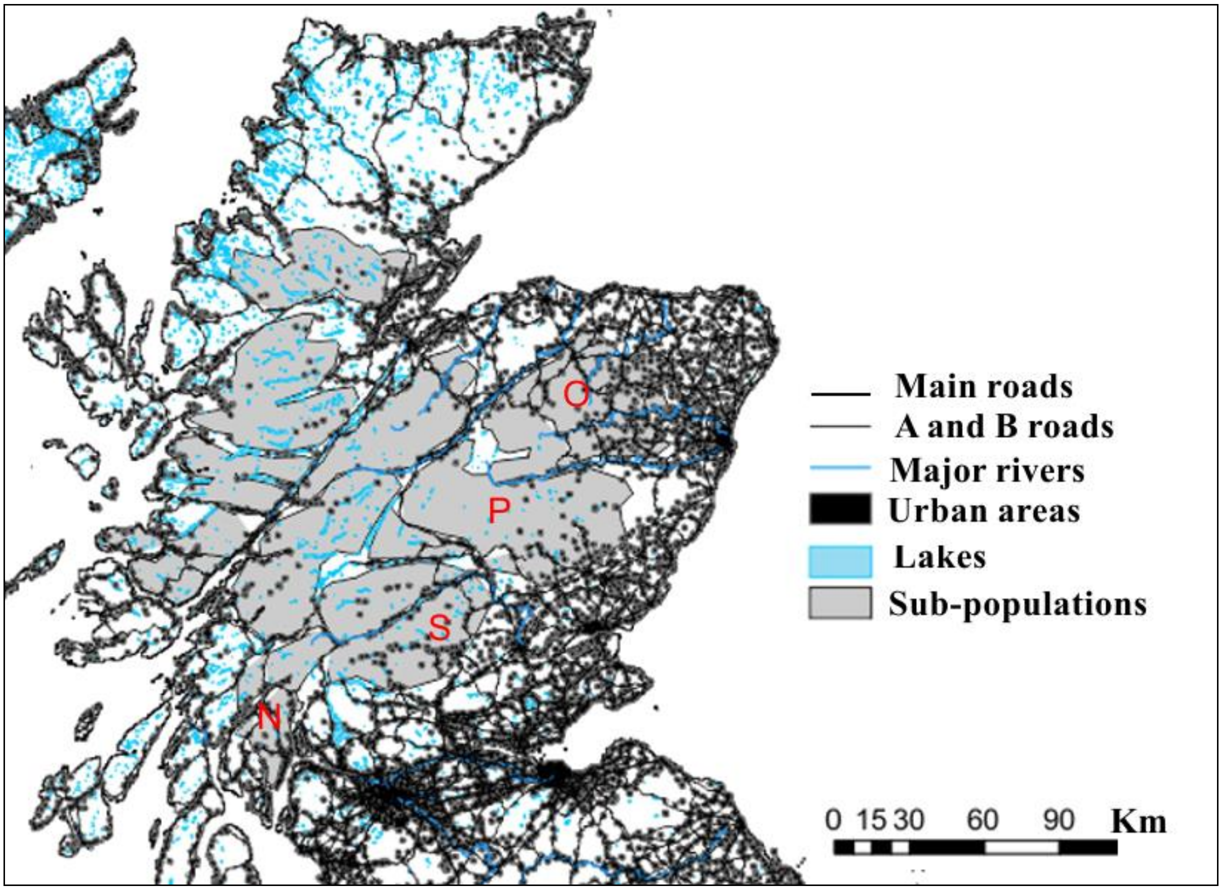
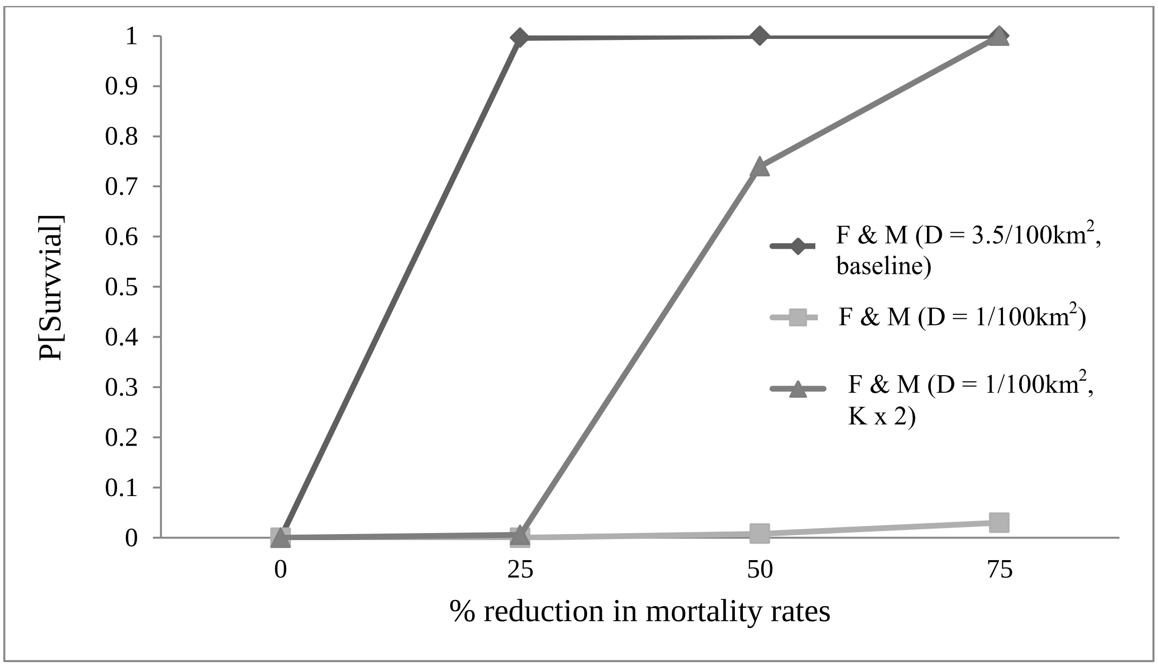


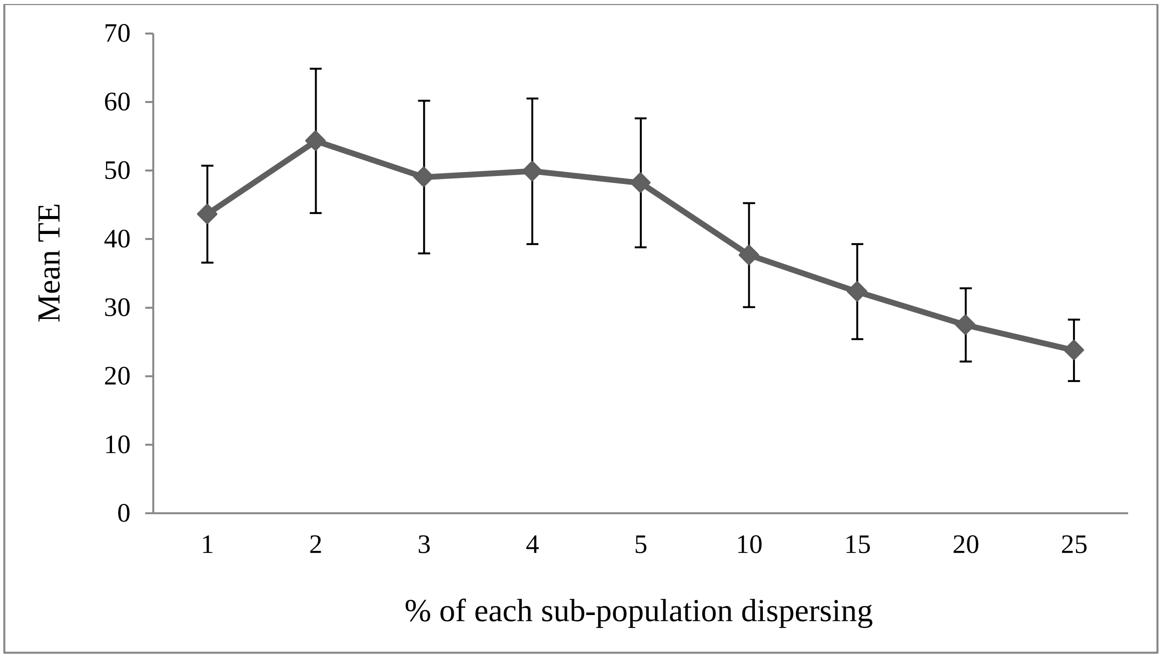
Figure 6.5 Increase in the probability of 4 of the sub-populations surviving at year 100 (P[Survival] when the mortality rates of females and males are reduced from 0% - 75%. The graph also shows how population survival is 100% when carrying capacity (K) is doubled even at the smallest population size (Density = 1 wildcat/100 km^2) if female and male mortality rates are reduced by 75%.



