INSIGHTS INTO WILDCAT’S ECOLOGICAL REQUIREMENTS IN SCOTLAND:
A MULTI-SCALE APPROACH

ANDRÉ PINTO DA SILVA

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A MULTI-SCALE APPROACH

ANDRÉ PINTO DA SILVA

Dissertação orientada por:

Doutor Luís Miguel Rosalino
(Centro de Biologia Ambiental, Universidade de Lisboa)

Ms. Kerry Kilshaw
(Wildlife Conservation Research Unit, Oxford University)

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This dissertation should be cited as:

To all who supported a dreamer...

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Dear all,

This section was perhaps one of the most difficult to write. In part because I have so much to thank some of you for that is unfair to choose just one reason to show gratitude and impossible to list them all. To others, transforming the feelings into words involves wrestling with the emotions involved. I will try to not forget anyone and of course I will include all of you who were important not just for the development of this thesis but also those who were essential for all my personal and scientific formation and therefore essential to the way I faced and carried out this work. To acknowledge all of you, I decided to start as everything began and finish in the most recent events – this thesis. Meanwhile this is also a way to avoid that the structure of these words might be understood as mirror of the importance and contribution of each one of you. In fact, I consider the role of each one unique and consequently precious and irreplaceable.

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Abstract

The effect of scale on species distribution has been highlighted by several authors and indicates the necessity of incorporate multi-scale approaches in conservation analyses. Several populations of European wildcat (*Felis silvestris silvestris*) are suffering considerable threats and thus conservation measures are vital. Conservation decisions have been based on the available information. However, most of wildcat studies have been conducted at fine scales, and thus may only represent part of the full picture. This thesis aims to provide the first insights on ecological factors constraining wildcat distribution in Scotland at local and national level. Several models based on food, land cover, disturbance, topographic and climatic variables were built to explain wildcat distribution at both scales. The results show that wildcat presence is influenced by the interaction of different types of environmental variables. At broad-scale, rabbit presence and rodent diversity showed to be the strongest factors influencing the species occurrence. However, a negative association was detected between rodent diversity and wildcat locations at finer scale, but conversely locations were associated with higher rodent abundance. Rabbit abundance was not detected as an influent factor at this level. Regarding land cover features, whatever the scales considered, wildcats benefited from higher habitat diversity. Wildcat presence at both scales was related to grassland patches and negatively associated with heather moorland. At local-level wildcats seem to be associated with woodland patches and riparian habitats. Disturbance influence was not detected, at least directly, at broader scale, but human settlements were positively associated with wildcats at finer scale, while closer distance to roads was related to lower wildcat occurrence. A direct influence of climatic conditions on the target species was not detected. However, areas theoretically associated with smoother climatic features were related to wildcat presence at broad scale. According with our main findings, the definition of special areas for wildcat conservation in Scotland should take into account multi scale approaches. At broader scales, areas should incorporate food rich patches (rabbits and rodents), specific land cover (e.g. woodland and grasslands) and less mountainous areas (topographic characteristics), while at the individual level areas showing higher levels of prey availability, heterogeneous land cover and few disturbance features should be the main target for assuring wildcat long term persistence.

**Keywords:** European Wildcat *Felis silvestris silvestris*, Ecological Requirements, Broad and Fine Scale, Wildcat Conservation
Os factores ecológicos que determinam a distribuição de espécies têm sido estudados ao longo do tempo. Contudo recentemente tem crescido a incorporação de diferentes escalas de análise em estudos que pretendem avaliar quais os factores que limitam ou potenciam a ocorrência das espécies. Tem sido verificado que diferentes resultados podem emergir de análises a diferentes escalas e que estratégias de conservação podem beneficiar de uma abordagem multi-escala. As estratégias de conservação delineadas para os carnívoros têm sido baseadas no conhecimento científico acumulado durante vários anos de estudos. Porém na maioria das espécies este conhecimento provêm maioritariamente de estudos à escala local. O gato bravo Europeu Felis silvestris silvestris tem uma distribuição generalizada e é globalmente considerado como espécie pouco preocupante em termos de conservação. Contudo populações regionais deste felídeo, como a população escocesa, têm vindo a sofrer várias ameaças, nomeadamente a perda e fragmentação de habitat e a hibridação com o gato doméstico Felis catus. A população escocesa de gato-bravo tem sido considerada como uma das populações com maiores taxas de hibridação e foi historicamente marcada pela perseguição activa e afectada pela transformação da paisagem. Actualmente a distribuição da população encontra-se restrita ao norte da Escócia e recentes estimativas apontam para uma população possivelmente criticamente ameaçada, com apenas 400 indivíduos apresentando o padrão de pelagem tipicamente associado ao gato bravo ‘puro’. Nesta situação, acções de conservação são urgentes. Contudo, é reduzida a informação disponível sobre os factores ecológicos que determinam a distribuição do gato bravo na Escócia. Esta tese foi desenvolvida com o objectivo de fornecer dados, a diferentes escalas, relativamente à interacção do gato bravo com o ambiente na Escócia e ser um ponto de partida para futuros trabalhos que permitam colmatar esta lacuna de informação. Com este objectivo desenvolveram-se, a uma escala nacional e local, diversos modelos baseados em variáveis ecológicas contendo informação sobre alimentação, cobertura do solo, perturbação, topografia e clima. A análise à escala nacional foi implementada no norte da Escócia, região fundamental para a preservação da biodiversidade no Reino-Unido. Esta zona é dominada, a Oeste, por planícies altas de urze e pradarias com mosaicos de coníferas e folha caduca a baixas altitudes. A Este, a região é maioritariamente composta por mosaicos de floresta intercalados com campos agrícolas. Esta zona é caracterizada pela topografia irregular, com a altitude a poder variar significativamente em curtas distâncias. Na análise à escala local, foram realizadas campanhas de foto-armadilhagem em três áreas localizadas no Norte e Nordeste Escocés. Ao nível local a abundância e diversidade de presas foi aferida através de sessões de armadilhagem de micromamíferos e transectos para contagem de indícios de presença de coelho. Os resultados obtidos neste trabalho sugerem que, em ambas as escalas, a presença do
gato bravo foi influenciada pela interacção de variáveis relacionadas com a disponibilidade de presas, cobertura do solo, perturbação humana e topografia do terreno. A avaliação da influência da abundância de presas na distribuição de gato-bravo à escala nacional não foi possível devido a inexistência deste tipo de dados em toda a extensão da área de estudo. Contudo a disponibilidade de presas revelou-se um factor fundamental para a presença da espécie, em ambas escalas, embora os resultados tenham revelado um diferente padrão. Na análise à escala nacional a presença de coelho e a diversidade de roedores revelaram-se os principais factores para explicar a presença de gato bravo. Já na escala mais fina, a abundância de coelhos não se revelou um factor influente na distribuição do gato e a diversidade de roedores teve uma influência negativa na presença de gato. Contudo, as localizações de gato foram positivamente associadas a uma maior abundância de roedores. A influência da disponibilidade de presas na presença e distribuição de gato bravo poderá afetar os tipos de cobertura seleccionados por este felídeo, uma vez que a sua presença foi relacionada com habitats usualmente associados a maior diversidade e abundância de presas. A espécie parece beneficiar, em ambas as escalas, da heterogeneidade dentro da matriz, nomeadamente do mosaico de floresta de folha caduca e coníferas, com áreas de pradaria. A presença de gato bravo a nível nacional e local parece estar negativamente associada com zonas de urzel. Ao nível local, a existência de habitat ripários poderá ainda beneficiar a presença da espécie. Relativamente ao efeito da perturbação humana na distribuição espacial do gato-bravo, verificou-se que, à escala nacional estes factores não influenciaram a presença da espécie. Porém ao nível local, a espécie apresentou uma associação negativa com a presença de estradas e positiva com aglomerações humanas. A topografia do terreno poderá ainda ser outro factor importante para a distribuição da espécie, nomeadamente à escala nacional. A influência positiva de áreas pouco montanhosas na presença de gato poderá estar associada com condições climatéricas mais amenas, características destas áreas. A influência deste factor não foi detectada à escala local. Comparativamente com o observado em outros estudos efectuados noutras áreas de distribuição da espécie, estes resultados salientam a necessidade de heterogeneidade de habitats para ocorrência do gato-bravo, algo que tem sido recentemente observado, por outros autores, no Sul e Centro da Europa. Relativamente ao efeito da perturbação, o gato bravo na Europa Central tem sido influenciado negativamente pela presença de estradas e zonas urbanas. Porém, no presente estudo não foi detectada uma relação clara entre o gato-bravo e as estruturas artificiais (ex. estradas), mas os resultados parecem indicar a sua maior importância ao nível local. Já a procura de áreas associadas a um clima menos severo está de acordo com a distribuição desta espécie, limitada a regiões com estas características, em países de maior latitude. Os resultados aqui apresentados podem ser um valioso instrumento para o delineamento de estratégias de conservação a diferentes escalas e os modelos construídos ser utilizados no mapeamento de áreas com maior adequabilidade para a espécie. Estes modelos permitirão não só fomentar estratégias de conservação mais
direcionadas e eficazes, como aumentar a capacidade de predizer a ocorrência de uma espécie de difícil de detecção, beneficiando futuras amostragens de campo.

**Palavras-chave:** Gato Bravo *Felis silvestris silvestris*, Escala Nacional e Local, Requerimentos Ecológicos, Conservação
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Introduction

Carnivore conservation

In recent years there has been a huge development of tools to study the causes, effects and solutions of biodiversity loss (e.g. the incorporation of genetics in conservation – Oliveira et al. 2008). Although large funds are now available for this purpose, they are still insufficient to fund all the necessary research. Thus, the scientific community has to prioritize targets for conservation (Mace et al. 2007). However, economic reasons are not the only factor to take into account when dealing with conservation issues. For example, since the human population is always linked to the loss of biodiversity (although the degree and type of influence may differ between regions), humans assigned values to biodiversity (utilitarian values such as economic, aesthetic, recreational or tourist; or Intrinsic value like Ecocentric and Biocentric ethic, Lindenmayer & Burgman 2005) play a key role in conservation.

Carnivores (i.e. members of order Carnivora) have been suggested as a central target group for conservation actions, due to their top position in the ecosystem and their large spatial requirements, allowing them to be used as keystone and/or umbrella species (Noss et al. 1996; Kerr 1997; Gese 2001; Gittleman et al. 2001; Carroll et al. 2001). Additionally, as they have elements that fulfil the emotional part of the equation, mainly due to their aesthetic value (e.g Felids, Canids and Ursids), they are strong motivators for attracting non-scientific members of the public into conservation actions. This role is usually associated with large carnivores, but in particular situations, can also be assumed by small or medium sized carnivores. For instance in the United Kingdom where Brown Bear Ursos arctos, wolves Canis lupus and Eurasian Lynx Lynx lynx are now extinct, medium-sized carnivores like the otter Lutra lutra and wildcat Felis silvestris have assumed the role of flagship species (Battersby 2005).

The success of conservation plans is closely linked with the available ecological knowledge. A deep knowledge of carnivore ecological determinants may be an essential auxiliary tool to: predict the distribution and expansion of alien species (e.g. American Mink Mustela vison) (Macdonald & Rushton 2003; Hammershøj et al. 2006); to detect the occurrence of cryptic or rare species difficult to survey like the flat-headed cat (Wilting et al. 2010); and to predict feasible areas for reintroduction, identifying simultaneously potential conflicts with human activities (Schadt et al. 2002; Carrol et al. 2003; Steury & Murray, 2004, Kissling et al. 2009).
Species distribution and the study of how environmental factors influence such distribution has been a research target for many years (Rushton et al. 2004). Common patterns of species distribution are difficult to assess due to the inter-population variability of ecological requirements and inter and intra-species relationships. In carnivores, this is more challenging since many species have worldwide distributions and inhabit a wide range of different environments (e.g. Eurasian badgers – Neal & Cheeseman, 1996). Nevertheless, factors such as food availability, land cover spatial structure, human disturbance or the interaction between them (e.g. Karanth et al. 2004; Michalski & Peres 2005; Kent et al. 2011a), appear to be essential determinants of carnivore presence in a region.

Carnivores are mainly predators and usually stand on the top of the food web. Thus, one of the main factors explaining their presence is their use of the available trophic resources (Carbone & Gittleman 2002). For instance, diet is considered the most direct interface between felids and their environment (Macdonald & Loveridge 2010). Within this interaction, prey abundance appears to be highly related with carnivore occurrence, and since prey biomass is correlated with abiotic factors (e.g. temperature, rainfall, nutrients availability and seasonality – Macdonald & Loveridge 2010) carnivores are directly (e.g. arctic fox Alopex galopus – Prestrud 1991) and indirectly influenced by these factors. For instance, some species show a close association with one main prey, despite consuming different trophic resources, and might shape their distribution and daily movements according to their main prey occurrence (e.g. cheetahs Acinonyx jubatus follow Thomson’s gazelle Eudorcas thomsonii during their migration in Serengeti dry season - Durant et al. 2010). Another good example is the Iberian-lynx Lynx pardinus, whose dependence on its main prey (the European rabbit Oryctolagus cuniculus) is so strong that it not only requires rabbit presence, but is also dependent on high rabbit abundance (up to 4.6 rabbits/ha in spring, Palomares 2001).

Nevertheless, some species can show some degree of variability on their diets (e.g. red fox Vulpes vulpes) which allow them to adapt to environmental changes (e.g. Contesse et al. 2004). Such variability may even occur in the same individual during different life stages (Iriarte et al. 1991, Loveridge et al. 2010). Additionally, size and abundance of prey can change spatial requirements within a carnivore species. For instance, Eurasian lynx (Lynx lynx) populations that prey mainly on forest ungulates, show a totally different spatial ecology when compared to those that prey mainly upon wild rabbits (Nowell & Jackson 1996).

Some species like the American marten Martes americana are habitat specialists (Hargis & Bissonnette 1997; Wilbert et al. 2000), but other species are more generalist and use different types of land cover during distinct periods of the year (e.g. breeding – Fernández & Palomares 2000) and shelter Jerosch et al. 2010). Habitat availability can therefore be a constraining
factor on carnivores’ presence. For instance Rosalino et al. (2005) showed that the presence of the Eurasian badger *Meles meles* in Mediterranean woodlands was not limited by a lack of food or water but instead by lack of suitable den sites. Diggable soil is therefore an essential factor for this species occurrence. Moreover, in other parts of the distribution range the species is also highly correlated with woodlands (Long et al. 1983). Other species, however, demonstrated that spatial availability is not always necessarily related with areas of suitable habitat. When enough prey is present, other species, like wolves *Canis lupus*, can tolerate areas theoretically less suitable (e.g. areas with high road density Merril 2000). Habitat features can also provide important structures that can play a fundamental role in population connectivity, such as corridors, essential for animal dispersion and therefore for the maintenance of genetically healthy populations (Rabinowitz & Zeller 2010; Zeller et al. 2011).

Human disturbance is another factor important to consider when studying the distribution of a particular species. For instance, Klar et al. (2008) found that the probability of wildcat presence dropped significantly within 200m distance of human-made structures (roads and human settlements). A similar relationship was highlighted for other carnivores in different environments, such as common genets *Genetta genetta*, African wild dogs *Lycaon pictus* and grizzly bears *Ursos arctos* (Woodroffe 2000; Galantinho & Mira 2009). Furthermore, Real et al. (2003) found that in Argentina human influence can be more relevant in explaining carnivore occurrence than spatial and environmental factors. Nevertheless, human actions can have different impacts. Traditional practices in agriculture, for example, can provide field heterogeneity and improve areas for prey abundance (e.g. landscape mosaics improve number of edges between fields and might improve rabbit abundance – Palomares 2001) and are considered more suitable for wildlife. On the other hand, intensive agriculture promotes field homogeneity and marked habitat transformation which may have a deleterious effect on carnivores (Ferreira et al. 2010) and other species. Moreover, there is a direct impact of human disturbance factors that threaten carnivore survival. For example, the increase in density of human built linear structures (e.g. roads and highways) may enhance the frequency of animal-vehicle collision, and consequently road kill mortality (Grilo et al. 2009). Also large dams may have negative effects on predators, by increasing the access of humans to less disturbed areas and the landscape deforestation, changing habitat characteristics (e.g. from lotic to lentic water systems), and increasing mortality in the water transference channels (Santos et al. 2008).

**The effect of scale on species distribution analyses**

Increasingly concern in updating the methodology to obtain more reliable estimates on species distributions is notorious. However, several studies on carnivore distribution do not take
into consideration the scale used to assess the distribution patterns. However, ecologists have realised in the last decades that ecological processes are scale dependent (Cushman & McGarigal 2002). Scale is characterized by both extent and grain (cell size). Extent is often considered as the overall area encompassed by a study, whereas grain is the size of the individual units of observation, commonly named sampling units (Wiens 1989). Variation in grain and extent influence data variability, which may induce several consequences in the analysis of factors affecting species spatial distributions (Wiens 1989). For example, grain increase is normally associated with the proportions of spatial heterogeneity lost to the study resolution. At the same time when grain is constant and extent increases, greater spatial heterogeneity may be incorporated, depending on the homogeneity level present in the area. Due to such effects, results among studies focusing on the same species, but using different extents and grains may differ. For instance, broad-scale influences of habitat selection may override the local effects of interspecific competition (see flycatchers example in Wiens 1989).

By realizing this scale bias some studies have looked into environmental factors importance at different scales, at both qualitative and quantitative levels (Saab 1999; Grand & Cushman 2003; Grand & Mello 2004; Kent et al. 2011a). For example, Schaefer et al. (2000) showed that caribou philopatry patterns (Rangifer tarandus caribou) differed when analyzed at the scale of the total caribou range and at the seasonal range level. Another example was mentioned by Kent et al. (2011a), that verified the importance of different variables at different scales, showing that U.S mammal species composition at coarse scales is largely affected by climate and land-use-land cover variables. However, the study verified that at finer scales land use-land cover variables showed a sizeable effect on the species composition. The results confirm the theoretical predictions of Wiens (1989) that the climate effect is more evident at coarser scales and its’ importance is diminished at finer scales due to the higher importance of biological interactions. Wiens (1989) also mentioned that although pattern variations between scales occur, the way such patterns change is not linear. To describe such unclear patterns the author used the designation of scale-domains. These domains are characterized by a gradient of scales (portion of the scale spectrum) where the factors explaining species distribution are consistent. However, between different domains, such determinants can markedly change. This notion is important when interpreting results, since models built within a domain may only be valid within the respective gradient of scales, with extrapolations being doubtful (Wiens 1989).