6.4.2.5. Dispersal

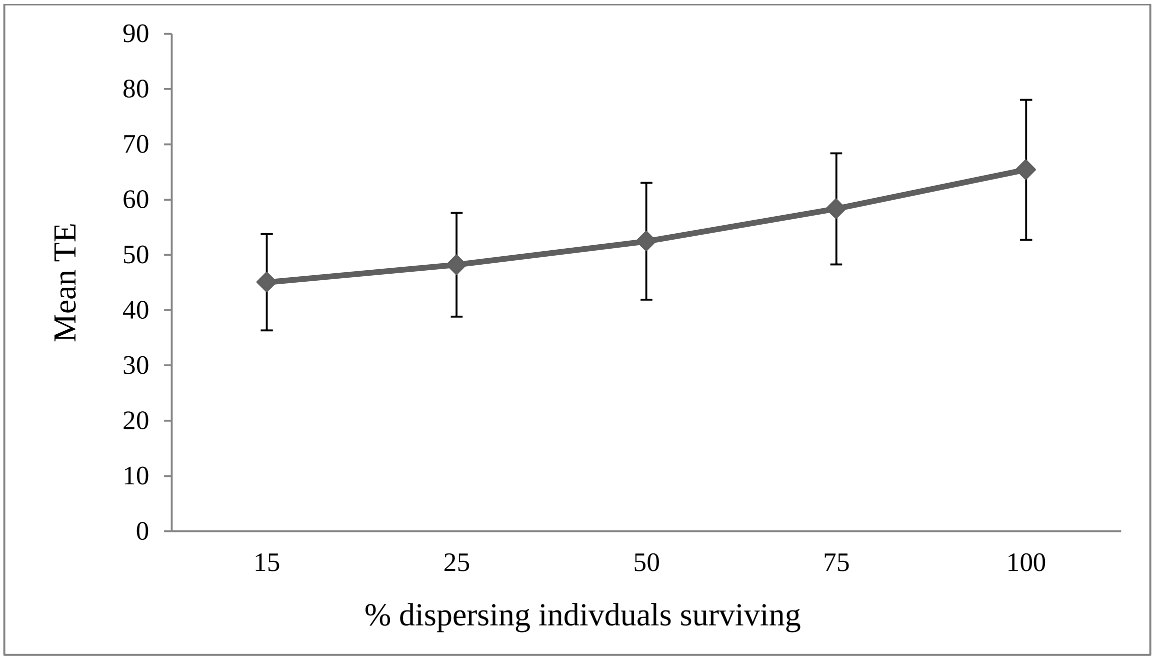
As the percentage of individuals dispersing out of a sub-population into another sub-population increased, the time to extinction decreased (Figure 6.6) with a zero probability of survival (SE = 0) under all scenarios. If 25% of each sub-population dispersed annually then the metapopulation would be extinct after only 23.8 (SD = 4.47) years.

Figure 6.6 Reduction in the mean time to extinction of the metapopulation (mean TE) as the percentage of individuals dispersing from each sub-population increases. Error bars show the standard deviation of the mean TE. Baseline model = 5% of individuals disperse.



Increasing the probability of survival of dispersing individuals from 25% to 100% resulted in an increase in the mean time to extinction, but still did not result in population viability, with the metapopulation going extinct after 65.39 (SD = 12.68) years (Figure 6.7) and the probability of survival zero (SE = 0) under all scenarios.

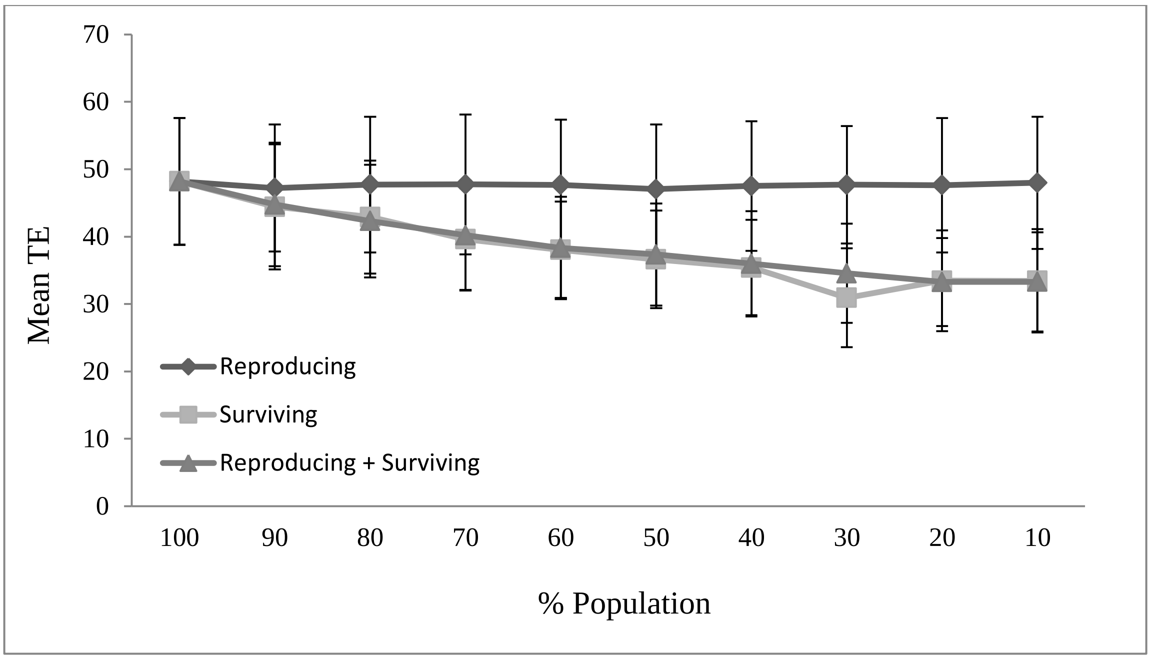
Figure 6.7 Increase in the mean time to extinction of the metapopulation (mean TE) as the percentage of individuals dispersing that survives increases. Error bars show the standard deviation of the mean TE. Baseline model = 25% of dispersing individuals survive.



6.4.2.6. Catastrophes

A catastrophe occurring with a probability of 1/15 every year did not have an impact on overall population viability even if only 10% of the metapopulation was able to reproduce. A reduction in the percentage of the population surviving had a greater impact, resulting in the overall mean time to extinction falling from 48.2 (SD = 9.39) years (baseline metapopulation) to 33.29 (SD = 7.35) years when only 10% of the remaining population survived and were able to reproduce (Figure 6.8). Probability of survival at year 100 was zero (SE = 0) under all scenarios. However, this impact could be mitigated by supplementing 1M and 1F annually for the duration of the simulation, resulting in 100% metapopulation survival after 100 years.

Figure 6.8 Decrease in the mean time to extinction of the metapopulation (mean TE) as the percentage of the population reproducing, surviving or both decreases as a result of a catastrophe occurring with a probability of 1/15 every year. Error bars show the standard deviation of the mean TE. Baseline model = 100% of the population reproduces and/or survives.