The available information indicates that multiple scales and domain analyses can suggest different factors explaining distribution patterns. This approach allows conservation decision-makers to have a clear understanding of how to define conservation actions, depending on the scale used (Cushman & McGarigal 2002). Nevertheless, multiple scale analyses can face some obstacles, namely the lack of reliable data at large extents, which in carnivores may be a common feature.
Target Species

European wildcat

The target species in this study is the European wildcat (Felis silvestris silvestris Schreber, 1775), a subspecies that belongs to the Felis silvestris group, taxonomically classified in the family Felidae, within the order Carnivora.

The modern wildcat (F. silvestris) is believed to have originated approximately c. 0.45-0.35 Ma, during the middle Pleistocene, from Martelli’s wild cat (F. (s.) lunensis Martelli, 1906), which occurred in Europe in the late Pliocene to 2Mya ago (Kurtén 1965; Kitchener 1991; Yamaguchi et al. 2004a; Macdonald et al. 2010).

According with a recent phylogeographical study (Driscoll et al. 2007), the modern wildcat is considered a polytypic complex that gave origin to five different lineages: European Wildcats (F. s. silvestris Schreber, 1775), African Wildcats (F. s. lybica Forster, 1780), Southern African Wildcat (F. s. cafra Desmarest, 1822), Asian Wildcats (F. s. ornata Gray, 1830) and Chinese Alpine Steppe cat (F.s. bieti Milne-Edwards, 1872). The acceptance of ornata and cafra as subspecies, with F. bieti, F.silvestris and F.lybica elevated at the species level is also accepted (Driscoll & Nowell 2009; Kitchener and Rees 2009). These results support the uncertainty in defining the cat’s taxonomical group, with different studies suggesting various classifications (Randi & Ragni 1991; Nowell & Jackson 1996), which were accepted by several authors (Sunquist & Sunquist 2002, Macdonald et al. 2004)

The taxonomic variability of the F. silvestris group is closely related with the broad distribution range, being probably one of the most widespread felid species on earth, since it is
present from China, Mongolia and India in Asia to Iberian Peninsula and Scotland in Europe, and with a broad distribution in Africa. Along the initial distribution range the wildcat suffered several threats that resulted in local extinctions and have reduced and fragmented the global population, as the current isolated populations in India and Saudi Arabia show (Nowell & Jackson 1996).

The unclear taxonomic situation of the European Wildcat causes some problems in the attribution of a conservation status. At the moment, the species is globally classified by the World Conservation Union (IUCN, 2010) as Least Concern. Nevertheless, according with the IUCN criteria, the wildcat appears to be Vulnerable in Portugal (Cabral et al. 2005) and Near-threatened in Spain (Palomo et al. 2007), although with vulnerable status in particular regions of the country such as the Basque Country. In Scotland, recent estimates indicate a possible critically endangered population. At the European level the wildcat is protected under the Council Directive 92/43/EEC of 21 May 1992, being included in the Annex IV, which lists the conservation of natural habitats and of wild fauna and flora requiring strict protection within the EU. The species is also protected under the Convention on International Trade in Endangered Species (CITES Appendix II, UNEP-WCMC 2006)

In Europe, the wildcat is morphologically characterized by a bushy and blunt-ended tail and a grey-brown coat colour with well-defined pattern of black or dark brown stripes (Nowell & Jackson 1996), and was once widely distributed throughout the continent, being only absent in Scandinavia and north-eastern Europe (Stahl & Artois 1994; Heltai et al. 2006; Driscoll & Nowell 2009). Presently, the species has a smaller and fragmented distribution range, with isolated populations in high latitude countries such as Scotland, Germany and France, with one half of the current distribution range in the Mediterranean region (Lozano et al. 2003). Slovakia, Poland and Ukrainian populations form one continuum, recognised as the Carpathian population (Driscoll & Nowell 2009).

Human expansion, and the consequent destruction and fragmentation of the habitat and direct persecution of the wildcat, from the 17th century up to recent days, are believed to be the main reasons for the species decline along the distribution range (Stahl & Artois, 1991; Sunquist & Sunquist, 2002; McOrist & Kitchener 1994; Jerosh et al. 2010). However, these factors may have allowed feral cats (resulting from the species domestication in the Near East with the expansion of the agricultural village system in the Fertile Crescent, at least, 9,000 years ago - Vigne et al. 2004; Driscoll et al. 2007) to establish populations in the natural environments. Nowadays, the growing number of small and isolated natural wildcat populations, the changes in land cover and the decline of prey availability are factors that can promote the contact with feral cats (Hertwig et al. 2009; Sarmento et al. 2009) and may result in higher levels of introgression, the flow of alleles from one species to another (Frankham et al. 2002). The contact between wild, feral and domestic cats can also be a threat for wild populations due to diseases
transmission (such as feline virus), commonly found in domestic and feral cats (McOrist et al. 1991; Nowell & Jackson 1996; Leutenegger et al. 1999; Račnik et al. 2008; Daniels et al. 1999; Fromont et al. 2000; Ferreira et al. 2010).

Current extent of hybridisation in Europe is not totally clear. High rates of interbreeding are suspected to occur in Scotland and Hungary (Beaumont et al. 2001; Daniels et al. 2001; Pierpaoli et al. 2003; Kitchener et al. 2005), in opposition to what is described for Italy, Germany and Portugal (Randi et al. 2001; Pierpaoli et al. 2003; Oliveira et al. 2008; Eckert et al. 2010). However, in Germany regional high rates of hybridization in scattered subpopulations has been detected (Hertwig et al. 2009). Hybridisation with the domestic cat is now considered one of the species main threats and the main concern in management and conservation plans, particularly in regions with higher human densities (Nowell & Jackson 1996; Daniels et al. 1998; O’Brien et al. 2009).

The impact of habitat loss and fragmentation is still a fundamental threat to the species (Sthal & Artois 1994, Nowel & Jackson 1996). These landscape processes were responsible for wildcat populations reaching minimum levels during the 20th century (McOrist and Kitchener, 1994; Lozano et al. 2007). The recovery of some local populations was only possible due to the decrease of direct persecution and habitat recovery from the 1990s (Lozano et al. 2007). Anthropogenic actions can hinder the recruitment of new individuals into a population (e.g. during dispersion movements) and consequently may reduce the probability of establishing new population nucleus.

Direct persecution was also one of the causes for the species disappearance in the past, specifically due to fur-trade and persecution by gamekeepers in hunting areas (Stahl & Artois 1994; Nowell & Jackson 1996; Lozano 2008). Nowadays, this threat seems to be diminishing. However, carnivore control, namely feral-cat and red-fox control, is still a risk for the wildcat, due to possible by-catches. This threat of accidental trapping, enhanced by the morphological similarities with hybrids and feral cats, that are not legally protected, can also increase the number of unintended kills of wildcats during carnivore control. Therefore, this threat should be considered, as it was confirmed in Scotland and Spain (Corbett 1979; McOrist & Kitchener 1994; Lozano 2008). In Scotland it is suspected that active persecution still occurs in response to the belief that wildcat predate on livestock and game birds. Also non-selective traps, such as snares used to legally control red fox populations, are a technique still used during predator control and, therefore, are a threat for wildcats (Macdonald et al. 2010).

Invasive species, populations reinforcements and overpopulation (e.g. deer population) can also cause some pressure on wildcat habitat and consequently on the wildcats’ main prey. Taking into account that feline densities are sensitive to prey densities fluctuations (O’Donoghue et al. 2010), this factors can have a considerable impact and should be investigated as a threat to wildcats (Lozano 2008). Field data has corroborated this idea, by detecting a
negative relationship between the presence of ungulates and the presence of European rabbits, small mammals and wildcats in typical Mediterranean ecosystems (Lozano et al. 2007).

**The Scottish Population**

The wildcat has been present in Britain since the early Holocene, when it was widespread throughout mainland Britain. These populations were descendant of continental European ancestors isolated after the separation of the Britain isles from mainland Europe during the sea level rise in the last glacial age, approximately, 8000-9500 radiocarbon years (Yalden 1999; Yamaguchi et al. 2004b; Driscoll et al. 2007). Traditionally, this isolation is assumed to be the basis of the differences towards wildcats inhabiting central Europe, namely regarding morphological characteristics, such as a darker coat colour and bolder stripes on the legs and flanks (Kitchener et al. 1995; Kitchener et al. 2005). This variation led the earlier taxonomists to describe the Scottish wildcat (*Felis silvestris grampia*, Miller 1907) as a different subspecies (Beaumont et al. 2001). Recent authors (Kitchener et al. 1991) have accepted this subspecies and the analysis of the skull morphology showed that British and Continental Europe wildcats were closely similar forms, suggesting that the Scottish wildcat was a representative of the European wildcat (Yamaguchi et al. 2004a). Another recent study (Driscoll et al. 2007) incorporated the Scottish population in *Felis s. silvestris* population, which is currently accepted by the IUCN (Driscoll & Nowell 2009).

The disappearance of the wildcat from southern Scotland, England and Wales occurred by the mid-late 19th century and at this period the species was also becoming scarce across Scotland (Taylor 1946; Langley & Yalden 1977). The simultaneous effect of habitat loss, and active persecution are therefore believed to have almost resulted in extinction of the species in the United Kingdom (Kilshaw et al. 2010).

In Scotland the distribution range was confined to the north and north-east Highlands by the 1920s. Nevertheless, the species probably re-occupied the central Highlands during the period between the World War I and II due to the reduction of persecution and, specifically, with the establishment of the Britain Forestry Commission in 1919 (McOrist & Kitchener 1994; Davis & Gray 2010). During this period forests were replanted and started to re-grow providing cover and increasing prey-abundance. By the early 1960’s wildcats were found in the Scottish Highlands with the most numerous records from Inverness-shire and parts of Aberdeen-shire, Angus, Moray, Nairn, Perth and Argyll (Jenkins 1962; Corbett 1979).

The latest Scottish wildcat survey (2006-08) conducted by Scottish Natural Heritage (SNH) (Davis & Gray 2010) suggested wildcat strongholds in Ardnamurchan, Cairngorms, Black Isle and Aberdeen-shire, suggesting that the species would be more abundant in east than in the west part of the country as it was predicted by Easterbee et al. (1991). Nevertheless, iso-
lated nucleuses were found in the west (Davis & Gray 2010). The major roads connecting Glasgow and Edinburgh are believed to be the southern boundary of the wildcat distribution (Balharry & Daniels 1998).

Despite low human density in the Northern Scotland, hybridisation is an important component of the current wildcat menaces in Scotland due to the high levels of introgression that are suspected to occur. Different approaches have been taken to address this question and differentiate domestic and wildcats, namely morphological, immunological, behavioural and genetic, (French et al. 1988; Hubbard et al. 1992; Daniels et al. 2001; Beaumont et al. 2001; Yamaguchi et al. 2004b; Kitchener et al. 2005).

New genetic approaches have been tested (Daniels et al. 2001; Beaumont et al. 2001; Driscoll et al. 2007) and genetic differentiation between different groups of wild-living cats seems to be valid. Five different types of cats (wildcats; wild/hybrid; hybrids; hybrid/domestic and domestic) living in wild were defined (Beaumont et al. 2001). Recently, morphological features and genetic data were compared (Kilshaw et al. 2010) and the use of microsatellites markers showed that groups identified according with pelage classification appear to have some degree of genetic differentiation and therefore the use of the strict pelage classification proposed by Kitchener et al. (2005) seems to be a reliable method to differentiate individuals genetically different from domestic cats. Kitchener et al. (2005) proposed a pelage score method based on seven main pelage characteristics (7PS): extent of the 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; which could enable the differentiation between domestic, hybrids and wild cats. Additionally, eight pelage characters (see Kitchener et al. 2005 for details) were suggested in order to confirm preliminary identification using the 7PS. According with this method each pelage feature is scored from 1 to 3 (1=domestic; 2=hybrid/intermediate aspect; 3= wildcat). An animal is considered wildcat when scores 19 or more in 7PS, simultaneously with no scores of 1 in any of these 7PS, neither in the additional 8PC. Under this strict ID, cats with high presence of wildcat characteristics can be identified. However, due to the identification difficulty during field observations, a relaxed definition (Score of 14 or more with no scores of 1 for the 7PS and 8PC) was simultaneous proposed (Kitchener et al. 2005). Is important to consider that under the Strict ID individuals identified as wildcats will not show any traits of domestic cats, but under the Relaxed ID animals will not show traits of domestic cats but may present hybrid characteristics (Kilshaw et al. 2010).

Despite being a well-documented population, accurate population numbers are unknown (Davis & Gray 2010). Harris et al. (1995), using wildcat sightings, reported the existence of 1000 to 4000 individuals living in the wild. A recent scrutiny (Kitchener et al. 2005) using a conservative approach of only considering animals features associated with the ‘pure’ wildcat (see: Kitchener & Easterbee 1992; Daniels, 1997; Yamaguchi et al. 2004a) suggested that may-
be only 400 individuals meeting those criteria could be found in wild. Nevertheless, this estimate may be slightly biased since a large proportion of the data used for this estimate is based on a road kill survey data and, therefore, may be more likely to detect hybrids and domestic cats due the proximity to human settlements (Kilshaw et al. 2010).

Since 1988, the Scottish wildcat population is protected in the UK under Schedule 5 and 6 of the Wildlife and Countryside Act. It is also under Schedule 2 of the conservation regulations. The species is also integrated in UK BAP list of Priority Species and Habitats, the Scottish Biodiversity List and was included on Scottish Natural Heritage’s Five Year Species Action Plan (Scottish Natural Heritage, 2007).

In Scotland wildcats may show slightly different morphological characteristics than their Continental counterparts. Thus, while in the Scottish population body size ranges from 49.5 to 65.3cm and the weight between 2.5 and 7.1 kg (Macdonald & Barrett 1993; Sunquist & Sunquist 2002), the overall European population shows wider morphometric intervals (body size: 48-68cm; weight: 1.6-8kg) (Macdonald & Barrett 1993). This insular population consumes a large number of prey, although the European rabbit constitutes the bulk of the diet, when available [e.g. Corbett (1979) detected a frequency of occurrence of rabbit remains in approximately 90% of wildcat faeces] (Kolb 1977; Corbett 1979; Hewson 1983). Moreover, several small mammals species, namely mice and voles, are also an important resource, present in almost 20% of the faeces (e.g. Corbett 1979), particularly when rabbits are absent (Hewson 1983, Corbett 1979). Nevertheless birds, amphibians, fishes, insects (less often) and, occasionally, cattle and roe-deer calves (Corbett 1979; Macdonald & Barrett 1993) may also be predated.

Due to its morphologic characteristics and feeding habits the wildcat can inhabit forest environments, being able to use a wide variety of strata, from the underground levels, to the arboreal stratum. In Scotland, the wildcat has been associated with pine forest dominated areas, with a preference for stream edges and woodland habitat types and avoidance of pasture and heather moorland habitats. The species tend to use the edges between mixed fields, where lago-morphs are usually more abundant. Inversely, they may use less mature forestry plantations, whose stands are less suitable for small mammals (Easterbee et al. 1991). Home ranges are highly variable, reaching significant differences within Scotland (e.g. 175ha in Glen Tanar region in the east and up to 1800ha in Ardnamurchan peninsula in the west; Corbett, 1979; Scott 1993). Like most felids, Scottish wildcats are solitary and both sexes appear to establish independent territories, marked by visual and scent marks (using scent glands secretion and urine), except during the mating season (January to March) when territories overlap (Corbett et al. 1999; Macdonald & Barrett 1993; Nowell & Jackson 1996). Densities are usually low, although different values have been estimated throughout the country, ranging from 3 individuals /10km², in Deeside on the Glen Tanar estate, (Corbett 1979) to 0.1 individuals/10km² in the western peninsula of Ardnamurchan (Scott et al. 1993).
Study Aims

The need for information on the multi-scale constraints of wildcat presence in Scotland, which is crucial for designing and mapping suitable areas for this species conservation, has become a major research priority. Thus, to fulfil this gap, the present thesis aims to study the environmental determinants (habitat, prey and landscape related factors, including the presence of Human infrastructures) shaping the wildcat distribution in Scotland, at two different scales, by providing data to answer the following questions:

a) What are the determinant factors that best predict wildcat distribution in Scotland? Are these factors different to those identified in other areas of the species range?

b) Are the patterns of wildcat distribution constant across scales? i.e. is the wildcat distribution constrained by the same parameters in a micro and macro scale analysis?

References


Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. & Deplazes, P. (2004) - The diet of urban foxes (Vulpes vulpes) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mammalian Biology, 69, 81–95.


Hewson, R. (1983) - The food of wild cats (Felis silvestris) and red foxes (Vulpes vulpes) in west and north-east Scotland. *Journal of Zoology* (Lond.) 200: 283–289.


Lozano, J. (2008) - Ecología del Gato montés (Felis silvestris) y su relación con el Conejo de monte (Oryctolagus cuniculus). Tesis doctoral, Facultad de Biología Universidad Complutense de Madrid.


Rosalino, L.M., Macdonald, D.W., Santos-Reis, M., (2005) - Resource dispersion and badger population density in Mediterranean woodlands: is food, water or geology the limiting factor? *Oikos* 110, 441-452


Saab, V. (1999) - Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis.


Scottish Natural Heritage (SNH) (2007) - A Five Year Species Action Framework: Making a difference for Scotland's species. 84. Scottish Natural Heritage.


Study area

Wildcat distribution, at two different spatial levels, was assessed by implementing a study simultaneously conducted at a broad/national and fine/local scale. Large scale analysis was carried out within the Highlands and Grampian regions of Scotland. The local scale study was conducted at three different areas (Kinveacky, Gartly forest and Black Isle) located in Inverness-shire, Aberdeen-shire and Ross-shire respectively, in the North of Scotland (Figure 1).

The Highlands and Grampian regions are located in the North and Northwest region of Scotland and are surrounded by the Atlantic Ocean at North and West and by the North Sea in the East (Figure 1).

Due to the geographic location of both regions, climate is predominantly cold temperate and influenced by the maritime West coast (Met Office 2011). Over the Highlands, the mean annual temperature can vary between 8.5ºC in low lands and a considerable lower temperatures at higher altitudes (e.g. Ben Nevis, the highest point in Scotland with 1344m, has a mean annual temperature around 0ºC). The Grampian region is slightly warmer, with a mean annual temperature varying between 6ºC, at higher grounds, and 9ºC at low altitudes. During the winter extreme temperatures (max. recorded -27.2ºC) can occur in both regions of Scotland. January and February are usually the coldest months in both areas (minimum daily temperature varying from 2ºC to -1ºC, depending on the altitude). Warmest temperatures are found in July and August, were maximum daily temperature can range from 20ºC, at low altitudes, to 16ºC at higher plains (Met Office 2011). As a result of the Atlantic influence, precipitation is sharper during winter months. Nonetheless, it can occur during every season of the year. While over the Highlands an average annual rainfall higher than 1700mm is registered, in the Grampian region ranges between 500-1700mm (Met Office 2011). The occurrence of snowfall is usually restricted to the period between November and April, although occasional brief falls can occur in upland areas in October and May. Snowfall period can vary between 40 to 100 days per year (Met Office 2011).

The Highlands comprise a large aggregate of different landscapes, as a result of the different land management and animal grazing schemes. Original habitats such as pine (Pinus sp.), birch (Betula sp.) and oak (Quercus sp.) woods and lower grasslands patches, are now considerably fragmented and reduced to small portions of their original range (Habron 1998; Quine et al. 2002). 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). Meanwhile, human presence in Scotland and particularly across the Highlands, is very low (0.08 person ha⁻¹) when compared to other parts of the UK or other European countries. Such low density is the result of the forced historical population exodus known as the clearances to the coastal large cities (Devine 1983; SCROL 2011).
The West and East areas of northern Scotland show dissimilar landscape. The West is particularly dominated by mountains with numerous glens and open heather/grassland moorlands. On the other hand, the East is smoother in terms of topography, being mainly composed of arable and pasture fields, used considerably for agriculture and livestock production (SNH 2002). Improved, heavily grazed land and unimproved grasslands are important and extensive habitats in Scotland, and a main support to livestock herds, in particular, cattle and sheep. Heather moorlands composed of Calluna vulgaris are widespread throughout Scotland and can occur associated with other types of land covers such as scrub (namely broom Cytisus scoparius and gorse Ulex europaeus) or woodland patches. In both regions original woodlands are mainly composed of the common pine (Pinus sylvestris) and birch forests (Betula spp.). Oak woodlands (Quercus spp.) are also present but their distribution is sparser. Both birch and oak woodlands can occur interspersed within pine forest areas (MLURI, 1993). Lochs, rivers, streams and freshwater reservoirs are commonly found and widespread through this region (Harrington et al. 2010). Timber extraction plays an important economic role in the region and forested areas, particularly Norway spruce, Picea abies, whose production stands are widely explored. This management results in a mix of young and mature forested areas. Therefore the Highlands are presently a complex mosaic of patches with different uses and purposes. The numerous field margins and hedgerows created by that heterogeneous spatial structure are an essential resource for wildlife (SNH 2011).

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. Hunting is also an important activity in this region, focused mainly on wild rabbits Oryctolagus cuniculus, grouse shooting Lagopus lagopus and deer stalking (namely roe deer Capreolus capreolus and red deer Cervus elaphus). Additionally, the introduced pheasant is reared in high numbers as a game species.

To provide ideal conditions for red grouse, an important game species in this region, moorland patches are frequently burned to create a mosaic of young and mature plants that respectively supply food and shelter for this species. Moreover, predator control is carried out to reduce the losses of game species by minimizing the predation impact on these birds. Other wild species management is also implemented. Although game managed and a popular hunting target in the study area, deer populations are a highly abundant (Clutton-Brock et al. 2004).

The region is an essential stronghold of the UK biodiversity since it hosts about 75% (455 species) of the UK priority species that can be found in Scotland (Highland Bap, 2010). Due to its role for the protection of biodiversity, the region encompasses the Cairngorms National Park and 21 Natural Reserves (NNRs) (SNNR 2011). Scotland is determined to restore original ecosystems and the most recent result of such effort is the newly introduced beaver Castor fiber population in Knapdale Forest, central Scotland. The geographical location allows Scotland and the Highlands to have a highly diversified bird community, in particular, migratory seabirds. Nevertheless
inland woodland areas are also an important resource for other bird species, such as the reintroduced Capercaillie *Tetrao urogallus* and the endemic Scottish crossbill *Loxia scotica*. Also the upland regions provide ideal habitat for golden eagles *Aquila chrysaetos*. Carnivore community is composed of nine species (weasel *Mustela nivalis*, stoat *Mustela erminea*, polecat *Mustela putorius*, American mink *Neovison vison*, pine marten *Martes martes*, otter *Lutra lutra*, badger *Meles meles*, red fox *Vulpes vulpes* and wildcat *Felis silvestris silvestris*) (Arnold 1993; NBN 2011). In this region the small and medium sized mammals community also include 7 small rodent species (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 *Oryctolagus cuniculus*, brown *Lepus europaeus* and mountain hare *Lepus timidus*).

**Study areas used for the local scale study**

The local scale study was conducted in three different areas (Kinveacky and Black Isle – Highlands region and Gartly forest – Grampian region) with approximately 32km² each (Figure 1).

Kinveachy site (57°16'29"N, 3°50'21"W) is located in the Seafield and Strathspey Estates in Inverness-shire, within the Northwest area of the Cairngorms National Park. The Estate also includes 57.6km² of land classified as Sites of Special Scientific Interest (SSSI). The region is primarily used for nature tourism, deer stalking and grouse shooting. As a result of these activities and since some parts of the Estate are recognized as key sites for Capercaillie conservation, predator control is carried out (Seafield & Strathspey Estates, 2001). The study site is mainly covered by large patches of pine forest (41%), mixed with numerous and smaller patches of heather moorland (39%). The area also presents significant grassland areas (15%), occasionally surrounded by broad-leaved woodland (5%). Residual areas of bog and inland bare ground can occur. With an average altitude of 340m, the region is crossed by the primary road A9 and is located 3.5 kilometres from Carrbridge village, a settlement with 700 inhabitants (SCROL 2011).

Gartly forest site (57°21'37"N, 2°45'53"W) is located in Aberdeenshire and is mainly classified as Forestry Commission land, being particularly managed for timber extraction. Thus, the site is mostly composed by a mosaic of felled and non-felled patches of Norwegian spruce (34%). 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. Broad-leaved woodlands are barely represented within this site (3%). Relatively to the main human settlements, Gartly is located 8km south of Huntly town, a city with 4.400 inhabitants (SCROL 2011).
The Black Isle is a small peninsula located in Ross-shire, Northeast Inverness. The peninsula is mainly used for agricultural, with large arable fields. The study site (57°36'40"N, 4°13'24"W) lays in the Black Isle forest that, as with Gartly, is Forestry Commission land, mainly used for Norwegian spruce plantation (45%). Several pasture (22%) and arable fields (17%) surround the forested land. Dwarf shrub areas (11%) occur mixed within the coniferous plantation. Broad-leaved areas are scarce within the site (5%). The village of Cullicudden and the locality of Fortrose (1.100 inhabitants) are the closest main human aggregates, located at 3km distance.

Gartly and Black Isle forests are restricted to visitors in motorized vehicles and only used for trekking and dog walking.
Figure 1 – Location of the study areas within the Highlands (A) and Grampian (B) regions of Scotland, and spatial structure of the main land cover types in each study areas used for the macro-scale (Highlands and Grampian regions of Scotland) and local-scale (Kinveachy, Gartly and Black Isle) analysis.
References


NBN (2011) - National Biodiversity Network: Species records at 10km or better that fall within or overlap Highland (Administrative) <http://data.nbn.org.uk/> Downloaded on 06 May 2011.


CHAPTER 3 – BROAD SCALE DETERMINANTS OF WILD-CAT DISTRIBUTION IN SCOTLAND
Wildcat distribution in Scotland: food really matters

André P. Silva¹, Kerry Kilshaw², Luís M. Rosalino¹

² Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanti-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire OX13 5QL, UK

Abstract

European wildcat Felis silvestris silvestris (Schreber, 1775) populations are suffering considerable threats and conservation actions are vital. In Scotland the design of Special Areas of Wildcat Conservation (SAWC) was recommended as a priority conservation action, however few studies have addressed wildcat ecological requirements. We examined data from the recent Scottish wildcat survey (2006-2008) and National Biodiversity Network (NBN) Gateway to study wildcat ecological determinants on a broad scale. Presence and absence data from 71 sampling units (10x10km) were used to generate models capable of explaining wildcat occurrence in Scotland. Models were built based on four pre-established hypotheses using Generalized Linear Mixed Models (GLMM-Logit). We used Receiver Operating Characteristics (ROC) curves to validate the final average model which included the variables present within the confidence set of models created according our hypotheses. Presence of European rabbit and higher rodent diversity contributed positively to wildcat presence. Larger grassland covered areas were also positively associated with wildcats. The species was negatively associated with heather moorland and sampling units with few numbers of grassland patches. Secondary watercourses and elevation range also contributed negatively to wildcat presence. Forested areas and human disturbance factors were not associated with the best explanatory models. These results indicate that the species could benefit from heterogeneity within the landscape matrix reinforcing recent descriptions of the wildcat as non-strictly forest species, an idea that has also arisen in other regions of the European wildcats’ range. As a result we concluded that less mountainous areas with a heterogeneous environment constituted by grassland and woodland areas and where rabbits and a higher diversity of small mammals are available might be key habitats for wildcats and consequently should be considered priority areas to be designated as SAWS to enhance wildcat conservation in Scotland.

Keywords: Wildcat Felis silvestris silvestris, Scotland, broad scale, ecological determinants, wildcat conservation
Introduction

The prediction of species distribution is a key factor in conservation biology, particularly for species difficult to survey and highly threatened (Rushton et al. 2004) such as carnivores. As top predators, carnivores are common targets for conservation action (Gittleman et al. 2001; Carroll et al. 2001). They are threatened by a whole range of factors, many of them anthropogenic, which can result in direct (habitat loss) and indirect (non-natural fluctuations in prey densities) landscape changes. Understanding the ecological requirements of a species can be useful in predicting how these landscape changes can affect population survival and distribution. Spatial modelling is a tool commonly used to assess the environmental determinants affecting species spatial distribution and can be useful to design conservation strategies (Macdonald and Rushton 2003; Rushton et al. 2004) for species such as carnivores where data may be scarce or difficult to obtain.

The European wildcat is found in Africa, Asia and Europe and is considered one of the most numerous and widespread small felid species (Kitchener & Rees, 2009). Despite being classified as Least Concern by the IUCN (Driscoll & Nowell 2009), regional populations of the European wildcat Felis silvestris silvestris (Schreber, 1775) are facing considerable threats and some have already become locally extinct (Nowell & Jackson 1996). In Scotland, surveys show that the wildcat has declined (Easterbee et al. 1991; Balharry & Daniels 1998; Battersby 2005; Davis & Gray 2010) and recent estimates indicate the possibility of a critically endangered population with only 400 individuals with typical wildcat pelage pattern remaining (Kitchener et al. 2005). The population has suffered mainly from habitat loss and active persecution (McOrist & Kitchener 1994), but is currently most affected by hybridisation with the domestic cat Felis catus (McOrist & Kitchener 1994; Beaumont et al. 2001; Daniels et al. 2001). The wildcat is currently protected within the UK under the Schedules 5 and 6 of the Wildlife and Countryside Act, 1981 (as amended in 1988) and it was also added to the revised UK BAP list of Priority Species (Macdonald & Tattersal 2004) and the Scottish Natural Heritage’s Five Year Species Action Plan, as a species for conservation action (SNH 2007). At a European level is listed on Annex IV of the European Habitats Directive (Kitchener et al. 2005).

Conservations strategies for this species were highlighted in the recent action plan (Macdonald et al. 2004), one of which was the classification of Special Areas of Wildcat Conservation (SAWCs). Application of such strategies relies on a good knowledge of species-environment interactions. However, only a few studies to date have focused on the ecological requirements of this species in Scotland (e.g. Corbett 1979; Scott et al. 1993; Daniels et al. 2001). A similar situation exists in Continental Europe with only a few published studies on wildcat ecological requirements existing (e.g. Wittmer 2001, Lozano et al. 2003; Klar et al. 2008; Jerosch et al. 2010). The majority of available information derives from fine scale ap-
proaches, either in terms of grain or extent. Coarse scales studies (e.g. Ferreira et al. 2010) are scarce throughout Europe despite the importance of looking at the determinants that constrain species presence at multiple scales (Wiens 1989) in order to understand how individuals use the landscape.

Factors affecting wildcat distribution appear to vary throughout the species range, but populations are predominantly affected by food, habitat, human induced disturbance or extreme environmental conditions (Stahl & Leger, 1992). For example, European Wildcat distribution, in general, is known to be coupled with prey species distribution, in particular, distribution of the European rabbit Oryctolagus cuniculus (Corbett 1979, Lozano et al. 2003, Malo et al. 2004). This is particularly apparent in Southern Europe, where rabbits constitute the largest proportion of the wildcats’ diet (e.g. Gil-Sánchez 1998). Although rabbits are a preferred prey species across the wildcats range, even in higher latitudes, wildcats can persist in areas where rabbits are scarce or absent by preying on other species, such as small mammals or birds (e.g. Scott et al., 1993; Lozano et al. 2006). Studies from Scotland have shown that the wildcat uses a wide range of different habitats, such as coniferous and broad-leaved woodlands, grassland and scrub patches (Corbett 1979; Daniels et al. 1998; Scott 1993). In Germany wildcat presence appears to be limited to areas in close proximity to forest, forest ecotones and meadows (Klar et al. 2008), whereas in Mediterranean areas Lozano et al. (2003) highlighted the importance of scrub areas. The use of these protective covered areas is believed to be related to shelter (Wittmer 2001; Klar et al. 2008). Since the available information show that this species is a habitat generalist (with regional adaptation to the landscape – e.g. Klar et al. 2008), individuals might benefit from a certain degree of heterogeneity in the landscape matrix. For instance, Klar et al. (2008) showed that edges between forest and watercourses or meadows influence wildcat presence and individuals avoided human structures such as roads (Klar et al. 2008). However, Scott et al. (1993), in Scotland, mentioned movements of individuals near human settlements and Jerosch et al. (2010) found that wildcats might tolerate disturbance through habituation. It is important to clarify the relationship between wildcats and areas of high human influenced areas, since these regions may act as source of wildcat hybridization, due to the contact with domestic cats (Nowell & Jackson 1996; Daniels et al. 1998; Yamaguchi et al. 2004; O’Brien et al. 2009). This factor is highly relevant, since hybridization is considered one of the main threats to wildcat conservation in Europe (Nowell & Jackson 1996; Oliveira et al., 2008).

Climatic features were also previously linked to wildcat presence, with studies showing that wildcats may avoid using areas with deep snow (Mermod & Liberk 2002). However, in Scotland, areas with lower temperature were associated with wild-living cats showing the typical wild morphological pattern (Daniels et al. 1998).

The aim of this study was to identify the environmental factors currently affecting wildcat distribution in Scotland at a broad scale, which might be useful in identifying priority areas
for the species long-term persistence. Since a significant part of available information on the ecological requirements for this species is derived from several studies across Europe (e.g. Klar et al. 2008; Monterroso et al. 2009), and that even within Scotland the landscape varies significantly from east to west, we did not exclude, in advance, factors identified as important to wildcat presence elsewhere. Therefore, to fulfil our aim we tested the following hypotheses: 1) wildcat presence depends on food resources; 2) distribution is affected by landcover features since those can provide important direct (e.g. shelter) and indirect (e.g. prey presence) resources; 3) human disturbance negatively affects wildcat occurrence, with wildcats avoiding humanized areas; and 4) wildcat presence is dependent on the interaction of several factors related with food, land cover characteristics, topography, climate and anthropogenic disturbance.

Methods

Study area

The study covered 7200km$^2$ in the northern and north-eastern part of Scotland including the Highland and Grampian regions (Figure 1). Climate is predominantly cold temperate and influenced by maritime West coast. January and February are the coldest months with mean daily minimum temperatures varying from about 2°C on west-facing coasts to less than -1 °C over the higher ground. Extreme minimum temperatures can occur during winter (e.g. -27.2 °C). July and August are the warmest months with mean daily maximum temperatures at low levels around 19 °C and less than 16 °C over the higher grounds. Rainfall is significantly higher (annual rainfall of at least 1700 mm) on the West comparing to the Eastern regions (700mm). Snowfall can occur and be persistent up to 100 days between November and April (http://www.metoffice.gov.uk/climate/uk/ns/ accessed on 06 May 2011).

Due to the climatic differences, the landscape composition varies between the West and East parts of the study area. The West region is more mountainous and humid and characterized by the presence of heather moorland/peatland mosaics. Inversely, in the East the landscape is dominated by lower mountain reliefs, commonly used for agriculture and pastures (MLURI, 1993). Woodland areas represent between 9 to 13% of land area (MLURI, 1993) and are present throughout both regions, being mainly composed of Scots pine *Pinus sylvestris* and birch forests (*Betula* spp.), although oak woodlands (*Quercus* spp.) can also occur (SNH 2011). Timber extraction is the main economic activity in woodland areas and Norway spruce *Picea abies* is extracted. These woodland areas occur within a matrix of open arable and grassland areas at low altitude, being replaced by heather (*Calluna* spp. and *Erica* spp.) and grass moorlands at a higher elevation. Scrub areas, particularly, common broom *Cytisus scoparius* and common gorse *Ulex europaeus* can be found interspersed with grassland habitats. Numerous rivers, small watercourses and lochs are distributed across the country. Human presence in Scotland, and partic-
ularly in the highlands, is low with an average of 0.08 person ha⁻¹ (Devine 1983; SCROL 2011). Road network length is low (<730km/1000km²) and no motorways are present within the study area (Scottish Transport E-statistics, 2008). The region encompasses the Cairngorms National Park which is considered a primary area for UK biodiversity conservation (Highland BAP 2010). The area’s carnivore guild encompasses 9 species (weasel Mustela nivalis, stoat Mustela erminea, polecat Mustela putorius, American mink Neovison vison, pine marten Martes martes, otter Lutra lutra, badger Meles meles, red fox Vulpes vulpes and wildcat Felis silvestris silvestris), supported, among other trophic resources, by the presence of 3 lagomorphs (European rabbit Oryctolagus cuniculus, brown-hare Lepus europaeus, mountain-hare Lepus timidus), and 13 small mammals species (8 rodent and 5 insectivorous), including the bank vole Myodes glareolus, field vole Microtus agrestis, European water vole Arvicola amphibius and the wood mouse Apodemus sylvaticus (Arnold 1993).