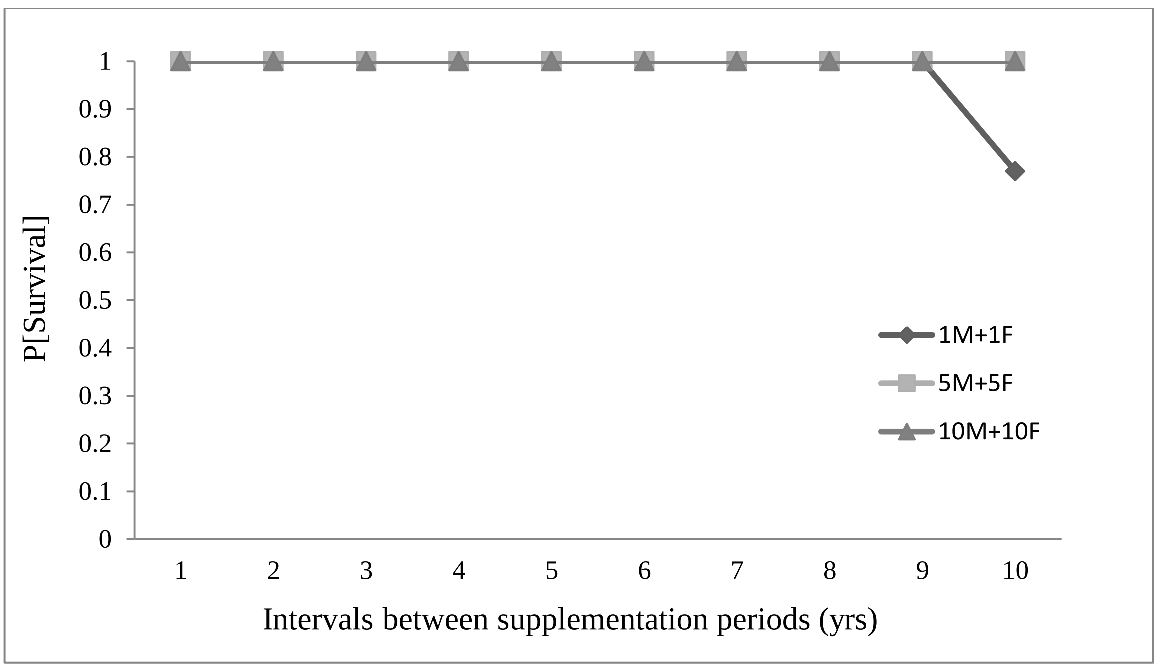
6.4.2.7. Supplementation

Annual supplementation of just 1 male and 1 female resulted in meta-population viability after 100 years. However, even supplementing 10 males and 10 females annually over 100 years, did not result in all the sub-populations surviving; mean time to extinction for four of the smaller sub-populations was; sub-population I = 53.8 years (SD = 33.2) with a probability of survival at year 100 of 0.99 (SE = 0.01), sub-population J = 1.67 years (SD = 1.04) with a probability of survival at year 100 of 0.43 (SE = 0.02), sub-population K = 2.52 years (SD =

2.11) with a probability of survival at year 100 of 0.64 (SE = 0.02) and sub-population Q = 44.04 years (SD = 28.54) with a probability of survival at year 100 of 0.98 (SE = 0.04).

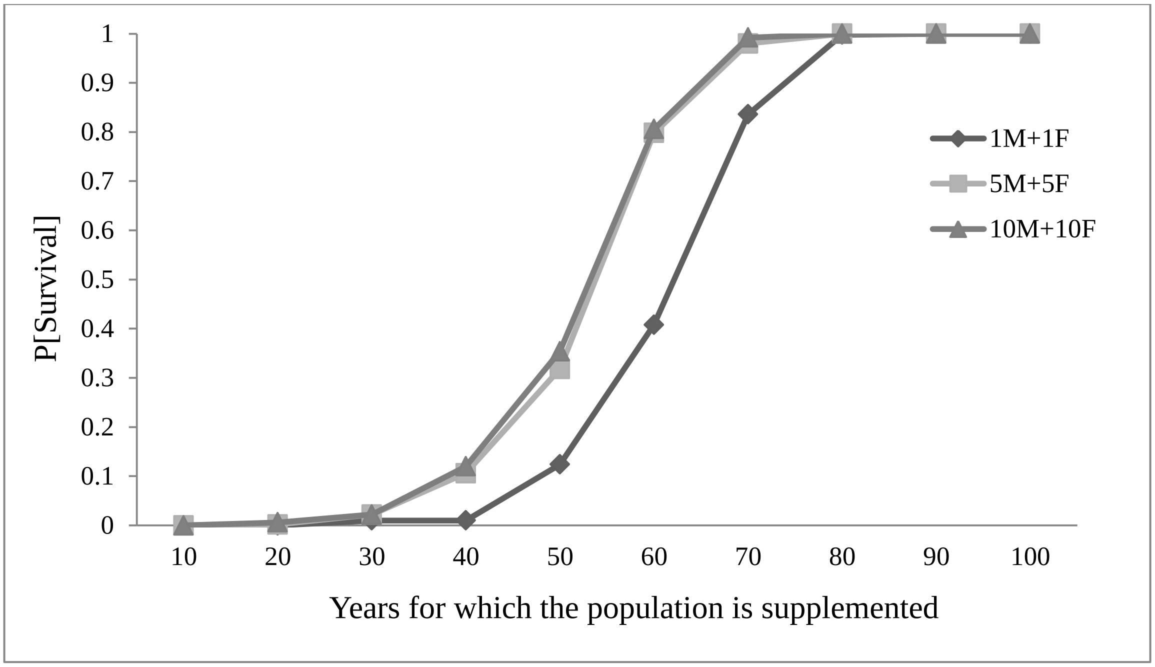
The model showed that if the intervals between supplementation are increased then a greater number of individuals needed to be supplemented in order to ensure long term viability over the 100 year simulation (Figure 6.9). If only 1M + 1F are supplemented, then meta-population viability is ensured if supplementation occurs at intervals ≤ 9 years.

Figure 6.9 Probability of population survival (P[Survival]) when 1M and 1F are supplemented into each sub-population at different yearly intervals.



Reducing the years over which annual supplementation occurred (< 70 years) resulted in a rapid reduction in the mean probability of survival, even if more individuals are supplemented (Figure 6.10).

Figure 6.10 Probability of population survival (P[Survival]) when the duration of yearly supplementation varies from 10-100 years and the number of male and female wildcats supplemented increases from 1-10.



6.4.2.8. Summary of parameters modelled

The models indicated that the parameters that had a large impact on population viability and the time it took for the metapopulation to go extinct included the initial population size based on the local wildcat population densities, the sex ratio of kittens born and mean litter size, increasing carrying capacity, the percentage of the population dispersing and what percentage of those survived. Reducing female + male mortality rates and/or supplementing the population with captive bred individuals resulted in long-term population viability.

6.5. Discussion

The baseline model indicated that the current population is not viable over >50 years. Small population sizes are vulnerable to extinction as a result of genetic problems (e.g. inbreeding, decreased genetic variability), demographic fluctuations (e.g. variation in births and deaths) and environmental fluctuations (e.g. due to disease, predators, food supply, natural catastrophes) (Primack, 1993). Population viability was only assured if specific management action occurred including reducing mortality rates and supplementing the population on a long-term basis.

For example, reducing mortality rates of adult wildcats, resulted in metapopulation viability, even at low population sizes and if brought about in only a few of the sub-populations. Main anthropogenic threats facing the Scottish wildcat that could be managed to reduce mortality include persecution, disease transmission from feral domestic cats and road traffic accidents (Corbett, 1979; McOrist *et al.*, 1991; McOrist & Kitchener, 1994a; Harris *et al.*, 1995; Daniels, 1997). For example, road traffic accidents have been reported to be a significant factor influencing mortality rates across the European wildcat's range (Riols, 1988; Lüttmann *et al.*, 1997; Grilo *et al.*, 2009). Studies on the European wildcat have shown that wildcat mortality on roads can be reduced through the use of appropriately placed landscape bridges, underpasses and viaducts, specially designed wildcat proof fencing and habitat alterations, such as restoring habitat surrounding crossing points to habitat known to be preferred by wildcats (Lüttmann *et al.*, 1997; Jungelen, 2005; Klar *et al.*, 2005). As discussed in Chapter 1, persecution of the wildcat has been a problem for centuries and has been identified as a specific threat in Scotland, particularly in areas of grouse rearing (Kitchener, 1995; Balharry & Daniels, 1998; Macdonald *et al.*, 2004). Recent initiatives in Scotland have involved increasing education and awareness campaigns through the Scottish Gamekeepers Association to help gamekeepers identify wildcats from feral domestic cats in the field (e.g. Hetherington & Campbell, 2012). Wildcats can also be infected by common feline diseases (McOrist *et al.*, 1991; Stahl & Artois, 1991; Daniels *et al.*, 1999; Fromont *et al.*, 2000) including the FeLV (feline leukaemia virus) which is almost always fatal (McOrist *et al.*, 1991; FAB, 2008). Increased steps are currently being put into place to try and reduce the numbers of unneutered feral domestic cats across the Scottish wildcat's range (e.g. www.wildcathaven.org; SNH, 2013), and in many cases, feral cats are also being vaccinated against the most common feline diseases. Small and/or fragmented populations of endangered species are thought to be particularly vulnerable to diseases and infections resulting from interactions with infected animals (Macdonald, 1993) and actions like these could therefore help decrease the risk of mortality in wildcats from disease transmission. Reducing mortality overall is therefore, clearly an important management action to ensure population viability, but different sub-populations are likely to be exposed to different mortality risks that need to be assessed separately.