Figure 1 – Study area location. Sampling units (10x10km), showing wildcat records and pseudo-absences, are presented together with the main habitats within the region
Wildcat data

Wildcat distribution on a broad scale was evaluated using a sampling square unit (SU) of 10x10km, corresponding to the 10km squares of the British National Grid system. Data for the response variable were collected on a binary basis taking values of 0 (absence of the focal species) and 1 (presence of the focal species). Presence data was extracted from the latest Scottish wildcat survey carried out by Scottish Natural Heritage (SNH) between 2006 and 2008 (Davis & Gray 2010) and the National Biodiversity Network (NBN) gateway (http://data.nbn.org.uk/). Due to the species morphological similarity with the domestic cat, possible misidentifications by observers, especially in field conditions, may occur (Davies & Gray 2010). Therefore only records classified as “probable wildcat” (the finest classification in this survey, corresponding to cats with the highest probability of being true wildcats) in the SNH dataset were taken into consideration. All these accounts were from experienced and trusted observers such as gamekeepers and landowners and assessed through interviews. Also during this survey and when possible (e.g. when photographic records were available) the records were assessed using the pelage classification method developed by Kitchener et al. (2005). Data from the NBN dataset were derived from several environmental organizations databases such as the Biological Record Centre (BRC) and the National Trust for Scotland (NTS). In both datasets records were considered between the years of 1989-2010 and were only used when at least the source and the date of the record was available. Additionally, wildcat presence’s squares were only considered if data on prey availability were simultaneously accessible. Moreover, if prey records dated several years or decades before the considered period, those squares were also excluded. This conservative approach intended to minimize the bias associated with temporal and spatial mismatch of predator/prey data. All records used were georeferenced. The study area for the current analysis was defined as the 100km squares of the British National Grid encompassing the positive wildcats records used.

Once presence data was restricted to particular areas of the highlands, and to avoid selecting pseudo-absence data (we considered pseudo-absence because although no detection was registered, it is impossible to be completely sure that the species was absent) from significantly different landscapes (e.g. the Scottish lowlands), we randomly selected forty 10x10km squares where the wildcat was not detected within the study area.

Explanatory variables

According to the hypotheses previously considered four different types of ecological descriptors were tested to explain wildcat distribution - food availability, land cover characteristics, human disturbance and topographic and climatic features (Table 1). Descriptors were se-
lected by reviewing the available information on the spatial and ecological requirements of the species (Appendix 1).

To assess the influence of food availability, and due to the lack of reliable data on every possible wildcat prey in Scotland, we selected, based on bibliographic information available, five key prey species previously identified in other studies as influencing wildcat presence or diet across the wildcat distribution range. The species selected were: one lagomorph (European rabbit), and four rodents’ species (bank vole, field vole, European water vole and the wood mouse). Presence/pseudo-absence data was collected for each sampling unit for the period between 1980 and 2009 (to encompass the time period of wildcat data compilation). Data were clustered into two main categories. Rabbits (Rb_p) were separated from small mammal species as they are known to form a larger percentage of the wildcats diet and therefore may have a distinct influence on the predator’s distribution, when compared to the small mammal species selected (Corbett 1979, Biró et al. 2005, Lozano et al. 2006). Thus, while rabbit data was transformed into presence/pseudo-absence, rodents’ data were grouped in a single variable (Rod_div) since we did not find any bibliographic evidence of particular prey selection towards these species. Species occurrence data were collected using the National Biodiversity Network gateway. Only georeferenced and dated data were considered.

We used several variables to describe the structure of the four main land covers: coniferous woodland, mixed/broad-leaved forest, grassland and heath moorland. Thus, within each 100km² sampling unit (SU) we assessed the proportion of area covered by each land cover type (Confor_a, Mixfor_a, Grass_a, Heather_a). Since the study region encompasses numerous inland water areas, this proportion was calculated in relation to the total land area of each sampling unit. Number of patches per landcover (Confor_p, Mixfor_p, Grass_p, Heather_p) and the mean patch size (Confor_pma, Mixfor_pma, Grass_pma, Heather_pma) were also assessed. Habitat heterogeneity of each SU was estimated using the number of habitat classes within each 10x10km squares (N_hab) as a surrogate. Land cover data were obtained from the 1990 and 2000 Land Cover Maps (Fuller et al.1994; Fuller et al. 2002) downloaded from the Centre for Ecology & Hydrology (CEH) gateway (https://gateway.ceh.ac.uk/, accessed on June 2011). Both maps are parcel-based thematic classification of satellite image data from the Landsat sensor covering the entire United Kingdom with a 1km resolution, where each pixel provides data on the dominant land cover. Since our positive records dated from a considerable period of time and to avoid possible discrepancies associated with describing the landscape based on the characteristic of a landcover map produced in a very different time period, we used land cover maps from different time series (LCM 1990 and LCM 2000). This approach allows us to have the best possible approximation to landscape reality of each time period. Therefore to characterize the landscape within the sampling units, we used the LCM 1990 for records before year 2000 and
the LCM2000 for records after that year. Due to a high number of classes considered in these land cover maps, we clustered some to reduce complexity. Thus, of the 25 habitats subclasses available, we merged: categories “improved”, “neutral”, “setaside”, “calcareous” and “acid grass” into a main category corresponding to “grassland covered areas”; subclasses “dense dwarf shrub heath” and “open dwarf shrub heath” into a one main class labelled “heath moorland areas”. Areas, patches number and mean dimensions per habitat class were estimated using ArcGIS 9.3 (ESRI, Redlands, California).

Another component of the landscape that has often been identified as important for carnivore survival in human-shaped environments are riparian woodlands (Virgós, 2001). This landscape structure can play an important function on the dispersion and persistence of carnivores’ species and is often considered for wildcat conservation (Klar et al. 2008). Hence, we assessed the influence of these structures on the species distribution (Water_main and Water_sec). Watercourses with more than 8 meters at their widest point (e.g. primary rivers and canals) were classified as Water_main, whereas watercourses with less than 8 meters wide at widest point, such as secondary and minor rivers, were considered as Water_sec. Data for these variables was acquired using the Ordnance Survey (OS) Strategi map, a small-scale (1:250000) and digital vector map, developed for regional analysis, that contains, among other layers, the different types of rivers within the UK. The map was downloaded from the OS open data website (https://www.ordnancesurvey.co.uk/opendatadownload/products.html, accessed on May 2011).

Human disturbance has been identified by some authors as an important factor constraining wildcat distribution at different scales (Klar et al. 2008, Ferreira et al. 2010). Consequently, we decided to evaluate the effect of urban areas (Urb_a, Urb_p and Urb_pma) and roads (Rds_main and Rds_sec) on wildcat regional distribution. Urban settlements and roads location was extracted from the same Ordnance Survey (OS) Strategi map used in the landscape features descriptor. Due to possible differential ecological effects of road types, layers corresponding to primary and A roads in the Strategi map were grouped as main roads (Rds_main), representing mainly double carriageway roads. B and minor roads were clustered in secondary roads (Rds_sec), corresponding to single carriageway roads. Urban areas, number of patches and its dimension and roads extent for each 10x10km square were calculated using software ArcGIS 9.3. In the Human disturbance factors’ group, the presence of sporting estates (Sport_est) within the sampling units was also included. Sporting estates are used in Scotland for deer and game bird hunting and cover large areas of the study site. Most sporting estates have carried out, and still carry out, predator control as part of their regular activities, which has in the past resulted in intense persecution of the wildcat in these areas. Sporting estates locations were assessed using the sporting estates map produced by the project “Who Owns Scotland” (http://whoownsscotland.org.uk/).
Environmental temperature may also affect the presence of wildcats, since individuals morphologically more associated with wild or less hybridized cats may be more adapted to colder climates (Daniels et al. 1998). For example, wildcats are thought to have a larger body size and denser coats, which enables them to survive under extreme climate conditions (Daniels et al. 1998). Elevation range was also evaluated since areas with higher range of altitudes may offer the possibility of seasonal movements, benefiting wildcat persistence during different times of the year (e.g. use of higher areas as refuge during the breeding season and use of lowlands during winter harsh conditions [Mermod & Liberek 2002, Ferreira et al. 2010]). This factor can be relevant, namely in Scotland, where landscape slope can change drastically within a short distance. Topographic and climatic data from current conditions (1950-2000) were obtained from the WorldClim database (Version 1.4, http://www.worldclim.org/current) (Hijmans et al. 2005). This database comprises a set of climate grids with a spatial resolution of 1 km² obtained from monthly temperature and precipitation values from 4,000 worldwide climate stations. We calculated the mean annual temperature (Mean_tc) and elevation range (Elev_range) for each of the 70 sample units. Annual mean temperature was calculated by averaging the mean monthly temperatures within each square. Elevation range was estimated through the variation between maximum and minimum altitude within sampling units. Calculations were performed using the Spatial Analyst extension in software ArcGIS 9.3.

**Statistical analyses**

One of the most important bias in spatially explicit data is associated with spatial autocorrelation, i.e. violation of the assumption that the observations in each sample are independent of one another. Thus, we evaluated data spatial autocorrelation by using Moran’s I index, to test if geographical location of sampling sites was influencing the response variable. In order to avoid multicollinearity between explanatory variables we tested pair-wise correlations using Spearman correlation (Zuur et al. 2007) and dropped one of the variable of each pair highly correlated (r>0.7) (Hosmer & Lemeshow 2000). Excluded variables were selected based on their lower correlation coefficient with the response variable and their ecological meaning.

To assess each descriptor influence in explaining wildcat’s distribution, we used a Generalised Linear Mixed Models (GLMM) approach (Zuur et al. 2009; Bolker et al. 2009), incorporating spatial positioning of sampling units as random effects (since autocorrelation was significant – see results below). We ran several different sets of models (Appendix 2), built according our defined hypothesis. Within each set we tested the main effect of each variable and all variables combinations between them.

The high number of variables within the land cover descriptor (Table 1), was reduced using a Principal Component Analyses (PCA), and the main independent principal components
were used to describe variables within this descriptor. These PCA scores were then included as predictors in the following GLMM procedures (Rushton et al. 2004).

Akaike Information Criterion for reduced sample sets (AICc) was used to rank the obtained models and all models with ΔAICc<2 (i.e., ΔAICc – difference between the AICc of a model and the lowest AICc) were considered as plausible models to best fit the observed data. The Akaike weight was calculated to assess the probability of a model being the best model (Burnham & Anderson 2002). Interaction between descriptors (fourth hypothesis) was evaluated using the variables within the model with smaller AICc and the most frequent variable in all best models of each remaining descriptor. This procedure was used instead of incorporating all variables present in the top model within each descriptor to avoid overparameterization (Grueber et al. 2011). Model averaging was performed to calculate average parameter estimates using models within the confidence set (ΔAICc<2) as suggested by Burnham & Anderson (2002). These estimates were then used to obtain predicted values using the logistic regression model.

Due to the lack of an independent dataset to test the model, validation was carried out using the predicted values obtained with parameters’ average estimates. We used the Receiver Operating Characteristics (ROC) curves, obtained by plotting true positive proportion of classifications (sensitivity values; 1—false-negative rate) on the y-axis against the false positive proportion (1—specificity [true negative proportion]) values on the x-axis (Fielding & Bell 1997; Pearce & Ferrier 2000). The Area Under this Curve (AUC) indicates overall ability of the model to accurately predict the data used to create it (Pearce & Ferrier 2000). AUC values of 0.5–0.7 usually indicate low accuracy (i.e., no better than a null model), values of 0.7–0.9 indicate useful applications and values >0.9 indicate high accuracy (with AUC=1.0 equal to perfect accuracy; Swets 1988; Pearce & Ferrier 2000).

All statistical analyses were implemented in R statistical software V. 2.13.1 (R Development Core Team 2005, Vienna). Morans’I test was carried out using “ape” package (Paradis et al. 2004) and PCA were carried out using “labdsv” package (Roberts 2010). GLMMs and model averaging were produced using “lme4” and “MuMIn” packages (Bates et al. 2011; Bolker et al. 2009).
Table 1 – Detailed description of the explanatory variables (including the minimum and maximum values registered).

<table>
<thead>
<tr>
<th>Descriptor</th>
<th>Variable (code)</th>
<th>Description</th>
<th>Data Range (min - max)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Food availability</strong></td>
<td>Rabbit presence (Rb_p)</td>
<td>Presence/absence of rabbits</td>
<td>(0/1)</td>
</tr>
<tr>
<td></td>
<td>Rodents diversity (Rod_div)</td>
<td>Alpha (α) diversity (5 key rodents species selected)</td>
<td>(0-4)</td>
</tr>
<tr>
<td></td>
<td>Coniferous area (Confor_a)</td>
<td>Area of all coniferous patches per land area (km²)</td>
<td>(0-0.49)</td>
</tr>
<tr>
<td></td>
<td>No. of coniferous patches (Confor_p)</td>
<td>Number of coniferous woodland patches per land area (no./km²)</td>
<td>(0-0.10)</td>
</tr>
<tr>
<td></td>
<td>Coniferous patches size (Confor_pma)</td>
<td>Mean area of coniferous woodland patches (km²)</td>
<td>(0-0.33)</td>
</tr>
<tr>
<td></td>
<td>Mixed forest area (Mixfor_a)</td>
<td>Area of all mixed forest patches per land area (km²)</td>
<td>(0-0.08)</td>
</tr>
<tr>
<td></td>
<td>No. of mixed forest patches (Mixfor_p)</td>
<td>Number of mixed forest patches per land area (no./km²)</td>
<td>(0-0.06)</td>
</tr>
<tr>
<td></td>
<td>Mixed forest patches size (Mixfor_pma)</td>
<td>Mean area of mixed forest patches (km²)</td>
<td>(0-4)</td>
</tr>
<tr>
<td></td>
<td>Heather moorland area (Heath_a)</td>
<td>Area of all heather moorland patches per land area in (km²)</td>
<td>(0-0.98)</td>
</tr>
<tr>
<td></td>
<td>No. of heather moorland patches (Heath_p)</td>
<td>Number of heather moorland patches per land area (no./km²)</td>
<td>(0-0.13)</td>
</tr>
<tr>
<td></td>
<td>Heather moorland patches size (Heath_pma)</td>
<td>Mean area of heather moorland patches (km²)</td>
<td>(0-0.97)</td>
</tr>
<tr>
<td></td>
<td>Grassland area (Grass_a)</td>
<td>Area of all grassland patches per land area (km²)</td>
<td>(0-0.92)</td>
</tr>
<tr>
<td></td>
<td>No. of grassland patches (Grass_p)</td>
<td>Number of grassland patches per land area (no./km²)</td>
<td>(0-0.13)</td>
</tr>
<tr>
<td></td>
<td>Size of grassland patches (Grass_pma)</td>
<td>Mean area of grassland patches (km²)</td>
<td>(0-0.87)</td>
</tr>
<tr>
<td></td>
<td>Habitat diversity (N_hab)</td>
<td>No. of habitat classes</td>
<td>(2-9)</td>
</tr>
<tr>
<td></td>
<td>Main watercourses (Water_main)</td>
<td>Extent of canals and main rivers per land area (km)</td>
<td>(0-0.19)</td>
</tr>
<tr>
<td></td>
<td>Secondary watercourses (Water_sec)</td>
<td>Extent of secondary and minor rivers per land area (km)</td>
<td>(0.35-1.29)</td>
</tr>
<tr>
<td><strong>Human disturbance</strong></td>
<td>Urban patches area (Urb_a)</td>
<td>Mean area of urban settlements (km²)</td>
<td>(0-0.08)</td>
</tr>
<tr>
<td></td>
<td>No. of urban patches (Urb_p)</td>
<td>Number of urban patches per land area (no./km²)</td>
<td>(0-0.31)</td>
</tr>
<tr>
<td></td>
<td>Size of urban settlements (Urb_pma)</td>
<td>Sum of all urban patches areas per land area (km²)</td>
<td>(0-0.80)</td>
</tr>
<tr>
<td></td>
<td>Main roads (Rds_main)</td>
<td>Extent of primary and non-primary A roads per land area (km)</td>
<td>(0-0.47)</td>
</tr>
<tr>
<td></td>
<td>Secondary roads (Rds_sec)</td>
<td>Extent of B and minor roads per land area (km)</td>
<td>(0-2.22)</td>
</tr>
<tr>
<td></td>
<td>Sporting Estates (Sport_est)</td>
<td>Presence of sporting estates (hunting areas)</td>
<td>(0/1)</td>
</tr>
<tr>
<td><strong>Topographic and climatic features</strong></td>
<td>Mean annual temperature (Mean_t)</td>
<td>Mean annual temperature (ºC)</td>
<td>(3.88-8.72)</td>
</tr>
<tr>
<td></td>
<td>Elevation Range (Elev_range)</td>
<td>Difference between max. and min. elevation (m)</td>
<td>(91-1235)</td>
</tr>
</tbody>
</table>
Results

Aggregation and spatial autocorrelation was detected among geographic locations of sampling units (Moran’s I = 0.084, z-Normal I= -0.015; p<0.001). Of the initial set of 25 explanatory variables we excluded 8 variables (Confor_pma, Mixfor_p, Mixfor_pma, Heath_pma, Grass_pma, Urb_p, Urb_pma, Rds_sec) within landscape and disturbance descriptors, due to high correlation with other variables within the set. The first three principal components of the PCA performed to resume information contained in the landscape descriptors, explained 56% of variance. The first component (PC1) represents a gradient between areas with large extensions of heather moorland habitat (positive scores) and sampling units with high number of different habitats and associated with the presence of coniferous and mixed woodland and grassland patches (negative scores) (Table 2). The second axis (PC2) represents a gradient between regions with large areas of grassland habitat (negative scores) and areas with higher number of grassland patches and heather moorland area associated with presence of secondary watercourses (positive scores) (Table 2). Finally, the third component (PC3) differentiates areas with high number of dwarf shrub patches and secondary water courses (only significant scores) (Table 2).