Supplementation of the metapopulation had one of the strongest impacts on population viability, with the supplementation of only 1 male and 1 female annually into each sub-population required to secure long-term population viability. However, the model was very sensitive to the longevity of supplementation, indicating that long-term management of the wildcat population would be required unless other steps are taken such as in combination with decreasing sub-adult and adult mortality. Currently, based on the most recent genetic tests, out of 35 individuals in the Scottish wildcat captive breeding programme tested, the majority have been deemed suitable for breeding from (H. Dickson, pers comm., 2015). This number is greater than previously reported (Kilshaw & Macdonald, 2009) and steps are currently being put into place to further bolster the captive population through removal of a small number of individuals from the wild in order to develop a captive population of genetically robust individuals that will be suitable for release into the wild (H. Dickson, pers comm., 2015). Management of the existing wildcat population through supplementation may therefore become a reality in the near future.

Varying the initial population size had a large impact on the time it took for the metapopulation to become extinct. Reported densities of the wildcat vary widely from east to west and from areas of high to low prey availability (Corbett, 1979; Scott *et al.*, 1993; Kilshaw *et al.*, 2015a) and can therefore have a large impact on the viability of local sub-populations. Many factors have been shown to limit population size including predation, lack of prey/food resources, persecution and competition with other species (e.g. Mills *et al.*, 2006). Although the initial decline of the Scottish wildcat is attributed partially to habitat loss, in particular the loss of forested areas, and partially to hunting for fur and persecution (Kitchener, 1995, Langley & Yalden, 1977; McOrist *et al.,* 1991; Tapper 1992), it is currently though to be at greatest risk from hybridisation with feral domestic cats and hybrids. As detailed in Chapter 3, hybrids and feral domestic cats are found throughout the wildcat's current probable range and may negatively affect wildcat densities in a number of different ways; for example direct competition for resources, lost breeding potential through mating with the wrong cat type, disease transmission and loss of genetic variability due to hybridisation (Mendelssohn & Yom-Tov, 1987; McOrist *et al.*, 1991; Hubbard *et al.*, 1992; McOrist & Kitchener, 1994b). Reducing the numbers of hybrids and feral domestic cats in the smaller sub-populations in particular could have significant overall positive results on the wildcat's viability there.

Some reproductive traits had a large impact on population viability including sex ratio of kittens born, the mean litter size and the percentage of females breeding annually. In litters with higher male: female ratio, smaller mean litter size and lower percentage of females breeding, a reduction in the time it took for the metapopulation to become extinct was observed. It is not known what the sex ratio of wild populations are, but captive data suggests an average sex ratio of 50:50 (Kilshaw & Macdonald, 2009) which has also been noted in other felids in the wild (e.g. Henriksen *et al.*, 2005). Some studies have shown that females in better condition produce more of the larger, costly sex (males) to be reared (Tella, 2001; Clout *et al.*, 2002; Cameron, 2004) or that more males are produced in low-quality habitats (Goltsman *et al.*, 2005) and larger females tend to have larger litter sizes (Clutton-Brock & Harvey, 1978). Clearly, more information on what conditions may result in skewed sex ratios or large litter sizes in the wildcat and therefore influence local population viability are required.

Here, the percentage of females breeding annually also had a large impact on population viability. Factors affecting female breeding success in carnivores in general include age, for example, in the Iberian lynx (*Lynx pardinus*), Henriksen *et al.* (2005) found that young females and those >12 years old had reduced breeding success, they also suggested that human-related stress (such as during the hunting season) can affect individual reproductive success. Piñeiro *et al.* (2012) noted that in one of Spain's National Parks, stress levels in the European wildcat were higher during gestation periods and dispersal of young as a result of increased tourist pressure. Reproductive success can also be related to nutritional status (e.g. Elowe & Dodge, 1989). Rabbits are the preferred prey species of the European and Scottish wildcat (Corbett, 1979; Sarmento, 1996; Malo *et al.*, 2004; Lozano *et al.*, 2006) but rabbit populations can be heavily affected by disease including Myxomatosis and Rabbit Haemorrhagic Disease (RHD). For example, Myxomatosis was introduced into eastern Scotland in 1954 (Brown *et al.*, 1956) and was found throughout most of the country during the following year (Thompson & Wordon, 1956) with up to 99% mortality seen in some populations. Immediately after myxomatosis an increase in the incidence of wildcat predation on poultry was observed and several dozen wildcats were killed (Thompson & Wordon, 1956). Disease of rabbits can therefore have a direct impact on wildcats both dietary and in relation to persecution. Sudden crashes in local rabbit populations could therefore have a significant impact on breeding success and survival of local female wildcats. Providing populations that experience sudden crashes or even where prey density is low with food could aid reproductive success. For example, food supplementing a small population of Iberian lynx allowed reproduction and kitten survival in areas with very low prey density (López-Bao *et al.*, 2010). Hybridisation with feral domestic cats or hybrids will also affect the percentage of females breeding in terms of wasted breeding effort.

Almost no data exist on dispersal rates of wildcats, yet the models here show the percentage of individuals dispersing and the percentage of dispersers surviving have a large impact on the viability of the metapopulation. The typical dispersal distance of a Scottish wildcat is thought to be 4km (Green, 1991) and radio tracking studies in Germany on the European wildcat found that male sub-adults will disperse between 9-10 months old, and females at 12 months old, although they may often stay within their mother's (the natal) territory (K. Hupe pers comm., 2009). The same study also found that only 20% of juveniles

(<12 months) and 60% of sub-adults (<24 months) survived annually. Dispersing young also appear to be particularly susceptible to road mortalities (PMVC, 2003). Understanding the factors that result in dispersal and result in the mortality of dispersing individuals is therefore important as it could help reduce the barriers affecting dispersal between sub-populations. It is also vital to determine how far dispersing individuals travel as this will have important implications on the connectivity between different sub-populations and therefore their sustainability in the long-term.

Surprisingly, increasing the carrying capacity of the sub-populations had only a negligible effect on overall population viability unless it was also included with a decrease in adult mortality rates. Here carrying capacity was estimated from the initial population sizes but as stated in the methodology this probably does not accurately reflect the number of wildcats that can be supported by each area. Carrying capacity is often calculated in terms of prey preference and abundance (e.g. Hayward *et al.*, 2007). A study on the European wildcat estimated that in theory 2-3 adult rabbits or 4 juveniles would fulfil an adult wildcats' daily energetic needs. Or, in areas where rabbits are not present or in low abundance, wildcats would need approximately 30 small rodents daily to fulfil their needs (Malo *et al.*, 2004). The Scottish wildcat will likely have similar energetic requirements and the carrying capacity of each sub-population may therefore vary considerably depending on the availability of rabbits and on the quality and amount of rodent habitat. Model outputs would therefore be more accurate through the use of precise prey density data. Carrying capacity may also be influenced by the densities of feral domestic cats and hybrids in each population as these will compete for much of the same prey species, effectively reducing overall carrying capacity for wildcats in the area.

An obvious limitation of this modelling process was that impact of hybridisation was not incorporated into the model and as noted above, hybridisation could affect several of the parameters including female breeding success and population size. However, in general, the models have highlighted the urgency of collating local data on; population densities, factors that influence reproductive success and mortality as well as how often dispersal occurs, where individuals disperse to and what factors might affect their survival. Importantly, the modelling also demonstrated that population viability can be achieved with a combination of different management techniques, although long-term efforts would be required. The modelling also suggest that overall metapopulation survival could still be obtained if management methods are concentrated on either the smallest populations (e.g. supplementation) or those at greatest risk (e.g. such as reducing road traffic accidents).

Chapter 7

7.0 General Discussion and Conclusions

The main aims of this thesis were to examine the status of the Scottish wildcat (*Felis silvestris silvestris*) by establishing the current distribution of wildcats, hybrids and feral domestic cats (*F.s.catus*), to map potential hybridisation risk, and to estimate the current population size and long term population viability of the population. The results and their relevance for conservation of the wildcat are discussed in more detail below.