Forty-eight models were built to predict wildcat distribution and test the four considered hypotheses. The first set of models produced was based on the combination of predictors within each variable’s category. Among those models, the one that better performed in explaining wildcat presence in each SU was a food related model incorporating rabbit presence and rodent diversity (Table 3). This model was more robust than those including each variable separately (Appendix 2). Within the other variables’ categories, some predictors were always included in the best models for each category (i.e. those with ∆AICc smaller than 2). Thus, PC2 (landscape), sporting estates (disturbance), elevation range and annual mean temperature (Topography and climate), were used to produce hybrid models, which included the interaction between food model’s variables and those predictors (PC2, Sport_est, Elev_range and Mean_tc). From this new set of models only the ones incorporating PC2 and Elev_range revealed a similar discrimination power, i.e. food, food+land cover food+elevation models’ ∆AICc was lower than 2 not allowing selection of a single best model (Burnham & Anderson, 2002). These three models compose the model confidence set.

Model-averaged parameter estimates, calculated in function of AIC weights of the three best models, revealed that rabbit presence, a higher number of rodent species and larger areas of grassland (PCA2 negative scores) had a positive effect on the wildcat presence. Inversely a smaller diversity of rodents, more steeper areas (higher elevation range) and areas with higher number of grassland patches and heather moorland, associated with presence of secondary watercourses (PCA2 positive scores), contributed negatively to wildcat presence.
Model validation using the model built under logistic regression and incorporating model-averaged parameter estimates, revealed high accuracy when evaluated using Receiving Operating Characteristics curve (AUC=0.949 ± 0.029). This result indicates similar values between observed and predicted wildcat presence using this model. Both sensitivity (capacity to correctly predict species presence - 93.5%) and specificity (capacity to correctly predict species absence - 92.5%) showed high values.

Table 2 – Loadings and explained variance of the three first axis of the principal component analysis (PCA) performed to resume information within land cover descriptor.

<table>
<thead>
<tr>
<th>Land cover variables</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>N_hab</td>
<td>-0.435</td>
<td>-0.039</td>
<td>0.004</td>
</tr>
<tr>
<td>Confor_a</td>
<td>-0.368</td>
<td>0.279</td>
<td>0.154</td>
</tr>
<tr>
<td>Confor_p</td>
<td>-0.427</td>
<td>0.075</td>
<td>-0.047</td>
</tr>
<tr>
<td>Mixfor_a</td>
<td>-0.325</td>
<td>0.212</td>
<td>-0.097</td>
</tr>
<tr>
<td>Grass_a</td>
<td>-0.213</td>
<td>-0.674</td>
<td>0.103</td>
</tr>
<tr>
<td>Grass_p</td>
<td>-0.345</td>
<td>0.307</td>
<td>-0.144</td>
</tr>
<tr>
<td>Heath_a</td>
<td>0.409</td>
<td>0.335</td>
<td>-0.137</td>
</tr>
<tr>
<td>Heath_p</td>
<td>-0.081</td>
<td>0.066</td>
<td>0.830</td>
</tr>
<tr>
<td>Water_main</td>
<td>-0.149</td>
<td>0.278</td>
<td>-0.229</td>
</tr>
<tr>
<td>Water_sec</td>
<td>0.163</td>
<td>0.358</td>
<td>0.417</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>1.762</td>
<td>1.175</td>
<td>1.058</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>3.106</td>
<td>1.382</td>
<td>1.118</td>
</tr>
<tr>
<td>Proportion of Variance</td>
<td>0.310</td>
<td>0.138</td>
<td>0.111</td>
</tr>
<tr>
<td>Cumulative explained variance (%)</td>
<td>31.05</td>
<td>44.87</td>
<td>56.05</td>
</tr>
</tbody>
</table>
Table 3 – Best models considered within each descriptor. For each model Deviance and Akaike’s information criterion (AIC) are presented. Models were ranked in function of AIC value corrected to small sample size (AICc); Variation between each model AICc and the lowest AICc within the set (ΔAICc) and the relative likelihood of each model (Akaike weight) are also presented; Best model is presented in grey.

<table>
<thead>
<tr>
<th>Descriptors</th>
<th>Models</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Akaike weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null model</td>
<td></td>
<td>97.07</td>
<td>103.4</td>
<td>63.06</td>
<td>0.00</td>
</tr>
<tr>
<td>Food</td>
<td>Rb_p + Rod_div</td>
<td>24.45</td>
<td>42.77</td>
<td>0.41</td>
<td>0.246</td>
</tr>
<tr>
<td></td>
<td>PC1 + PC2 + PC3</td>
<td>85.27</td>
<td>98.59</td>
<td>57.23</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>PC2 + PC3</td>
<td>88.53</td>
<td>99.45</td>
<td>58.49</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>PC1 + PC2</td>
<td>88.81</td>
<td>99.73</td>
<td>58.77</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>PC2</td>
<td>91.75</td>
<td>100.40</td>
<td>59.71</td>
<td>0.00</td>
</tr>
<tr>
<td>Landcover</td>
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<td>85.27</td>
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<td>57.23</td>
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<td></td>
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<td>99.45</td>
<td>58.49</td>
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<td>99.73</td>
<td>58.77</td>
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<tr>
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<td>PC2</td>
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<td>100.40</td>
<td>59.71</td>
<td>0.00</td>
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<td>Human disturbance</td>
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<td>46.23</td>
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</tr>
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<td>88.14</td>
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<td>Sport_est + Rds_main</td>
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<td>88.19</td>
<td>47.23</td>
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<td>0.00</td>
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<td>Food + disturbance</td>
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<td>Food + elevation</td>
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<td>22.31</td>
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<td>0.263</td>
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<td>24.44</td>
<td>45.39</td>
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Table 4 – Model-averaged parameters estimates of variables within the model confidence set, with respective standard errors (SE) and confidence intervals (CI).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
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<th>Lower CI (95%)</th>
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<td>Rb_p</td>
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<td>Rod_div 1</td>
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<td>45.40</td>
<td>62.21</td>
<td>-114.84</td>
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<tr>
<td>Rod_div 2</td>
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<td>116.83</td>
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<td>Rod_div 3</td>
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<td>Rod_div 4</td>
<td>19.800</td>
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<td>Elev_Range</td>
<td>-0.060</td>
<td>0.07</td>
<td>0.07</td>
<td>-0.19</td>
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</tbody>
</table>


**Discussion**

Wildcat presence in Scotland, at a broad scale, was influenced by the conjunction of different variable types (food, land cover and topography dependent variables), corroborating our fourth hypothesis, i.e. this felid presence is dependent on the interaction of several factors. Specifically, regions with a high diversity of rodents and rabbits, smooth elevation range and a mix of grassland and woodland patches were most suitable to wildcats.

As stated, sampled units with confirmed wildcat presence were mainly associated with higher rodent diversity and rabbit presence. Both variables alone did not build better explanatory models and led us to conclude that the simultaneous presence of these two prey categories may be beneficial for wildcat persistence on a broad scale. The species close relation with prey presence has also been detected in other regions of the species range (e.g. Portugal - Monterroso *et al.* 2009; Ferreira *et al.* 2010), but had not yet been documented as a broad-scale determinant in Scottish populations. These results are supported by previous studies that have reported that, in northern Scotland, wildcats prey mostly on rabbits and small mammals (Corbett 1979). The simultaneous presence of both types of prey may be beneficial since it allow wildcats to cope with the seasonal and unexpected fluctuations of prey populations that may occur (Merritt *et al.* 2001). Rabbit consumption may be important for the wildcat because the highest biomass values compared to smaller sized rodent prey species. This in combination with evidence that wildcats preferentially hunt rabbits that are sick (e.g. due myxomatosis) or young (and thus more easily captured) (Corbett 1979), make rabbits one of the most profitable species in terms of energy. At the same time, areas with higher diversity of small mammals may play an important role in supporting wildcats during winter periods, when rabbits are normally present at lower population levels, particularly during long periods of snow cover (Trout *et al.* 2000).

Wildcat presence was also positively associated with “grassland covered areas”. Corbett (1979) recorded the use of these areas by this felid while hunting and has associated this use with the fact that these patches had higher abundance of rabbits. Nevertheless, the possible benefit to the species survival associated with the presence of a land cover that support high prey abundances (e.g. grassland), may be outcompeted by the increase of the probability of encounters with feral domestic cats (and the likelihood of hybridization, one of the wildcats’ main threats – Oliveira *et al.* 2008). For example, in France, grassland areas were used by all types of wild-living cats, whereas other habitat types, such as woodland areas, were more likely to be used by wildcats (Germain 2007). Daniels *et al.* (2001) in Scotland suggested that wild-living cats avoided pasture areas, a result that can be understood since these areas are heavily grazed and thus less suitable for rodents and rabbits. In the Scottish landscape “grassland covered areas” are frequently found close to mosaics of arable fields, where farms usually occur, and thus it is impossible to extend Daniel and collaborators’ conclusion to the remaining Scottish territory.
due to the lack of information on habitat selection of hybrids and feral cats. Such information is, therefore, crucial to prioritize areas with higher conservation value. These results support evidence that the wildcat should not be seen as strictly a forest species (e.g. Klar et al. 2008; Lozano et al. 2010). In fact, the species appears to benefit from a heterogeneous matrix of grassland and woodland patches. Although we did not detect any influence of woodland area in wildcat presence in our study area, other studies in Scotland confirmed the use of these forested areas (Corbett 1979; Scott 1993; Daniels et al. 2001).

Heather moorland areas were negatively associated with wildcat presence, as previously recorded with wild-living cats in Scotland (Daniels et al. 2001). In this study the negative influence may be related to the fact that larger areas of heather moorland were associated with smaller patches of grassland. Heather moorland areas are also generally open and exposed areas which may represent a risk (e.g. predators and harsh climatic conditions) for wildcats and their main prey. In addition, heather moorland is heavily managed to provide more suitable habitat for grouse, an important game bird, which includes annual burning and predator control, making this habitat less attractive for the wildcat. Secondary watercourses and higher elevation range also contributed negatively to wildcat presence. Secondary watercourses are normally associated with riparian habitats, which usually have high prey diversity (Virgós 2001) and have been considered an important factor for wildcat presence (Klar et al. 2008). Nevertheless, we found a negative association of these areas with wildcat presence at broad scale. This may be related to outdoor activities (e.g. fishing) practiced in the Scottish rivers and their associated disturbance. Areas with a higher elevation range have been suggested as possible wildcat refuges since they are usually less disturbed (Mermod et al. 2002; Ferreira et al. 2010) Nonetheless, we detected a negative association between wildcat occurrence and steeper areas. One possible explanation for this is that human population density in Scotland is low enough to allow wildcats to tolerate disturbance, and therefore they do not need to select mountainous areas, where the climate and prey availability are usually less suitable; another possible explanation is that steeper or mountainous areas are significantly less populated than the lowlands and, therefore, the detection probability during a survey using sightings is lower in mountainous areas. On the other hand these areas are more frequented by game keepers who are more likely to see a wildcat when they are out in the field looking for other predators. This last hypothesis, if true, may indicate that our data might be biased towards lowland and more humanized areas. It is known that the use of data from Atlas and surveys based on sightings can be affected by some errors, such as those due to non-homogeneous sampling (Macdonald et al. 2008).

Although confident in the robustness of the analysis, we recognize the bias associated with this type of data, namely when dealing with species difficult to detect, like the wildcat. In such situations, true absences are difficult to obtain. Moreover, the morphological similarity with feral and hybrid cats might cause additional errors. The extent of such possible error is
unknown since it depends on the dissimilarity of habitat selection patterns of wild-living cats, which is not yet confirmed in Scotland. Nevertheless, if a bias towards humanized areas is present we would expect wildcat occurrence to be associated with urban areas and roads, something that we did not detect.

The application of our averaged wildcat presence model (based on food availability, land cover and topography dependent variables) to other Scotland regions may be useful, but should be used with caution, since our data did not allow us to explore other effects that may affect wildcat distribution. For example, an effect that was not possible to test, due to the lack of reliable prey data, was the influence of the surrounding sampling units on positive records. For instance, an area suitable for wildcats according with this model may be less appropriate if the surrounded region is a non-suitable area. The surrounding environment may have a considerable impact on wildcat distribution since it can constrain connectivity between suitable areas. However, the lack of connectivity effect on wildcats is unknown at this scale. On the other hand, the use of prey abundance, instead of species diversity should be a more reliable and accurate measure of the area’s trophic carrying capacity, and, when available, should be incorporated in future modelling procedures.

Currently, sightings and road-kills are the main method of collecting broad scale data on the wildcat in Scotland. Thus, conservation actions and urgent decisions will have to be based on this type of information. Therefore, we are aware of the possible associated bias affecting our data, but we believe that the first insights into wildcat’s ecological determinants at a broad scale in Scotland, presented in our study, will be a useful first approach that may motivate future local studies.

References
Bates, D., Maechler, M., & Bolker, B. (2011) - lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39.


SNH (2007) - A Five Year Species Action Framework: Making a difference for Scotland’s species. 84. Scottish Natural Heritage


## Appendix 1 – Review of the factors previously identified by other authors as influencing wildcat distribution and selected as explanatory variables for the modeling process

<table>
<thead>
<tr>
<th>Variables used in the present study</th>
<th>Authors</th>
<th>Study Location</th>
<th>Main habitat</th>
<th>Study aims</th>
<th>Sample type</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Confor_a</td>
<td>a) Corbett (1979)</td>
<td>a) Glen Tanar, East Scotland</td>
<td>a) Wooded valley and open moorland</td>
<td>a) Spatial ecology</td>
<td>a) Radio-tracking</td>
<td>a) Wide selection of habitats (pine, birch, scrub, moors, farm). Core areas in pine forest and significant number of movements along forest edges and areas with scrub cover. Movements over open heather moorlands during summer.</td>
</tr>
<tr>
<td>Confor_p</td>
<td>b) Scott (1993)</td>
<td>b) Ardnamurchan, Scotland</td>
<td>b) Wood and grassland more wet areas</td>
<td>b) Spatial ecology</td>
<td>b) Radio-tracking</td>
<td>b) Use of young forestry plantations and gorse during the day with exploration movements in open ground and around farms and villages during the night.</td>
</tr>
<tr>
<td>Mixfor_a</td>
<td>c) Daniels et al. (2001)</td>
<td>c) Angus Glen, Scotland</td>
<td>c) Mixed and coniferous woodland + moor and grassland</td>
<td>c) Ecology and Genetics of wild-living cats</td>
<td>c) Radio-tracking</td>
<td>c) Wild-living cats preferred stream edge and woodland habitats and avoided pasture and heather moorland.</td>
</tr>
<tr>
<td>Mixfor_pma</td>
<td>d) Klar et al. (2008)</td>
<td>d) Southern Eifel, Germany</td>
<td>d) Forest, mainly coniferous</td>
<td>d) Habitat selection at local scale.</td>
<td>d) Radio-tracking</td>
<td>d) Presence of forest didn’t totally explains habitat use. Edges between forest and watercourses were also important.</td>
</tr>
<tr>
<td>Heath_a</td>
<td>e) Davis &amp; Gray (2010)</td>
<td>e) Scotland (10x10km scale)</td>
<td>e) -</td>
<td>e) Scottish wildcat survey (2006-08)</td>
<td>e) Wildcat sightings and interviews</td>
<td>e) Sightings in grassland along river margins with scrub and tree cover.</td>
</tr>
<tr>
<td>Heath_p</td>
<td>f) Confor_p (1979)</td>
<td>f) Continental scale</td>
<td>f) -</td>
<td>f) Biogeographical patterns of diet and scats</td>
<td>f) Revision of 15 diet studies</td>
<td>f) Selection of rabbits when present and small mammals when rabbits are absent. At high latitudes in Europe most of the small mammals consumed are Microtinae.</td>
</tr>
</tbody>
</table>

### Variables used in the present study:
- **Rb_p**: Rodent diversity
- **Rod_div**: Rodent diversity
- **Confor_a**: Conformity to a
- **Confor_p**: Conformity to p
- **Mixfor_a**: Mixfit to a
- **Mixfor_p**: Mixfit to p
- **Heath_a**: Heath to a
- **Heath_p**: Heath to p
- **Grass_a**: Grass to a
- **Grass_p**: Grass to p
- **N_hab**: Number of habitats
- **Water_main**: Water main
- **Water_sec**: Water secondary
### Variables used in the present study

<table>
<thead>
<tr>
<th>Variables</th>
<th>Authors</th>
<th>Study Location</th>
<th>Main habitat</th>
<th>Study aims</th>
<th>Sample type</th>
<th>Results</th>
</tr>
</thead>
<tbody>
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<td>Urb_a</td>
<td>a) Scott (1993)</td>
<td>a) Ardnamurchan, Scotland</td>
<td>a) Wood and grassland more wet areas</td>
<td>a) Spatial ecology</td>
<td>a) Radio-tracking</td>
<td>a) Movements around farms and villages during night.</td>
</tr>
<tr>
<td>Urb_p</td>
<td>b) Klar et al. (2008)</td>
<td>b) Southern Eifel, Germany</td>
<td>b) Forest, mainly coniferous</td>
<td>b) Habitat selection</td>
<td>b) Radio-tracking</td>
<td>b) Probability of wildcat habitat use decreases significantly near villages and moderately near roads and single houses.</td>
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<tr>
<td>Urb_pma</td>
<td>c) Davis &amp; Gray (2010)</td>
<td>c) Scotland (10x10km scale)</td>
<td>c) -</td>
<td>c) Scottish wildcat survey (2006-08)</td>
<td>c) Wildcat sightings and interviews</td>
<td>c) Records of wildcats were mostly found near human settlements and new housing developments.</td>
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<td>Rds_main</td>
<td>d) Ferreira et al. (2010)</td>
<td>d) Iberian Peninsula</td>
<td>d) -</td>
<td>d) Large-scale determinants of wildcat presence</td>
<td>d) Distribution data from Portugal and Spain atlas</td>
<td>d) In Atlantic area, non-natural areas and road-length contributed positively for wildcat presence. Elevation range was the most important predictor.</td>
</tr>
<tr>
<td>Sport_est</td>
<td>e) Jerosh et al. (2010)</td>
<td>e) Harz Mountains, Germany</td>
<td>e) Forest and Pastures</td>
<td>e) Selection of resting sites</td>
<td>e) Radio-tracking</td>
<td>e) Wildcat can habituate to human-made structures, detection of resting sites near forest roads and motorways</td>
</tr>
<tr>
<td>Elev_Range Mean_tc</td>
<td>a) Corbett (1979)</td>
<td>a) Glen Tanar, Scotland</td>
<td>a) Wooded valley and open moorland</td>
<td>a) Spatial ecology</td>
<td>a) Radio-tracking</td>
<td>a) Wildcats moved to lowland valleys during snow period.</td>
</tr>
<tr>
<td></td>
<td>b) Mermod &amp; Liberk (2002)</td>
<td>b) Jura Mountains, Switzerland</td>
<td>b) Forest, pasture and cultures</td>
<td>b) The role of snow cover for wildcat</td>
<td>b) Radio-tracking</td>
<td>b) Wildcats use highland areas if vertical migration is possible and mostly during summer, after the snow disappearance.</td>
</tr>
<tr>
<td></td>
<td>c) Daniels et al. 1998</td>
<td>c) Scotland</td>
<td>c) -</td>
<td>c) Morphological and pelage characteristics</td>
<td>c) Road casualties; Predator control; Live-trapping</td>
<td>c) Distribution of wild-living cats with characteristics normally associated with wildcat showed to be related with mean annual temperature</td>
</tr>
<tr>
<td></td>
<td>d) Davis &amp; Gray (2010)</td>
<td>d) Scotland (10x10km scale)</td>
<td>d) -</td>
<td>d) Scottish wildcat survey (2006-08)</td>
<td>d) Wildcat sightings and interviews</td>
<td>d) Records were generally from lowland areas.</td>
</tr>
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</table>
Appendix 2 - All models considered within each descriptor. For each model Deviance and Akaike's information criterion corrected to small sample size (AICc) are presented.