7.1. Current distribution and hybridisation risk

Here camera trap data indicated that wildcats appeared to be predominant in eastern Scotland and the Cairngorms National park, and parts of the western peninsula. The distribution of the Scottish wildcat suggested by this thesis is similar to that noted in the most recent Scottish wildcat surveys (Balharry & Daniels, 1998; Davies & Gray, 2010), but notably missing records from Ardnamurchan, the Black Isle and sites in the north that have previous recorded wildcats, even at low numbers. These observations from the Black Isle and far north in particular, are likely due in part to a drastic decrease in local rabbit (*Oryctolagus cuniculus*) populations at these sites. However, feral domestic cats and hybrids were found at all sites wildcats were photographed at, suggesting these cat types are widespread across the wildcat's potential current range indicating a high risk of hybridisation exists.

Until recently, unneutered feral domestic cats were assumed to be the primary source of hybridisation risk. Recent evidence suggests hybrids themselves may be more important for facilitating hybridisation (see Germain *et al.*, 2008). The data presented here confirm this; hybrids preferred much of the same habitat as wildcats. Hybrids overlapped in their distribution pattern with both feral domestic cats and wildcats, supporting recent suggestions that the hybridisation threat posed by hybrids is exacerbated by their acting as a bridge between wildcats and feral domestic cats. The presence of hybrids was the most statistically significant predictor of wildcat occupancy, indicating the importance of controlling the impact of both feral domestic cats and hybrids on the wildcat population.

The distribution maps produced here also highlight areas that could be targeted for conservation management to reduce hybridisation risk. For example, in 2013, Scottish Natural Heritage (SNH), the government body responsible for wildlife conservation in Scotland, launched a Scottish wildcat action plan with the aim of halving the decline of the Scottish wildcat through a variety of actions, including neutering and/or removal of feral domestic cats and hybrids in priority wildcat areas (SNH, 2013). Six wildcat priority areas were chosen based on recent survey work that identified areas that had wildcats present with suitable habitat that could support a viable population (20 female wildcats). The priority areas also considered potential barriers to dispersal, the feasibility of carrying out feral cat and hybrid neutering/control and whether local support for wildcat conservation in these areas was likely (Littlewood *et al.*, 2014). All of the priority areas identified by the Scottish wildcat Action Plan fall within one of the sub-populations identified in Chapter 6 supporting the identification of these areas. However, the occupancy modelling carried out here also indicates that feral domestic cats have their highest probability of occurrence in eastern Scotland, where the proportion of arable farmland and grassland is greatest and human presence is extensive. Wildcat populations bordering these areas, including for example, one of the priority areas identified by SNH (Strathbogie) could therefore benefit from intensive targeted control of feral domestic cats specifically in these areas. In comparison, hybrids appear to pose a greater challenge, occupying much of the same habitat as wildcats, and control of hybrids should be prioritised throughout the wildcat's probable distribution. Control of feral domestic cats and hybrids include neutering to reduce hybridisation, but ideally, removal of these cat types, especially hybrids from the local wildcat population would occur and these actions are highlighted in the recent Action Plan.

7.2. Population size and density estimates

The most widely quoted estimate of Scottish wildcat population size is 400 (Macdonald *et al.*, 2004). As noted previously, this estimate was extrapolated from the proportion of museum samples that had typical wildcat pelage and superimposed onto a population estimate of 3500 wildcats (Harris *et al.*, 1995) which itself was extrapolated from sightings data collected by Easterbee *et al.* (1991). Here, a combination of density estimates from this study and other studies (Corbett, 1979; Scott *et al.*, 1993; Daniels, 1997) and estimates of the amount of available habitat that could support 20 breeding female wildcats resulted in a population size estimate between 115-314 individuals. Recent studies that suggest a minimum viable population of several thousand individuals are required for the long-term survival of most vertebrate populations (Reed *et al.*, 2003; Traill *et al.*, 2007). The Scottish wildcat population is clearly in a perilous state.

Mean wildcat densities estimated here, which obviously determine the estimate of total population size, were 3.5/100 km^2. Other studies in Scotland have indicated densities range from 1/100 km^2 to 30/100 km^2 with wildcats in the east showing higher densities than the west (Corbett, 1979; Scott *et al.*, 1993; Littlewood *et al.*, 2014). This is thought to result from lower prey densities and poorer habitat in the west compared to the east of Scotland. Low local population size estimates may indicate that the wildcat population there is at risk of local extinction without intervention (Littlewood *et al.*, 2014) and this is supported by the population viability analysis (Chapter 6).

Home range estimates also varied between sites and were greater than those from previous studies (Corbett, 1979; Scott *et al.*, 1993; Daniels, 1997). Studies have shown that home range sizes may vary between sexes and seasons and in relation to prey availability (Corbett, 1979; Stahl *et al.,* 1988; Scott *et al.,* 1993; Liberek, 1999). Differences across different areas of Scotland have implications for the use of survey methods such as camera trapping. Typically, the maximum distance between camera traps is based on the diameter of the smallest recorded home range of a female wildcat, 17.2-1.75 km^2 (Corbett, 1979; Daniels, 1997) in order to maximise the probability of capture for all individuals in the surveyed area. As a result, camera traps have hitherto recommended to be placed no further than 1-1.5km apart and using a minimum of 20 camera trap stations has been recommended (Kilshaw *et al.*, 2015a). However, in areas of potentially lower wildcat densities and greater home range sizes (e.g. areas with a larger proportion of poorer quality habitat) an increase in the number of camera traps used to extend the overall survey area size could help maximise the number of individuals captured. This would result in more accurate density estimates and hence more accurate population size estimates on a local scale.

7.3. Monitoring methods

To date, a combination of road traffic accident (RTA) surveys, live trapping, radio tracking, scat surveys, interviews and questionnaires and more recently camera trap surveys have been used to collect data on “wild-living” cats in Scotland including wildcats and feral domestic cats (Corbett, 1979; Easterbee *et al.*, 1991; Scott *et al.*, 1993; Daniels, 1997; Balharry & Daniels, 1998; Davies & Gray, 2010; Hetherington & Campbell, 2012; Kilshaw *et al.*, 2015a). As discussed in Chapter 5, different methods have their uses and limitations and conservation managers should to take into account both the ability of a method to detect the species in question (e.g. MacKenzie *et al.*, 2006) as well as the logistical constraints.

Here, camera trapping appeared to be more than twice as effective at detecting wildcats as scat surveys. However, overall detection was greatest when data from both methods were combined. This has been observed in other carnivores, where combining different survey methods increased detection rates (see Campbell *et al.*, 2008). Multiple methods should be favoured for future wildcat surveys. Detection can be improved by carrying out the surveys in habitats expected to have a higher occupancy probability, by using linear features such as fence lines and tracks in the survey site and by maximizing the chances of recaptures occurring (e.g. through baiting camera traps or by improving scat survey techniques). In addition, both the occupancy modelling (Chapter 5) and SECR analysis (Chapter 4) noted that some trap response by wildcats to camera traps was evident, likely in response to the presence of bait (e.g. Kilshaw *et al.*, 2015a) and this sort of information can be useful in improving detection rates of future surveys such as through the use of bait or scent lures.

7.4. Long term population viability and management interventions

PVA modelling indicated that the baseline metapopulation is not viable unless management actions are taken to either reduce mortality rates or supplement the population with captive individuals. For example, supplementing the sub-populations with 1 male and 1 female every

1-9 years resulted in zero probability of extinction of the metapopulation over 100 years.. Other parameters that influenced population viability included sex ratio of kittens born, litter size and the percentage of females breeding annually, the percentage of the population dispersing and of those, the percentage surviving. In addition, the initial population size estimates had a clear impact on population viability, with higher density estimates resulting in larger population size estimates and increases in the mean time for the metapopulation to become extinct.

As noted in Chapter 6, data on these parameters from populations in the wild are limited to a very small number of studies, but are clearly important for population viability. Akçakaya (2000) identified that sensitivity analysis carried out in PVA modelling can help determine which parameters need to be estimated more precisely and help guide fieldwork efforts, helping to reduce logistic costs and effort. In this case, for example, parameters such as initial population size had a large impact on population viability as a result in the variation of density estimates used. However, only a few density estimates exist for the Scottish wildcat (Corbett, 1979; Scott *et al.*, 1993; this study, Chapter 4). Consequently, in order to improve model predictions for each sub-population and therefore the metapopulation as a whole, detailed survey work for each potential sub-population should ideally be carried out.