<table>
<thead>
<tr>
<th>Descriptor</th>
<th>Tested models</th>
<th>Deviance</th>
<th>AICc</th>
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<td>52.61</td>
</tr>
<tr>
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<td>Rb_p</td>
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<td>Rds_main</td>
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<td>94.89</td>
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<td><strong>Climate</strong></td>
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<td>82.96</td>
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<tr>
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<td>Elev_range</td>
<td>85.61</td>
<td>94.21</td>
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<td>95.27</td>
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<td>24.45</td>
<td>42.77</td>
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<td>52.61</td>
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<td></td>
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</tr>
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<td>Sport_est</td>
<td>82.35</td>
<td>90.96</td>
</tr>
<tr>
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<td>24.45</td>
<td>42.77</td>
</tr>
<tr>
<td></td>
<td>Rb_p + Rod_div + Elev_range</td>
<td>22.31</td>
<td>43.26</td>
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<tr>
<td></td>
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<td>36.84</td>
<td>52.61</td>
</tr>
<tr>
<td></td>
<td>Rod_div + Elev_range</td>
<td>35.93</td>
<td>54.25</td>
</tr>
<tr>
<td></td>
<td>Rb_p + Elev_range</td>
<td>47.80</td>
<td>58.73</td>
</tr>
<tr>
<td></td>
<td>Rb_p</td>
<td>53.40</td>
<td>62.01</td>
</tr>
<tr>
<td></td>
<td>Elev_range</td>
<td>85.61</td>
<td>94.21</td>
</tr>
<tr>
<td><strong>Food + Temperature</strong></td>
<td>Rb_p + Rod_div</td>
<td>24.45</td>
<td>42.77</td>
</tr>
<tr>
<td></td>
<td>Rb_p + Rod_div + Mean_tc</td>
<td>24.44</td>
<td>45.39</td>
</tr>
<tr>
<td></td>
<td>Rod_div</td>
<td>36.84</td>
<td>52.61</td>
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<td></td>
<td>Rod_div + Mean_tc</td>
<td>36.79</td>
<td>55.12</td>
</tr>
<tr>
<td></td>
<td>Rb_p</td>
<td>53.40</td>
<td>62.01</td>
</tr>
<tr>
<td></td>
<td>Rb_p + Mean_tc</td>
<td>51.76</td>
<td>62.69</td>
</tr>
<tr>
<td></td>
<td>Mean_tc</td>
<td>86.67</td>
<td>95.27</td>
</tr>
<tr>
<td><strong>Null model</strong></td>
<td></td>
<td>97.07</td>
<td>103.40</td>
</tr>
</tbody>
</table>
Local-level determinants of wildcat presence in Northern areas of Scotland

André P. Silva¹, Luís M. Rosalino¹, Neil Anderson², Kerry Kilshaw²


²Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanti-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire OX13 5QL, UK

Abstract

We studied the European wildcat (Felis silvestris silvestris Schreber, 1775) presence at the individual-level in relation to food, land cover, disturbance and topography features. Field campaigns to assess wildcat presence and prey surveys were carried out in three study areas across the northeast of Scotland. Wildcat records were collected using camera-trapping and prey data was assessed through rabbit transects and small mammal trapping. We used Generalized Linear Models (GLM-logit) to assess the best models explaining wildcat occurrence in our study sites. Model predictive accuracy was evaluated using Receiver Operating Characteristics (ROC) curves. Wildcats were only detected in two of the three study sites. Rabbits were mainly found in grassland habitats and rodents were more abundant in coniferous patches across the different sites. Wildcat presence was predicted by interactions between food, landcover and disturbance variables. The species was positively associated with rodent abundance and locations with higher habitat diversity, mainly composed of mixed and coniferous woodlands together with grassland patches. Wildcat presence was also positively correlated with camera traps located closer to watercourses and human settlements. On the contrary, the species was negatively linked with locations presenting higher diversity of rodents, dwarf shrub areas and closer distances to secondary roads. Our main findings suggest that wildcat conservation actions at local-scale may benefit from focusing on the availability of feeding resources and matrix heterogeneity. Additional features such as watercourses and roads may play an important role in shaping wildcat distribution at this scale.

Keywords: Wildcat, Scotland, individual-level requirements, rodents, grassland, woodlands, disturbance factors
Introduction

The European wildcat (*Felis silvestris silvestris* Schreber, 1775) population is threatened across most its distribution range by human-caused mortality (e.g. road kills, illegally persecution) and by habitat destruction and fragmentation (Langley & Yalden 1977, McOrist & Kitchener 1994, Nowell & Jackson 1996). Nowadays, one of the greatest threats to the European wildcat is hybridisation with domestic cat *Felis catus*, and several studies have focused their attention to this subject (e.g. Beaumont *et al.* 2001; Randi *et al.* 2001; Pierpaoli *et al.* 2003; Oliveira *et al.* 2008; O’Brien *et al.* 2009; Say *et al.* 2011). Thus, practical conservation actions are now vital to maintain regional populations (Driscoll & Nowell 2009). However, without the acquisition of robust ecological data on the species populations’ adaptation to regional environments, the success of such actions may be threatened. Some studies have addressed the species’ ecological requirements, namely in central Europe (Liberek 1999; Wittmer 2001; Biró *et al.* 2004; Klar *et al.* 2008; Jerosch *et al.* 2010) and in the Mediterranean region (Lozano *et al.* 2003; Virgós & Travaini 2005; Sarmento *et al.* 2006; Santos *et al.*, 2008; Monterroso *et al.* 2009). However, some of this studies (e.g. Lozano *et al.* 2003; Virgós & Travaini 2005; Santos *et al.*, 2008) are based on traditional non-invasive field-techniques (e.g. scats and track surveys, sightings information or road-kill casualties), which have revealed some limitations (Lozano *et al.* 2003) in collecting robust and reliable data samples (e.g. misidentification between feral and wildcats).

The advent of camera-trapping in animal ecology (Carey 1926; O’Connell *et al.* 2010) was a new opportunity to overcome many of the problems associated with studying rare and elusive species, in particular the collection of ecological data in relation to species presence (Monterroso *et al.* 2009; Sarmento *et al.* 2009; Anile *et al.* 2010; Emre Can *et al.* 2011). Such new developments can provide crucial information that can help identify and design priority areas for wildcat conservation. These areas can play an important role in minimizing habitat loss, population fragmentation and reduce or even prevent contact between wild and domestic forms. The importance and urgency of these areas were highlighted in the recent UK wildcat action plan (Macdonald *et al.* 2004).

In the United Kingdom, the wildcat distribution is currently restricted to northern Scotland and recent estimates indicate a possible critically endangered population of only 400 individuals showing the classical wildcat pelage pattern (Macdonald *et al.* 2004; Kitchener *et al.* 2005). The wildcat is legally protected within the UK under the Schedules 5 and 6 of the Wildlife and Countryside Act, 1981 (as amended in 1988) and at European level is listed on Annex IV of the European habitat directive (Kitchener *et al.* 2005).
Despite being a threatened, protected and a well studied population, available information on the main determinants affecting the wildcat presence in Scotland, at a fine scale, is sparse (Corbett 1979, Scott 1993, Daniels et al. 2001).

In other parts of its range, European wildcat presence is known to be related with prey availability (Corbett 1979; Monterroso et al. 2009) and although European rabbit Oryctolagus cuniculus is the preferred prey species in areas where it occurs, the wildcat can adapt to other prey species (Malo et al. 2004; Lozano et al. 2006) such as small mammals, which are essential prey in northern latitudes (Hewson 1983; Liberek 1999; Biró et al. 2005; Lozano et al. 2006; although some exceptions exist – see Sarmento 1996). Vegetation and disturbance features are also central aspects shaping wildcat distribution in Europe, namely within a context of landscape increasingly composed of agriculture mosaics, where individuals are often associated with land cover that offers protection (i.e. forests and scrubland - Klar et al. 2008; Monterroso et al. 2009). Human influence can have considerable impact on habitat structure and recently man-made structures, such as roads and human settlements, have been mentioned as critical factors to take into account in wildcat conservation (Klar et al. 2008; Klar et al. 2009).

The effect of scale can be crucial in conservation strategies since species can show different response at different scale levels (Wiens 1989; Kent et al. 2011). Recently, wildcat ecological requirements at broad scale in Scotland were addressed by Silva et al. (in prep), but no study is yet available that has specifically looked at constraints to the species presence at a local scale in Scotland. Therefore, to fulfil this lack of information, in this study we aim to expand the current available knowledge on determinants influencing wildcat presence at a local-scale by testing the importance of food, land cover, disturbance and topographic variables on wildcat occurrence. To do so, we tested 4 hypotheses based on the previously described factors identified by other authors as influential for wildcats occurrence, elsewhere in the species distribution range: 1) Food resources - wildcats select locations with higher prey availability; 2) availability of landcover features due their possible direct (e.g. shelter) and indirect (e.g. prey presence) importance; 3) presence of man-made structures (e.g. roads and human settlements) and 4) the interaction of food, landcover, human disturbance and topography features.

**Methods**

**Study area**

The study was performed on three sites: Kinveachy: 57°16'29"N, 3°50'21"W; Gartly forest: 57°21'37"N, 2°45'53"W; and Black Isle: 57°36'40"N, 4°13'24"W) across the Highlands and Grampian regions of Scotland. In terms of topography, the region comprises the highest high ground areas in UK (max. altitude of 1344m). However, elevation can vary significantly with low altitude plains near the coast. Higher fields within this region are primarily composed by inaccessible rocky areas, mixed with heath and grass moorlands. At lower altitudes, managed
landscape composed by arable mosaics of fields and pastures are commonly found in the eastern regions (MLURI, 1993). At this altitudes, bog and grassland patches, that can be associated to scrub areas mainly composed of common broom *Cytisus scoparius* and common gorse *Ulex europaeus*, occur interspersed with coniferous (mainly *Pinus silvestris*), broad-leaved (*Betula* spp) and mixed woodlands (MLURI, 1993). Oak woodlands (*Quercus* spp.) can be present, although showing a sparser distribution. Norwegian spruces *Picea abies*, are present for timber extraction (MLURI, 1993).

Gartly and Black Isle areas are managed by the Forestry Commission and are used for timber extraction, originating a mosaic of felled/non felled areas of Norwegian spruce. Both areas are surrounded by numerous arable fields and pastures used for agriculture and livestock. Kinveachy, on the other hand, is generally composed of Scots pine *Pinus silvestris*, heather moorland and dwarf shrub open areas and managed as a sporting estate. The three study sites were surrounded by a road network, generally composed of minor and secondary roads, showing low road traffic.

Climate is predominantly cold temperate and influenced by the Atlantic Ocean. Days of snowfall can vary between 40 to 100 days per year, with mean daily minimum temperatures in winter between 2°C to −1°C, and mean daily maximum in summer between 16–19°C. Mean

![Figure 1](image_url) – Location of the study areas (Black Isle, Gartly, Kinveachy) within Scotland, and spatial structure of the main land cover types in each study area.
annual rainfall can vary from 1700 mm (Western regions) to 700mm (Eastern regions) (http://www.metoffice.gov.uk/climate/uk/ns/ accessed on 06 May 2011).

**Wildcat data**

Between December 2010 and July 2011, we carried out camera trapping on the three study sites to examine the local spatial distribution of wildcats (Karanth & Nichols 1998; Sarmento *et al.* 2010; Negrões *et al.* 2010; Long *et al.* 2011). Areas were selected based on previous records of wildcats during the last Scottish wildcat survey (Davis & Gray 2010). A preliminary evaluation of each site was carried out through scats and track surveys, and by identification of areas with potential habitat for wildcat presence.

In each study area twenty camera trap stations, each composed of two camera traps remotely activated by heat and motion, were placed in a grid (5 x 4). Stations were placed 1-1.5km apart to ensure every individual wildcat within the study site had a >0 probability of capture (Karanth 1998). Occasional adjustments had to be made due to habitat feature constraints and landowner permissions. Distance between stations was determined based on previous information regarding the wildcats’ smallest home-ranges in Scotland, detected by Corbett (1979) and Daniels *et al.* (2001), and the distance moved by wildcats during a pilot camera-trapping study within the Cairngorms National Park area (Kilshaw *et al.*, in prep). The first trap location in each study area was chosen according to previous confirmed sightings of wildcats. To maximize our results, the remaining stations were placed in a grid around the first trap. Exact locations of each camera trap station in the field was dependent on local habitat features, evidence of prey and the presence of wildcat scats. Cameras were positioned about 20 cm above the ground, attached to trees or wooden posts, facing a bait station (bait and lure). Each bait station was composed of a wooden stake with a pheasant carcass attached to the top of the stake and Hawbaker’s wildcat scent lures no.1 and no.2 (S. Stanley Hawbaker & Sons Fort Loudon, Pennsylvania, USA) placed on a small piece of towel attached lower down. Scent lure and bait were, on average, 3 to 4m apart from the cameras. We used two distinct camera devices: 40 x Cuddeback® Capture digital camera (Cuddeback digital, Green Bay, Wisconsin, USA) – Kinveachy and Gartly site and 40 x Reconyx® 500 Hyperfire semi-covert IR (Reconyx Inc., Holmen, Wisconsin USA) – Black Isle site. Stations were active over approximately 60 days and were checked every 10-15 days to check batteries and replace bait. Each cat photograph was analysed and animals were classified into three different categories, using the wildcat pelage classification method (Kitchener *et al.* 2005): feral, hybrids and wildcats. Due to their marked morphological and behavioural differences when compared to the other wilder cats groups (Ferreira 2010), feral cats were excluded from data analyses. Due to the small sample size, hybrids were included in our dataset. Individual identification was made using the natural variation in wildcat pelage features (Anile *et al.* 2010; Emre Can *et al.* 2011; Kilshaw *et al.*, in press).
Wildcat presence was recorded on a binary basis, taking values of 0 (absence of the focal species) and 1 (presence of the focal species) at each trap site.

The boundaries of each study area were defined by a 1km buffer around the stations placed on the exterior lines of the camera trapping grid.

Prey surveys, diversity and abundance

We reviewed wildcat feeding habits in Europe to select the most important prey for this felid: European rabbits *Oryctolagus cuniculus* and small rodents (Corbett 1979; Hewson 1983; Liberek 1999; Biró *et al.* 2005; Lozano *et al.* 2006). Due to the different ecological requirements of rabbits and small rodents, we estimated the abundance of these preys in each study area using two different methods. Rabbit abundance was estimated through latrine counts (Palma *et al.* 1999; Trout *et al.* 2000; Palomares 2001) on four linear transects, approximately 2 km long that covered the main habitats in each study site. Main habitats (representing approximately 80-90% of the land cover units) were identified using the UK Land Cover Map 2000 (NERC - Centre for Ecology & Hydrology; http://www.ceh.ac.uk/LandCoverMap2000.html), with a 25m minimum resolution. Transects were divided in 100m sections and designed to take into account the habitat preferences of the species, namely soft ground and proximity to grassland patches, in order to maximize sampling success. Rabbit latrines were identified if more than 20 pellets were detected within a maximum distance of 2m, on either side of the transect (Virgós *et al.* 2003). Rabbit abundance in each habitat type was defined as the number of latrines per transect section (100m).

Rodent abundance was estimated using live-trapping (Flowerdew *et al.* 2004). The main habitats within each study area were surveyed using 30 Sherman live traps (LFATDG-Large Folding Aluminium Treadle and Doors Galvanized – 8 x 9 x 23 cm; H. B. Sherman Traps, Inc – Tallahassee, USA), placed on a 5 x 6 grid design, with traps 10m apart. Each habitat was trapped for four consecutive nights (Gurnell & Flowerdew 2006). Traps were baited with a mixture of porridge, bird seeds and worms, and lined with non-absorbent cotton wool to protect captured animals from hypothermia. Traps were checked twice a day (morning and afternoon). Captured individuals were identified, sexed, aged, and marked with a combination of hair clipping for individual identification (Gurnell & Flowerdew 2006). To avoid disturbing the camera-trapping, small mammal trapping was carried out before or after camera-trapping. Main habitats were sampled simultaneously in groups of two, due to the limited number of available traps (60).

The small mammal data was used to assess species diversity (defined as the number of species identified in each habitat type within each study area) and abundance. Rodent abundance in each habitat type was calculated using a relative abundance index (Eq.1):
\[ I_i = \frac{N_i}{T*R - \left( \sum C - r \right)} \times 1000 \]  
(Eq.1)

where \( N_i \) is the number of animals of the species \( i \) captured, \( T \) the number of available traps, \( R \) the number of daily inspections of traps, \( C \) the number of captures of other species and \( r \) the number of recaptures of species \( i \) (Pounds, 1981).

**Landscape characterization**

We used a 500m buffer to characterize the landscape surrounding each camera trap station. Buffer dimension was based on the wildcats’ core area values for Scotland (Corbett 1979). We used core area values, instead of home range, because it represents the maximum activity areas and allowed us to reduce possible associated error when assuming a home-range as a circular shape well bounded. Landscape variables (Table 1) were obtained from the Land Cover Map 2000 (Fuller et al. 2002). This map is a parcel-based thematic classification of satellite image data from the Landsat sensor, covering the entire United Kingdom, with a 25m resolution, where each pixel provides data on the dominant land cover. Of the 25 habitats subclasses available, “improved”, “neutral”, “setaside”, “calcareous”, and “acid” grass were merged into a main category corresponding to general grassland covered areas. Subclasses dense dwarf shrub heath and open dwarf shrub heath were also transformed into a main class identifying heath moorland areas. Distance from each trap site to human settlements, roads and watercourses were calculated from Ordenace Survey (OS) Strategi map. This fine-scale (1:250000) and digital vector map is developed for regional analysis and contains, among other layers, the spatial disposition of the different river types, roads and urban areas within the UK. Rivers with more than 8 metres at their widest point were classified as main watercourses, whereas watercourses with less than 8 metres wide at widest point, were considered secondary watercourses. Road types were associated in two categories: main and secondary roads, representing in general single and double carriageway roads, respectively. Strategi map was downloaded from the OS open data website (https://www.ordnancesurvey.co.uk/opendatadownload/products.html accessed on June 2011). All land cover variables metrics were estimated using software ArcGIS 9.3 (ESRI, Redlands, California).

To estimate prey availability within each 500m buffer we used the prey abundance indices found for each land cover type and calculated, in function of habitat proportion within the buffers, the average rodent and rabbit abundances. We used the same procedure, using species diversity detected for the main habitats within each study area, to calculate average rodent diversity.
**Statistical analyses**

A high number of variables can lead overparameterization of the models with possible unwanted consequences such as model nonconvergence, especially in cases of small sample sizes (Grueber et al. 2011). Moreover, it can also become difficult to find an optimal model, namely when variables show some degree of collinearity (Cabral et al. 2007). Thus, we firstly looked at the relationships between variables by assessing pair-wise correlations using Spearman correlation coefficient (Zuur et al. 2007). From the highly correlated variables (r>0.7), we retained those that had high ecological meaning, according to prior information on the species ecological requirements. Additionally, we proceeded to the reduction of land cover variables by using a Principal Component Analysis (PCA) (Zuur et al. 2007). This technique allows reducing original variables to a small number of independent principal components. The spatial position of each sampling point relatively to each independent component (PCA scores) was then incorporated in the modelling procedures, instead of the original variables values.

Another potential problem in the analysis of spatial data is the violation of independence between observations, which prevent the use of several model types. To look for spatial autocorrelation (SA) in wildcat presence data, we used the Moran’s I index. When autocorrelation is detected, several strategies such as incorporating spatial locations as random effects in generalized liner mixed models (GLMM), subsampling the data or the incorporating an autocovariate term, can be used to overcome the unwanted effect of increasing the probability of Type I errors (Segurado et al. 2006; Zuur et al. 2007).

In our case the subsampling strategy was not possible due to the small sample size. Therefore we tested the performance of GLMM, by incorporating the cameras spatial locations as random effects, and of a generalized linear models (GLM) incorporating trap locations as an ordinary variable. Nevertheless, in both strategies the effect of spatial locations overlapped the explanatory power of the variables selected to explain wildcat occurrence (see results below). Thus, since there is a lack of information regarding wildcat presence constraints at a local scale, and realising the effects of non-incorporating spatial autocorrelation and the weak relation between the response and explanatory variables, we decided to use GLM for testing all variable combinations to obtain some insights on the most important variables influencing wildcat distribution.

The most influential models were chosen using Akaike’s Information Criterion for reduced sample sets (AICc). The models with variation of $\Delta$AICc<2 constituted the final set of confident models (Burnham & Anderson 2002). The likelihood of each model to be the best explanatory model was assessed using Akaike weights.

Since several models fulfilled the above mentioned criteria ($\Delta$AICc<2), we assessed the coefficients of the environmental variables influencing wildcat’s presence by calculating parameter average estimates using a model averaging approach (Grueber et al. 2011). Logistic regres-
A regression model incorporating averaged parameters estimates was then used to predict wildcat occurrence within our study sites.

Predictive capacity of this final model was tested using Receiver Operating Characteristics (ROC) curves and the Area Under the Curve (AUC) was used as measure of model accuracy (Pearce & Ferrier 2000). AUC values of 0.5–0.7 usually indicate low accuracy (i.e. no better than a null model), values of 0.7–0.9 indicate useful applications and values of >0.9 indicate high accuracy (with AUC=1.0 equal to perfect accuracy; Swets 1988; Pearce & Ferrier 2000).

All statistical analyses were performed in R statistical software V. 2.13.1 (R Development Core Team 2005, Vienna). Morans’I test was carried out using “ape” package (Paradis et al. 2004) and PCA was carried out using “labdsv” package (Roberts 2010). GLMMs and model averaging were produced using “lme4” and “MuMIn” packages (Bates et al. 2011; Bolker et al. 2009).

Table 1 – Detailed description of the explanatory variables selected to explain wildcat occurrence.

<table>
<thead>
<tr>
<th>Categories</th>
<th>Variables (abbreviation)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>Rabbit abundance (Rb_a)</td>
<td>Average rabbit abundance in all habitats within the buffer</td>
</tr>
<tr>
<td></td>
<td>Rodent abundance (Rd_a)</td>
<td>Average rodent abundance in all habitats within the buffer</td>
</tr>
<tr>
<td></td>
<td>Rodent Alpha (α) diversity (Rd_d)</td>
<td>Average no. of rodent species in all habitats within the buffer</td>
</tr>
<tr>
<td>Landcover</td>
<td>Coniferous forest (Confor_%)</td>
<td>Percentage of coniferous forest</td>
</tr>
<tr>
<td></td>
<td>Broad-leaved/Mixed forest (Mix-for_%)</td>
<td>Percentage of broad-leaved/mixed forest</td>
</tr>
<tr>
<td></td>
<td>Grassland (Grass_%)</td>
<td>Percentage of area covered by grassland</td>
</tr>
<tr>
<td></td>
<td>Heather (Heath_%)</td>
<td>Percentage of area covered by heather</td>
</tr>
<tr>
<td></td>
<td>Habitat diversity (Hab_div)</td>
<td>No. of different habitat classes</td>
</tr>
<tr>
<td></td>
<td>Distance to watercourses (Dist_water)</td>
<td>Min. distance to nearest watercourse (m)</td>
</tr>
<tr>
<td>Disturbance</td>
<td>Urban area (Urb_a)</td>
<td>Urban area (m²)</td>
</tr>
<tr>
<td></td>
<td>Distance to minor roads (Dist_minor_rds)</td>
<td>Min. distance to nearest minor road (m)</td>
</tr>
<tr>
<td></td>
<td>Distance to settlements (Dist_sett)</td>
<td>Min. distance to nearest human settlement (m)</td>
</tr>
<tr>
<td>Topographic</td>
<td>Altitude (Alt)</td>
<td>Altitude of each trap station (m)</td>
</tr>
</tbody>
</table>

Results

Wildcats were recorded in 13 (21.6%) of the 60 trap locations. Of the positive records, 30% corresponded to locations only used by hybrids (N=4). The distribution of positive records among the different study areas was asymmetric with most captures (18.3% of the 13 locations)
in the Gartly study area. No wildcats were detected on the Black Isle area (Table 2). As a result, analysis of spatial distribution detected aggregation and spatial autocorrelation in our response variable (Moran’s $I = 0.286$, $z$-Normal $I = -0.017$; $p < 0.001$).

Across the three study areas, prey surveys revealed that rabbits were mainly associated with grassland covered areas and absent from coniferous patches. No rabbits were detected on the Black Isle area. Rodent abundance was higher within coniferous woodland areas, with grassland and heather patches having the lowest rodent abundance (Table 3).

Table 2 - Camera-trapping periods, efforts and wildcat captures during the three study sites campaigns.

<table>
<thead>
<tr>
<th>Area</th>
<th>Sampling period</th>
<th>Trap stations</th>
<th>Trap-nights</th>
<th>Trap stations visited</th>
<th>Photos</th>
<th>Captures</th>
<th>Individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kinveachy</td>
<td>Dec 2010 – Feb 2011</td>
<td>20</td>
<td>1460</td>
<td>2</td>
<td>13</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Gartly</td>
<td>Mar - Jun 2011</td>
<td>20</td>
<td>1327</td>
<td>11</td>
<td>79</td>
<td>24</td>
<td>5</td>
</tr>
<tr>
<td>Black Isle</td>
<td>May - July 2011</td>
<td>20</td>
<td>1200</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>60</td>
<td>3987</td>
<td>13</td>
<td>92</td>
<td>31</td>
<td>7</td>
</tr>
<tr>
<td>Average ± SE</td>
<td>20 ± 0.0</td>
<td>1329 ± 130.0</td>
<td>4.3 ± 5.8</td>
<td>30.6 ± 42.4</td>
<td>10.3 ± 12.3</td>
<td>2.3 ± 2.5</td>
<td></td>
</tr>
</tbody>
</table>

Table 3 – Rabbit and rodent abundance indices per habitat and rodent species captured within each study site.

<table>
<thead>
<tr>
<th>Area</th>
<th>Habitat type</th>
<th>Rabbits abundance (Latrines/100m)</th>
<th>Rodent abundance (Pounds index)</th>
<th>Rodent species captured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kinveachy</td>
<td>Coniferous wood</td>
<td>0</td>
<td>78.947</td>
<td>$A.\ sylvaticus$</td>
</tr>
<tr>
<td></td>
<td>Broad-leaved wood</td>
<td>0</td>
<td>0</td>
<td>$M.\ glareolus$</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>4.626</td>
<td>4.167</td>
<td>$M.\ agrestis$</td>
</tr>
<tr>
<td></td>
<td>Heather</td>
<td>0.792</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Gartly</td>
<td>Coniferous wood</td>
<td>0</td>
<td>79.497</td>
<td>$A.\ sylvaticus$</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>0.550</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Heather/Clear fell</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Black Isle</td>
<td>Coniferous wood</td>
<td>0</td>
<td>46.414</td>
<td>$A.\ sylvaticus$</td>
</tr>
<tr>
<td></td>
<td>Broad-leaved wood</td>
<td>0</td>
<td>37.500</td>
<td>$A.\ sylvaticus$</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>0</td>
<td>4.310</td>
<td>$M.\ glareolus$</td>
</tr>
<tr>
<td></td>
<td>Heather</td>
<td>0</td>
<td>12.605</td>
<td>$A.\ sylvaticus$</td>
</tr>
</tbody>
</table>

Multicollinearity analysis detected that Dist_main_rds was significantly correlated with rabbit abundance, and therefore was excluded from further analysis.
The two principal components (PC1 and PC2) of the Principal Component Analysis (PCA), used to reduce the number of variables within the land cover descriptor, explained 61.75% of data variability (Table 4). PC1 was associated to a gradient ranging from areas with the presence of mixed woodland, grassland cover and areas with higher number of different habitat types (negative scores), to areas located at greater distances to watercourses and with high density of coniferous woodland cover (positive scores). The second principal component (PC2) represents a gradient between trap locations surrounded by areas mainly covered by heather (negative scores) and traps within coniferous or mixed forest patches (positive scores).

The GLMM models produced by incorporating trap-locations as random effects revealed that variables chosen were incapable to explain wildcat distribution, since obtained models showed ∆AICc>2 relatively to the null model incorporating random effects (Appendix1). Thus, we applied GLM to test if there was any association between locations (X and Y variables) and any other landscape variable considered in the previous analysis that might be more important in explaining our results.

GLM models using trap-locations as an autocovariate term for accounting for SA, confirmed that wildcat occurrence in our dataset was mainly explained by the spatial distribution of the observation points, per se (Appendix1).

In the face of these results, and realising the mentioned problems associated with autocorrelation, but also aiming to recognise any trend in the data, we then built GLM models without incorporating trap-locations to identify the possible relations between the explanatory and response variables. Modelling all variable combinations, a final set of four models (∆AICc<2) was considered as those that best predict wildcat presence in our study areas (Table 5), if spatial autocorrelation is not accounted for. Model averaging carried out to search for relations between wildcat presence and the explanatory variables incorporated in the best models considered, showed that wildcat presence was positively associated with buffers where rodent’s abundance was higher, but negatively associated to areas with higher species diversity (Table 6). Additionally, wildcat presence was negatively related to PC1, showing that trap locations where the species was detected were characterized by a higher diversity of habitats, including grassland and mixed forest. Inversely, areas only covered by coniferous forest and distant form watercourses, were negatively associated with wildcat detection. Nevertheless, wildcats were more associated with forest patches (mixed and coniferous forest), than with open areas of dwarf shrub (PC2). Relatively to the two disturbance variables incorporated within the final set of models, wildcats were positively related with greater distances to secondary roads, but detected incloser distance to human settlements (Table 6).

Predictive capacity of the GLM average model tested using ROC curves revealed an area under the curve (AUC) of 0.89, showing that the average model reveals a good predictive
capacity. Sensitivity (92.3%), the true positive proportion of classifications, was higher than the true negative proportion of classifications (specificity = 85.1%).

Table 4 – Loadings and explained variance of the two first axis of the principal component analysis (PCA), performed to resume information within land cover descriptor.

<table>
<thead>
<tr>
<th>Land cover variables</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Confor_a</td>
<td>0.542</td>
<td>0.404</td>
</tr>
<tr>
<td>Mixfor_a</td>
<td>-0.334</td>
<td>0.347</td>
</tr>
<tr>
<td>Grass_a</td>
<td>-0.553</td>
<td>-</td>
</tr>
<tr>
<td>Heath_a</td>
<td>-</td>
<td>-0.802</td>
</tr>
<tr>
<td>Hab_div</td>
<td>-0.439</td>
<td>0.250</td>
</tr>
<tr>
<td>Dist_water</td>
<td>0.307</td>
<td>-</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>1.508</td>
<td>1.197</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>2.273</td>
<td>1.432</td>
</tr>
<tr>
<td>Proportion of variance</td>
<td>0.380</td>
<td>0.239</td>
</tr>
<tr>
<td>Cumulative explained variance (%)</td>
<td>37.890</td>
<td>61.750</td>
</tr>
</tbody>
</table>

Table 5 – Best models obtained. For each model Deviance and Akaike’s information criterion (AICc) are presented. Models were ranked in function of AIC value corrected to small sample size (AICc); Variation between each model AICc and the lowest AICc within the set (ΔAICc) and the relative likelihood of each model (Akaike weight) are also presented.

<table>
<thead>
<tr>
<th>Models</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Akaike weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>PC1 + Rod_a + Rod_d</td>
<td>37.77</td>
<td>46.50</td>
<td>0</td>
<td>0.38</td>
</tr>
<tr>
<td>Dist_set + PC1 + Rod_a + Rod_d</td>
<td>36.26</td>
<td>47.37</td>
<td>0.87</td>
<td>0.25</td>
</tr>
<tr>
<td>Dist_SECrds + PC1 + Rod_a + Rod_d</td>
<td>36.49</td>
<td>47.61</td>
<td>1.10</td>
<td>0.22</td>
</tr>
<tr>
<td>PC1 + PC2 + Rod_a + Rod_d</td>
<td>37.32</td>
<td>48.43</td>
<td>1.90</td>
<td>0.15</td>
</tr>
<tr>
<td>Full model</td>
<td>34.98</td>
<td>56.57</td>
<td>10.07</td>
<td>0.00</td>
</tr>
<tr>
<td>Null model</td>
<td>62.72</td>
<td>64.78</td>
<td>18.28</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 6 – Model-averaged parameters estimates of variables within the model confidence set, with respective standard errors (SE) and confidence intervals (CI).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Coefficient</th>
<th>SE</th>
<th>Lower CI (95%)</th>
<th>Upper CI (95%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.200</td>
<td>2.780</td>
<td>-7.74e+01</td>
<td>3.340</td>
</tr>
<tr>
<td>Dist_SECrds</td>
<td>2.1e-4</td>
<td>5.71e-4</td>
<td>-9.21e-04</td>
<td>1.340e-03</td>
</tr>
<tr>
<td>Dist_set</td>
<td>-2.61e-4</td>
<td>6.27e-4</td>
<td>-1.50e-03</td>
<td>9.82e-04</td>
</tr>
<tr>
<td>PC1</td>
<td>-1.570</td>
<td>0.655</td>
<td>-2.88</td>
<td>-0.261</td>
</tr>
<tr>
<td>PC2</td>
<td>0.061</td>
<td>0.278</td>
<td>-0.493</td>
<td>0.614</td>
</tr>
<tr>
<td>Rod_a</td>
<td>0.177</td>
<td>0.062</td>
<td>0.0539</td>
<td>0.300</td>
</tr>
<tr>
<td>Rod_d</td>
<td>-6.890</td>
<td>2.260</td>
<td>-1.14e+01</td>
<td>-2.360</td>
</tr>
</tbody>
</table>

Discussion

Several strategies can be used to deal with spatial autocorrelation (Segurado et al. 2006). However, some of them are dependent on sample size (e.g. subsampling of non-correlated observation points). In our case the only viable strategies were the use of GLMM and GLM model incorporating spatial locations. Due to the strong power of spatial locations explaining wildcat distribution the effect of other variables on the explanatory models was imperceptible in both methods.

The GLM used without account for traps spatial locations revealed four best models to explain wildcat presence in our study areas. Food availability, land cover and disturbance determinants were incorporated in those models. This result confirms that our fourth hypothesis is the one that better explained wildcat presence on a local level.

Wildcat occurrence was related to higher rodent abundance, but not to a higher rodent diversity. The relationship with rodent abundance confirms what was recorded in higher latitude countries, where rodents are considered the staple of a wildcat’s diet (Nowell & Jackson 1996). The negative relationship between wildcats and higher rodent diversity could suggest that wildcats are selecting one rodent species as main prey, and that the importance is prey quantity and quality. However, such behaviour was not detected in other regions of the species distribution, where the species is considered not to select any specific rodent (Stahl 1986).