Similarly, for example, reducing mortality rates of wildcats ensures long-term population viability but the impact different factors have on mortality rates are poorly understood. As a potential management option, the first process would be to evaluate the impact different mortality risks such as road traffic accidents have on the different population parameters, e.g. survival of dispersers or breeding success. Then these data could be re-input into the PVA modelling to reassess their impact (Akçakaya, 2000).

Overall, the PVA analysis indicates which aspects of the Scottish wildcat's biology require further research into and which direction management options could take in order to maximise population viability.

7.5. Conclusion

In summary, the results from this thesis indicate that the Scottish wildcat population is at risk from hybridisation from feral domestic cats and/or hybrids across all of its probable range. A population of the size estimated here is not viable in the long-term without management interventions. Different areas of the wildcat's current distribution will probably require different management initiatives. However, in order to implement these management techniques effectively, detailed information on local population parameters and the factors that influence these is also required. The study also provides support for the Scottish wildcat to have its status as Least Concern reassessed.

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Appendix 1a Classification used to score each pelage characteristic (adapted from Kitchener *et al.*, 2005).

Pelage Characteristic scored	**1 (Domestic)**	**2 (Hybrid)**	**3 (Wildcat)**
Dorsal line (1)	Absent/covers entire tail	Continues onto tail	Stops at base
Tail tip shape (2)	Tapered to point	Intermediate	Blunt
Tail bands (3)	Absent/joined by dorsal line	Indistinct or fused	Distinct
Broken stripes flank (4)	>50% broken or no marking	25-50% broken	<25% broken
Spots flank & HQ (5)	Many/no markings	Some	None
Stripes nape (6)	Thin/none	Intermediate	4 thick
Stripes shoulder (7)	Indistinct/none	Intermediate	2 thick
White chin (8)	White extensive on muzzle	White on chin	Buff or off white chin
Stripes cheek (9)	no dark stripes	Indistinct	3 clear, 2 fused
Spots underside (10)	Absent	Indistinct	Distinct
White Paw (11)	Extensive	Tuft	None
White flank (12)	Present	–	Absent
Colour tail tip (13)	Neither black or dark	Dark	Black
Stripes hind (14)	<4 or >7	–	4 to 7
Ear Colour (15)	Same as head	Weak ochre	Ochre/reddish

Appendix 1b Pelage scores of each of the cats caught on camera trap and identification under the Strict and Field ID's. Shows the 7PS (1-7) and 8PC (8-15) pelage characteristic each given a score of 1-3 (domestic-hybrid), UK = unidentifiable. The total 7PS score is given and the resulting Strict and Field ID of each cat (D = domestic, H = hybrid, W = wildcat). The 7PS characteristics are highlighted in grey.

Cat ID	Location	7PS							8PC								7PS	Strict ID	Field ID	Notes
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)				
Dom-01	Achlibster	1	2	1	1	2	2	1	1	1	UK	1	1	2	1	1	10	D	D	Tabby & white
Dom-01	Glen hurich	2	1	2	1	1	1	1	2	1	UK	2	3	1	1	1	9	D	D	Ginger & white
Dom-02	Glen hurich	1	2	1	1	1	1	1	2	1	1	1	3	2	2	1	8	D	D	Black & white
Dom-03	Glen hurich	1	2	2	1	1	1	1	UK	UK	UK	2	3	1	1	1	9	D	D	Ginger
Dom-04	Glen hurich	1	3	1	1	1	1	1	–	1	1	3	3	3	2	1	9	D	D	Black
Dom-05	Glen hurich	1	1	1	1	1	1	1	–	1	1	3	3	3	2	1	7	D	D	Black
Dom-01	Darnaway	2	2	2	1	2	1	1	2	1	UK	2	3	1	1	1	11	D	D	Ginger & white
Dom-02	Darnaway	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	8	D	D	Probable White
Dom-01	Dundreggan	2	2	2	1	1	2	2	3	3	UK	3	3	3	3	2	12	D	D	Known tabby domestic
Dom-01	Fearnoch	UK	UK	UK	1	1	UK	UK	1	1	UK	UK	UK	UK	2	1	2+	D	D	Black & white
Hyb-01	Fearnoch	1	2	2	UK	UK	UK	UK	3	UK	UK	3	3	3	UK	UK	5+	H	H	Unclear photo
Dom-01	Fetteresso	1	2	1	1	1	1	1	1	1	1	1	1	3	2	1	8	D	D	Black & white
Hyb-01	Fetteresso	1	2	1	2	2	3	2	3	3	UK	3	3	3	3	2	13	H	H	
Hyb-02	Fetteresso	3	2	3	1	1	3	2	3	3	UK	3	3	3	3	2	15	H	H	
Wild-01	Fetteresso	3	2	3	2	2	3	3	3	3	3	3	3	3	3	3	18	W	W	

Cat ID	Location	7PS							8PC								7PS	Strict ID	Field ID	Notes
		(1)	**(2)**	**(3)**	**(4)**	**(5)**	**(6)**	**(7)**	**(8)**	**(9)**	**(10)**	**(11)**	**(12)**	**(13)**	**(14)**	**(15)**				
Dom-01	Gartley	1	3	1	1	1	1	1	–	1	1	3	3	3	2	1	9	D	D	Large black
Dom-02	Gartley	2	2	1	1	1	1	1	2	2	UK	3	3	2	2	2	9	D	D	Brown/grey
Dom-03	Gartley	1	2	1	1	1	1	1	–	1	UK	3	3	3	2	1	8	D	D	Black
Hyb-01	Gartley	3	2	3	1	1	3	2	2	3	UK	UK	UK	3	1	3	15	H	H	Very spotty tabby
Wild-01	Gartley	3	3	3	2	2	3	3	2	3	UK	3	3	3	3	3	19	W	W	
Wild-02	Gartley	3	3	3	2	2	3	2	2	3	1	3	3	3	3	3	18	W	W	
Wild-03	Gartley	3	3	3	2	2	3	2	2	3	UK	3	3	UK	3	2	18	W	W	
Dom-01	Glen Isla	2	3	3	1	2	3	1	3	3	UK	3	3	3	1	2	15	D	D	Marbled tabby
Dom-02	Glen Isla	1	2	1	1	1	1	1	1	1	UK	1	1	1	2	1	8	D	D	White
Dom-03	Glen Isla	1	2	1	1	1	1	1	-	1	UK	3	3	3	2	1	8	D	D	Black
Dom-04	Glen Isla	2	2	2	1	1	2	1	3	3	UK	3	3	3	3	2	11	D	D	Tabby
Hyb-01	Glen Isla	1	2	1	1	2	2	2	3	3	UK	3	3	3	3	2	11	H	H	
Hyb-02	Glen Isla	3	2	3	1	1	2	1	3	3	3	3	3	3	3	2	14	H	H	
Hyb-04	Glen Isla	3	2	3	1	2	3	1	3	3	UK	3	3	3	3	2	15	H	H	
Hyb-05	Glen Isla	2	2	2	1	2	2	1	3	3	3	3	3	3	3	3	13	H	H	

Cat ID	Location	7PS (1)	(2)	(3)	(4)	(5)	(6)	(7)	8PC (8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	7PS	Strict ID	Field ID	Notes
Wild-01	Glen Isla	3	3	3	2	2	3	2	3	3	UK	3	3	3	3	3	18	W	W	
Wild-02	Glen Isla	UK	2	3	3	2	3	UK	3	3	UK	3	3	3	3	3	16+	W	W	
Wild-03	Glen Isla	3	2	3	2	2	3	2	3	3	UK	3	3	3	3	2	17	H	W	
Wild-04	Glen Isla	3	2	3	2	2	3	2	3	3	UK	3	3	3	3	3	17	H	W	
Wild-01	Kinveacy	3	3	3	3	3	3	2	3	3	U/K	3	3	3	3	3	20	W	W	
Hyb-01	Kinveacy	3	2	3	1	2	2	2	3	3	3	3	3	3	3	3	15	H	H	
Dom-01	Kinveacy	3	2	3	1	2	1	2	1	1	UK	1	1	3	1	2	14	D	D	Tabby, lots of white
Dom-01	Laggan	1	2	1	1	1	1	1	-	1	UK	3	3	3	2	1	8	D	D	Black
Dom-01	Letterewe	1	1	1	1	1	1	1	3	1	UK	3	3	3	2	2	7	D	D	Tortishell
Dom-02	Letterewe	1	3	1	1	1	1	1	1	1	UK	2	1	2	2	2	9	D	D	White & brown
Dom-03	Letterewe	1	2	1	3	2	1	1	U/K	U/K	UK	3	3	1	1	1	10	D	D	Grey tabby
Dom-04	Letterewe	U/K	2	1	1	1	U/K	U/K	3	2	UK	2	3	1	1	1	5	D	D	Ginger
Dom-01	Lochaline	2	2	2	1	1	2	1	1	3	UK	2	3	3	1	2	11	D	D	Tabby, white paws
Dom-02	Lochaline	1	1	1	1	1	2	2	3	1	UK	3	3	2	1	2	9	D	D	Marbled tabby
Dom-03	Lochaline	1	1	1	1	1	1	1	3	1	UK	3	3	2	1	1	7	D	D	Marbled tabby

Cat ID	Location	7PS							8PC								7PS	Strict ID	Field ID	Notes
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)				
Dom-04	Lochaline	1	1	1	1	1	1	1	2	1	UK	1	1	1	2	1	7	D	D	White
Dom-05	Lochaline	1	2	2	1	1	1	1	1	2	UK	2	3	2	1	1	9	D	D	Marbled tabby
Wild-01	Lochaline	3	2	3	3	3	2	2	3	3	UK	3	3	3	3	2	18	W	W	
Hyb-01	Lochaline	2	2	2	2	1	2	2	U/k	U/k	UK	3	3	3	1	U/k	13	H	H	
Dom-01	Spinningdale	1	3	1	1	1	1	1	1	2	1	1	1	2	2	2	10	D	D	Grey & white
Hyb-01	Spinningdale	2	2	2	2	2	2	2	1	3	UK	1	3	3	3	3	14	H	H	Tabby, white paws
Dom-01	Strontian	1	1	1	1	1	1	1	–	1	1	3	3	3	2	3	7	D	D	Black
Dom-02	Strontian	2	2	3	1	1	1	1	1	1	UK	1	1	3	2	1	11	D	D	Tabby, lots of white
Dom-03	Strontian	1	1	1	1	1	1	1	–	1	1	3	3	3	2	3	7	D	D	Black
Hyb-01	Strontian	3	U/K	U/K	2	1	2	U/K	2	3	UK	3	3	3	1	2	8	H	H	Tabby
Dom-01	Trossachs	2	2	2	2	3	2	UK	1	3	UK	1	1	2	2	2	13	D	D	Tabby, lots of white
Dom-02	Trossachs	1	1	1	1	1	1	1	1	1	UK	1	1	2	2	1	7	D	D	Grey & white
Hyb-01	Trossachs	1	2	1	3	2	3	2	3	3	UK	3	3	3	3	3	14	H	H	

Appendix 1c Example of some of the different cat types captured; Wildcats from Glen Isla (ISLA-Wild-01) and Gartley (GART-Wild-01), hybrids from Seafield and Strathspey (KIN-Hyb-01) and Gartley (GART-Hyb-01) and feral/domestic cats from Fetteresso (FETT-Dom-01) and Glen Hurich (GH-Dom-05).

Appendix 2 Results of the two-stage model selection process

The results of the model selection process for predicting the probability of occurrence for feral domestic cats, hybrids, and wildcats in Scotland. Model selection was developed as a two-stage process. In the first stage, the most suitable model structure was identified among three types; 1) a model where occupancy (Ψ), colonization (γ), extinction (ε), and detection (p) are held constant, 2) a model where the detection process is allowed to time-vary, and 3) a model where the occupancy process varies as a function of habitat covariates and the detection process is time-varying. The highest-ranking model based on Akaike's Information Criterion (AIC) was retained which then graduated to the next stage of the model selection process. In the second stage all possible combinations of models built from habitat covariates that are believed to be influential to feral domestic cats, hybrids, and wildcats were evaluated. Here the top-10 ranking models for each cat type displaying the number of parameters (*n*Pars), the AIC score, and the difference between each model and the top-ranking model (ΔAIC) are shown. Quadratic terms are featured by a 2 in superscript.

Feral domestic cats

Model	nPars	AIC	ΔAIC
(Stage 1)			
Ψ(c + m + g + go + e + u + a + e)γ(.)ε(.)p(d + d^2)	14	834.98	0.00
Ψ(.)γ(.)ε(.)p(d + d^2)	6	852.77	17.79
Ψ(.)γ(.)ε(.)p(.)	4	865.98	31.00
(Stage 2)			
Ψ(c + g + e + u + a)γ(.)ε(.)p(d + d^2)	11	832.07	0.00
Ψ(c + g + e + u + a + ed)γ(.)ε(.)p(d + d^2)	12	832.50	0.43
Ψ(g + go + e + u + a + ed)γ(.)ε(.)p(d + d^2)	12	833.45	1.38
Ψ(c + g + go + e + u + a + ed)γ(.)ε(.)p(d + d^2)	13	833.57	1.50
Ψ(c + g + go + e + u + a)γ(.)ε(.)p(d + d^2)	12	833.85	1.78
Ψ(c + g + e + u)γ(.)ε(.)p(d + d^2)	10	833.86	1.80
Ψ(c + m + g + e + u + a)γ(.)ε(.)p(d + d^2)	12	833.89	1.82
Ψ(g + go + e + u + ed)γ(.)ε(.)p(d + d^2)	11	833.97	1.90
Ψ(m + g + go + e + u + a + ed)γ(.)ε(.)p(d + d^2)	13	834.05	1.98
Ψ(c + m + g + e + u + a + ed)γ(.)ε(.)p(d + d^2)	13	834.12	2.06

c = coniferous woodland, m = mixed woodland, g = grassland, go = gorse, e = elevation, u = urban, a = arable, ed = edge, d = survey date

Hybrids

Model	nPars	AIC	ΔAIC
(Stage 1)			
Ψ(c + m + g + go + e + u + a + e)γ(.)ε(.)p(d + d^2)	14	727.81	0.00
Ψ(.)γ(.)ε(.)p(d + d^2)	6	748.91	21.10
Ψ(.)γ(.)ε(.)p(.)	4	755.73	27.92
(Stage 2)			
Ψ(g + go + e + u + ed)γ(.)ε(.)p(d + d^2)	11	723.44	0.00
Ψ(g + e + u + ed)γ(.)ε(.)p(d + d^2)	10	724.05	0.61
Ψ(c + g + e + u + ed)γ(.)ε(.)p(d + d^2)	11	724.11	0.68
Ψ(c + g + e + u)γ(.)ε(.)p(d + d^2)	10	724.42	0.98
Ψ(g + go + e + u + a + ed)γ(.)ε(.)p(d + d^2)	12	724.99	1.55
Ψ(c + m + g + e + u + ed)γ(.)ε(.)p(d + d^2)	12	725.05	1.61
Ψ(m + g + go + e + u + ed)γ(.)ε(.)p(d + d^2)	12	725.09	1.65
Ψ(c + g + go + e + u + ed)γ(.)ε(.)p(d + d^2)	12	725.12	1.68
Ψ(c + m + g + e + u)γ(.)ε(.)p(d + d^2)	11	725.13	1.69
Ψ(c + g + e + u + a + ed)γ(.)ε(.)p(d + d^2)	12	725.29	1.85

c = coniferous woodland, m = mixed woodland, g = grassland, go = gorse, e = elevation, u = urban, a = arable, ed = edge, d = survey date

Wildcats

Model	*n*Pars	AIC	ΔAIC
(Stage 1)			
Ψ(c + m + g + go + e + h + ed)γ(.)ε(.)p(d + d^2)	13	528.45	0.00
Ψ(.)γ(.)ε(.)p(d + d^2)	6	535.74	7.29
Ψ(.)γ(.)ε(.)p(.)	4	540.66	12.21
(Stage 2)			
Ψ(c + m + g + e)γ(.)ε(.)p(d + d^2)	10	524.00	0.00
Ψ(c + m + g + e + go)γ(.)ε(.)p(d + d^2)	11	524.86	0.86
Ψ(m + e + go)γ(.)ε(.)p(d + d^2)	9	525.20	1.20
Ψ(m + e + go + h)γ(.)ε(.)p(d + d^2)	10	525.25	1.25
Ψ(m + g + e + go + h)γ(.)ε(.)p(d + d^2)	11	525.37	1.37
Ψ(c + m + g + e + h)γ(.)ε(.)p(d + d^2)	11	525.94	1.94
Ψ(c + m + g + e + ed)γ(.)ε(.)p(d + d2)	11	526.05	2.05
Ψ(m + g + e + go)γ(.)ε(.)p(d + d^2)	10	526.10	2.10
Ψ(c + m + g +e + go + h)γ(.)ε(.)p(d + d^2)	12	526.50	2.50
Ψ(c + m + e + go + h)γ(.)ε(.)p(d + d^2)	11	526.92	2.92

c = coniferous woodland, m = mixed woodland, g = grassland, go = gorse, e = elevation, h = heather, ed = edge, d = survey date

Wildcats with feral domestic and hybrids

Model	*n*Pars	AIC	ΔAIC
(Step 1)			
Ψ(c + m + g + go + e + h + ed + f + hy)γ(.)ε(.)p(d + d^2)	15	513.99	0.00
Ψ(.)γ(.)ε(.)p(d + d^2)	6	535.74	21.75
Ψ(.)γ(.)ε(.)p(.)	4	540.66	26.67
(Step 2)			
Ψ(m + hy)γ(.)ε(.)p(d + d^2)	8	509.93	0.00
Ψ(m + go + hy)γ(.)ε(.)p(d + d^2)	9	510.27	0.34
Ψ(m + f + hy)γ(.)ε(.)p(d + d^2)	9	511.18	1.25
Ψ(c + m + hy)γ(.)ε(.)p(d + d^2)	9	511.26	1.33
Ψ(c + m + go + hy)γ(.)ε(.)p(d + d^2)	10	511.90	1.97
Ψ(hy)γ(.)ε(.)p(d + d^2)	7	511.92	1.99
Ψ(m + e + f)γ(.)ε(.)p(d + d^2)	9	511.94	2.01
Ψ(m + e + hy)γ(.)ε(.)p(d + d^2)	9	511.95	2.02
Ψ(m + go + f + hy)γ(.)ε(.)p(d + d^2)	10	512.08	2.15
Ψ(go + hy)γ(.)ε(.)p(d + d^2)	8	512.17	2.24

c = coniferous woodland, m = mixed woodland, g = grassland, go = gorse, e = elevation, h = heather, ed = edge, f = feral domestic cats, hy = hybrids, d = survey date

Appendix 3 Comparison of Mean Home Range estimates (km^2) for *Felis silvestris silvestris* across its range.

Country	Mean Home range size (km^2)		Source
	Male	**Female**	
European wildcat			
France (NE)	5.70	1.80	Stahl *et al.* (1988)
Germany	16.62	-	Wittmer (2001)
Germany (Saxony)	13.68	7.41	Götz and Roth (2005)
Portugal	-	2.89	Sarmento *et al.* (2006)
Portugal (S)	19.47	2.23	Monterroso *et al.* (2005)
Switzerland	37.00	4.10	Liberek (1996)
Hungary	8.07	4.26	Biro *et al.* (2004a)
Slovenia	13.86	7.69	Potočnik *et al.* (2005)
Spain (S)	10.50	5.00	Ballesteros-Duperón *et al.* (2005)
Scottish Wildcat			
Scotland (NE)	1.75	1.75	Corbett (1979)
Scotland (NE)	6.06	1.72	Daniels (1997)
Scotland (W)	9.90	8.5	Scott *et al.* (1993)

Appendix 4 Models run using the Single-Season Multi-Method model in PRESENCE. ($\psi(.),\theta(.), p(.)$) = null model, ($\psi(.),\theta(.), p(m)$) = constant model where m = method of detection used, r = recaptures, dd = Julian date, dd^2 = Julian $Date^2$, a = arable, mw = deciduous/mixed woodland, cw=coniferous woodland, gr=grassland, e=edge.

$\psi(.),\theta(.), p(.)$	$\psi(.),\theta(.), p(m+r+dd+dd^2)$
$\psi(.),\theta(.), p(m)$	$\psi(.),\theta(.), p(m+r+a)$
$\psi(.),\theta(.), p(m+r)$	$\psi(.),\theta(.), p(m+r+cw)$
$\psi(.),\theta(.), p(m+dd+dd^2)$	$\psi(.),\theta(.), p(m+r+ed)$
$\psi(.),\theta(.), p(m+a)$	$\psi(.),\theta(.), p(m+r+gr)$
$\psi(.),\theta(.), p(m+cw)$	$\psi(.),\theta(.), p(m+r+mw)$
$\psi(.),\theta(.), p(m+ed)$	$\psi(.),\theta(.), p(m+r+cw+mw)$
$\psi(.),\theta(.), p(m+gr)$	$\psi(.),\theta(.), p(m+r+gr+mw)$
$\psi(.),\theta(.), p(m+mw)$	$\psi(.),\theta(.), p(m+r+a+gr+e)$
$\psi(.),\theta(.), p(m+cw+mw)$	$\psi(.),\theta(.), p(m+r+a+mw+cw+gr+e)$
$\psi(.),\theta(.), p(m+gr+mw)$	
$\psi(.),\theta(.), p(m+a+gr+e)$	
$\psi(.),\theta(.), p(m+a+mw+cw+gr+e)$	
$\psi(.),\theta(.), p(m+dd+dd^2+a)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+a)$
$\psi(.),\theta(.), p(m+dd+dd^2+cw)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+cw)$
$\psi(.),\theta(.), p(m+dd+dd^2+e)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+gr)$
$\psi(.),\theta(.), p(m+dd+dd^2+gr)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+e)$
$\psi(.),\theta(.), p(m+dd+dd^2+mw)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+mw)$
$\psi(.),\theta(.), p(m+dd+dd^2+cw+mw)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+mw+cw)$
$\psi(.),\theta(.), p(m+dd+dd^2+gr+mw)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+mw+gr)$
$\psi(.),\theta(.), p(m+dd+dd^2+a+gr+e)$	$\psi(.),\theta(.), p(m+r+dd+dd^2+a+gr+e)$
	$\psi(.),\theta(.), p(m+r+dd+dd^2+a+mw+cw+gr+e)$

Appendix 5 Models run using the Single-Species Single-Season Method model in PRESENCE. (ψ(.),p(.)) = null model, r = recaptures, a = arable, mw = deciduous/mixed woodland, cw=coniferous woodland, f = felled, gr=grassland, g = gorse, e=edge, OF=OnFence, OT=OnTrack, OE=In Edge habitat, DT=Distance to track, EC=Edge in cover habitat, CC=Camera trap location in cover habitat, Su=Rural, U = Urban.

Model	s
ψ(.),p(.)	
ψ(.),p(a+mw+cw+gr+e)	
ψ(.),p(a+mw+cw+f+gr+g+e)	
ψ(.),p(CC)	
ψ(.),p(DT)	
ψ(.),p(EC)	
ψ(.),p(EC+CC)	
ψ(.),p(OE)	
ψ(.),p(OF)	
ψ(.),p(OF+OT)	
ψ(.),p(OF+OT+OE)	
ψ(.),p(OF+OT+OE+DT)	
ψ(.),p(OT)	
ψ(.),p(r+a+mw+cw+f+gr+g+e+DT)	
ψ(.),p(r+a+mw+cw+f+gr+g+e+OE)	
ψ(.),p(r+a+mw+cw+f+gr+g+e+OE+OF+OT)	
ψ(.),p(r+a+mw+cw+f+gr+g+e+OE+OF+OT+DT)	
ψ(.),p(r+a+mw+cw+f+gr+g+e+OF)	
ψ(.),p(r+a+mw+cw+f+gr+g+e+OT)	
ψ(.),p(rec+a+mw+cw+f+g+gr+e+OE+OT+OF+DT+SU+U+EC+CC)	
ψ(.),p(r+CC)	
ψ(.),p(r+DT)	
ψ(.),p(r+EC)	
ψ(.),p(r+EC+CC)	
ψ(.),p(r+OE)	
ψ(.),p(r+OF)	
ψ(.),p(r+OF+OT)	
ψ(.),p(r+OF+OT+OE)	
ψ(.),p(r+OF+OT+OE+DT)	
ψ(.),p(r+SU+U)	
ψ(.),p(SU+U)	