Regarding other feeding resources, rabbits have been mentioned as the preferred prey, when present, in other regions of the species distribution range (Lozano et al. 2006). Furthermore, Corbett (1979) also found in the north of Scotland that, although wildcats may prey upon small mammals, their main diet resource was rabbits. Nevertheless, despite the fact that no wildcats were found on the Black Isle site (the only study area where rabbits were not detected), rabbit abundance was not incorporated in our confidence set of models as an important variable in explaining wildcat occurrence. This situation may have two folded reasons: our low sample size and the fact that Gartly forest (i.e. the site with more wildcat records) had lower rabbit
abundance; the interaction of both reasons may have biased our results, by reducing the weight of explanatory power of the rabbit-related variable on wildcat occurrence. Nevertheless, other variables may suggest otherwise, since we detected that wildcat presence was associated with grassland covered areas, the habitat type were rabbits were mainly detected in our study sites. Therefore, we believe that although not totally explicit in our results, rabbit occurrence may be related to wildcat presence.

Camera traps surrounded by a higher diversity of habitats, composed of mixed woodland and grassland covered areas, were more associated with the species occurrence than those present in locations surrounded by heather moorland and large coniferous patches. Easterbee et al. (1991) suggested that wildcats make less use of mature forestry plantations, since they may be less suitable to small mammals. Instead, they tend to use the edges between fields where lagomorphs are likely to be more abundant. Nevertheless, in our study areas wildcats used coniferous and mixed woodland patches, but did not use heather moorland areas. The coniferous result might appear contradictory (see above). However, it seems that they avoid large coniferous areas that tend to be more homogeneous, but can cope with small patches of coniferous forest, whose wooded structure (and consequently protective cover) may overrule the negative effects of a low food land cover unit. Such a relationship had already been detected in wild-living cats by Daniels et al. (2001). Dwarf shrub areas revealed poor rabbit and rodent availability, and therefore may be less suitable for wildcats. Furthermore, these patches are usually associated with open and exposed areas, that wildcats tend to avoid, particularly during winter when they have trouble moving around in heavy snow cover (Mermod & Liberek 2002).

Wildcat presence was also related to areas closer to watercourses. These structures were already suggested as an important resource to carnivores (Virgós et al. 2001; Matos et al. 2009). They are usually associated with a higher diversity and density of rodent prey and, therefore, used by several carnivores’ species, including the wildcat (Klar et al. 2008).

Disturbance variables present within the models confidence set revealed an ambiguous relationship between wildcat distribution and man-made structures. Although wildcats showed a trend to use locations more distant from secondary roads (despite not being characterized by intense traffic), there seems to be an association between this felid detection and the proximity to human settlements. The wildcat is known to avoid roads in other parts of its range, mainly because of disturbance (Klar et al. 2009). However, the use of locations closer to human settlements conflicts with other studies results, such as those from Klar et al. (2008), in Germany. Nonetheless, wildcats in Scotland have been associated with human structures. For instance, Scott et al. (1993) mentioned wildcat movements around farms and villages during the night. The use of areas around human settlements may be related with the arable fields, the consequent higher availability of rodents (Verdade et al. 2011), and the existence of livestock in their vicinity. For instance, during camera trapping in Gartly (April-May 2011), several sheep herds
were giving birth and dead lambs were occasionally found in the fields, which could provide an alternative food source. Furthermore, we detected one lamb carcass eaten by a predator that was pulled out from the open fields to the woods. These evidences of a surplus of food source nearby human settlements, associated with the fact that wildcats can be opportunistic predators (Nowell & Jackson 1996), may be the reason why this felid was detected in areas closer to human settlements.

Despite the high accuracy capacity showed by this model we suggest that these results must be viewed with caution. The small sample size and the strong data spatial autocorrelation do not allow extrapolations of these results outside of our study sites (Segurado et al. 2006). Therefore, the model may not be representative of wildcat determinants in other areas of Scotland. We also believe that a larger sample size may help to better define the actual role of each variable and probably show the importance of rabbits, which have already been detected in other scales of analysis (Silva et al. in prep.). Nevertheless, in our study sites located across northern-east part of Scotland, the results appear to show that conservation actions and areas designed for wildcat protection at this scale level, should encompass areas composed of grassland and woodland patches with high rodent abundance. Special attention should be given to the potential effect of natural and artificial structures such as roads and watercourses. Although being a spatial and temporal snapshot of the wildcat requirements at local scale, our results should be considered a first insight into this felid’s ecology at lower scales and as a pilot study showing what should be improved to deepen the knowledge on wildcat-environment relationship at the individual-level.

References


Bates, D., Maechler M., & Bolker, B. (2011) - Linear mixed-effects models using S4 classe, package “lmer4”, CRAN.


Appendix

Appendix 1 – Best models considered using GLMM and GLM with autocovariate term incorporated X, Y variables. For each model Deviance and Akaike’s information criterion corrected to small sample size (AICc) are presented.

<table>
<thead>
<tr>
<th>Tested models</th>
<th>Deviance</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Best GLMM models</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1</td>
<td>x) + (1</td>
<td>y)</td>
</tr>
<tr>
<td>Rod_d + (1</td>
<td>x) + (1</td>
<td>y)</td>
</tr>
<tr>
<td><strong>Best GLM models incorporated (X,Y variables)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC2 + Rod_d + y</td>
<td>36.32</td>
<td>45.05</td>
</tr>
<tr>
<td>PC1 + x</td>
<td>38.94</td>
<td>45.37</td>
</tr>
<tr>
<td>Mean_alt + x + y</td>
<td>37.28</td>
<td>46.01</td>
</tr>
<tr>
<td>Dist_SECrds + PC2 + Rod_d + y</td>
<td>34.93</td>
<td>46.04</td>
</tr>
<tr>
<td>X</td>
<td>42.14</td>
<td>46.35</td>
</tr>
<tr>
<td>Dist_set + x</td>
<td>39.99</td>
<td>46.42</td>
</tr>
<tr>
<td>Dist_SECrds + Mean_alt + x + y</td>
<td>35.33</td>
<td>46.44</td>
</tr>
<tr>
<td>PC1 + Rod_a + x</td>
<td>37.75</td>
<td>46.48</td>
</tr>
<tr>
<td>PC1 + Rod_a + Rod_d</td>
<td>37.77</td>
<td>46.50</td>
</tr>
<tr>
<td>PC2 + Rod_d + x + y</td>
<td>35.54</td>
<td>46.66</td>
</tr>
<tr>
<td>PC1 + PC2 + x</td>
<td>37.93</td>
<td>46.66</td>
</tr>
<tr>
<td>PC1 + x + y</td>
<td>38.07</td>
<td>46.80</td>
</tr>
<tr>
<td>PC2 + Rb_a + Rod_d + y</td>
<td>35.83</td>
<td>46.94</td>
</tr>
<tr>
<td>Dist_SECrds + PC1 + x</td>
<td>38.31</td>
<td>47.04</td>
</tr>
</tbody>
</table>
Discussion

Wildcat presence

Our results clearly show that, at both scales (national and local), wildcat presence is influenced by the interaction of different types of environmental variables. Food and land cover characteristics of the landscape were associated with wildcat presence at both levels. Furthermore, while disturbance variables were found to be more related with wildcats at a local level; topographic factors were more associated with wildcat distribution at a broad scale. These results are in accordance with other studies (e.g. Kent et al. 2011), who have identified land cover variables as a factor that influence mammal species presence across different scales, where at broad scales, climatic features (which are influenced by topography) were found to have a stronger influence (Wiens 1989).

An essential factor explaining wildcat distribution at both levels was food availability. At a broad-scale rabbit presence and rodent diversity were the strongest factors influencing this felid occurrence. Despite the importance of food availability, a different pattern was observed at a local level. While rodent abundance was positively associated with wildcat presence, rodent diversity was negatively associated. However, we have to stress that it was impossible to investigate the importance of prey abundance at a broader scale, due to the lack of available data. We may suppose that, if available, this variable may influence wildcat presence. Furthermore, rabbit abundance was not an influential factor at the local level. Again, the type of data available may have affected these results. At a finer scale we used rabbit abundance instead of presence/absence, which allowed us to investigate in more detail the real importance of this prey for wildcat spatial distribution. Rabbit presence and abundance has been a factor associated with wildcat occurrence, although it was the first time that such relationship was detected at a broader-scale in Scotland, since the previous records were derived from finer scale information (e.g. Corbett 1979, Easterbee et al. 1991). Across other areas of the species distribution range, broad-scale relationships with prey variables, particularly rabbit presence and number of small mammals, have been already highlighted (e.g. Ferreira 2010).

The close association between wildcat and prey may be related with the detected importance of land covers structure at both levels. For example it would be expected that grasslands, as open areas and thus more exposed to predators and harsh climate conditions, would be less suitable habitats for wildcats. In fact heather moorlands, areas, equally open and exposed, were negatively associated with wildcat occurrence. However, grassland areas were positively associated with wildcat presence. In Scotland rabbits are normally associated with this land cover (Trout et al. 2000) and such association was detected during the local-level study. Also water-voles can be found in wet grasslands and can be additional food resource for wildcats.
This relationship between prey availability and grassland covered areas may influence wildcat presence in this land cover, which theoretically seems to be unsuitable. On the other hand, heather moorlands, less used by wildcat prey at a local-level, were at both scales negatively associated with wildcat presence. Wildcat locations were also associated with woodland patches, namely coniferous woods, as detected in other studies in Scotland (Corbett 1979, Daniels et al. 2001). At the individual level this may be related with a higher abundance of rodents. Nevertheless, these patches can also play a structural role in fulfilling other ecological requirements of the wildcat, namely shelter and easier ground for daily movements during snowfalls (Artois 1985, Mermod & Liberek 2002). The importance of both grassland and wooded areas seem to indicate a compromise between being protected and accessing food. The use of woodland and grassland edges suggested by Easterbee et al. (1991) in Scotland, corroborates this hypothesis.

Land cover types of a more restricted distribution, and often occurring in smaller size patches, such as riparian habitats, may also play an important role in wildcat distribution. Although, we detected a negative association on the broader scale, we found a positive influence at the local level. The importance of these riparian structures for carnivores in general, and for wildcats in particular, is normally associated with a higher diversity and abundance of prey and has been linked to the presence of carnivores (Virgós 2001; Klar et al. 2008). The importance of small land cover structures, such as linear habitat types, may be detectable at local-level, but broader scales analysis resolution may impede the identification of such structures or reduce their proportional importance as land cover unit.

Another important finding of this study was that, across the studied scales, wildcats benefited from higher habitat diversity. This result contradicts the historic assumption that the wildcat is primarily a forest species (Stahl & Leger 1992). However, this new perception of wildcats’-habitat association has already been suggested by other authors (e.g. Lozano 2010) across the species distribution range. Moreover, Easterbee et al. (1991) results may also suggest that this pattern can also be extended to Scotland. However, some caution is needed, because the detected pattern may be a result of a first stage response to recent habitat fragmentation, and not an effective selection for heterogeneity. It is necessary to understand if the species: 1) had already selected this heterogeneity within the matrix prior to the events that led to marked landscape changes, namely fragmentation and extensive loss of forested areas; or 2) changed its behaviour as a response to a surplus of food resources made available by the increase of agriculture areas and grassland fields, surrounding the remaining forest patches. Such understanding is crucial for designing and implementing conservation plans, since it can help clarify the species flexibility to landscape changes.

The impact of local-level factors on wildcat presence may be even more relevant when considering the influence of disturbance variables. Disturbance influence was not detected, at least directly, at a broader scale. Scottish highlands have a low population density and reduced
traffic and road network, which may result in a negligible effect (i.e. a small proportion of unsuitable areas within suitable matrix) of disturbance at this scale, inversely to evidence from the Spanish Mediterranean area, where a negative contribution of roads and non-natural areas on wildcat presence was detected (Ferreira, 2010). At a local-level some structures may cause considerable disturbance (e.g. local isolation of populations due to a barrier effect in areas intersected by road sections with high traffic volume). However this same road may not present a significant effect on wildcat distribution at broad scale (e.g. if the traffic volume in other road sections is lower or if crossing structures are present, even if not constructed for wildlife).

This negative relationship has already been detected in other European wildcat populations (e.g. Klar et al. 2009), where it can have a real impact on carnivores species survival (Grilo et al. 2009). Human settlements revealed a different pattern. Human settlements and roads, as a group, have been suggested to be an important disturbance factor in other wildcat populations (e.g. Klar et al. 2008). However, in Scotland authors do not agree on the role of this disturbance factor for wildcat presence. While Easterbee et al. (1991) indicates that wildcats avoid urban environment, Scott (1993) mentioned wildcat movements near farms and villages. In our local scale study wildcats were positively associated with human settlements. This proximity with non-natural areas may be the result of different, and perhaps interacting, factors, such as access to easier preys (e.g. cattle and sheep young), or the presence of reproductive feral cats in farms that can act as an attractant for wildcats. Nevertheless, all these possible causes for approaching humans settlements can vary significantly from region to region and even the effect of roads may vary significantly accordingly with the traffic volume. For these reasons, disturbance factors can play an important role in some areas (local-level), but their relevance may vary as function of the human presence level.

Finally, climatic conditions were already suggested by other authors, as determinants of species distribution, especially in coarse-scale studies, since at lower-level approaches the effect of these determinants can be overruled by biological interactions (Wiens 1989). Although a direct effect on wildcat distribution at a broad scale was not detected, some topographic features, namely less mountainous areas, were positively associated with wildcat occurrence. The selection of areas with these characteristics may be indirectly driven by the animals’ need to avoid areas with harsh climatic conditions and, therefore, is an indirect response to climatic features. Higher areas in Scotland are usually open and exposed, where low temperatures, snowfall and high winds can be frequent and intense during all seasons. The wildcat is known to be a species that avoid harsh climatic conditions (Nowell & Jackson 1996), which may be the reason why the studied species avoided higher latitudes countries (Nowell & Jackson 1996).

This study provided the first insights on the impact of ecological factors on wildcat distribution in Scotland and of the scale effect. It should be seen as a starting point to clarify our understanding on the impact of broad-scale and regional changes on wildcat conservation. A
clear knowledge of how the species responds to different scale factors will assure the development of more accurate predictive models, increasing the efficiency of conservation actions.

**Conservation implications**

According to our main findings, the definition of special areas for wildcat conservation in Scotland should take into account multi scale approaches. At broader scales, areas should incorporate food rich patches (rabbits and rodents), specific land cover (e.g. woodland and grasslands) and less mountainous areas (topographic characteristics), while at the individual level, areas showing higher levels of prey availability, heterogeneous landcover and few disturbance features should be the main target for assuring wildcat long term persistence.

As a consequence of the detected importance of food factors, wildcat conservation actions in Scotland should emphasize maintenance and reinforcement of prey populations. Such measures were already recommended to boost other carnivores’ populations (e.g. Palomares et al. 2001). One possible strategy to benefit rabbits and rodents, the wildcat main preys, could be to conserve and recover their key habitats. For example, revitalizing woodlands and reforesting open areas (but not grasslands), may induce rodent population enhancement. Simultaneously, the preservation of grassland covered areas, namely when associated with scrub and woodland, may be essential for rabbits recovery. Once rodents and rabbits are markedly affected by human actions, such as land transformation, a balanced land management may be crucial to create heterogeneity within the matrix and regulate prey populations. According to our results, intensive land transformation, leading to extensive and homogeneous areas with a singular land-use, is not ideal for wildcats, which appear to benefit from land cover heterogeneity. Traditional agriculture with less intensive land transformation, preserving prey populations and more heterogeneous land-uses, may be a sustainable way to reduce habitat homogenization by monocultures, and support wildcat populations (Moreno & Villafuerte 1995). Grassland and woodland patches should be encompassed within an ideal matrix, since they can simultaneously provide shelter and food resources for wildcats (and rabbits). Moreover, preservation of micro-habitats such as riparian areas can also potentially directly (e.g. shelter) and indirectly (e.g. prey) encourage wildcat presence.

Preventing and reducing rabbit diseases, such as rabbit haemorrhagic disease (RHD) and myxomatosis outbreaks, may be also crucial to maintain a sustainable prey levels. The influence of such outbreaks on wildcat populations can be severe, due to the importance of this food resource to wildcat occurrence.

Concurrently with food and land cover constraints, disturbance factors identified in our study should also be taken into account during wildcat conservation planning, as was already
recommended for other European populations of this felid (Klar et al. 2009). Nevertheless, further research on disturbance induced impacts is necessary, since the relationship between wildcat and human-made structures in Scotland is still not completely understood.

Finally, terrain topography can also be used as a tool to predict suitable areas for wildcat conservation. When used together with land cover maps, this feature can be an indirect way to identify areas exposed to harsh climatic conditions. However, this approach should be used cautiously since lower and flatter areas may also be associated with areas with higher human disturbance. The local scale habitat model may also present an advantage in a species where conservation genetics is fundamental. Local-scale models have been used with success in other species (Stenglein et al. 2011) to identify high probability areas of the species occurrence, improving the success of genetic samples collection in the field and precluding the need of other time-consuming techniques, such as radiotelemetry for this purpose.

**Future research**

The results presented in this thesis raised new questions, and thus the following subjects are suggestions for further research necessary to achieve a deeper knowledge on wildcat-environment relationship and enhance the wildcat conservation in Scotland:

- In order to have a clear understanding of how to use ecological-based measures to limit the contact between wild, hybrid and feral cats, and thus preventing hybridization, studies on the ecological requirements of the three different forms of wild-living cats in Scotland are urgent. Niche studies analyzing the possible overlap on trophic resources use and spatial and time patterns can be a useful tool for this purpose. The development of such studies should use a clear and reliable method to differentiate the three forms of wild-living cats. At the moment, researchers have some insights on the ecological requirements of wild-living cats, but further knowledge regarding the other cat forms is necessary. The absence of this kind of information when developing management plans may introduce a bias related to the high hybridization rates recorded in Scotland.

- At a local-level, is necessary to obtain solid information on the role of human-made structures. Are villages and agricultural environment surrounding these areas acting as contact regions with feral cats? Are these areas an essential resource of prey for wildcats during fluctuations of wild-prey populations? In an environment not highly humanized, such as Scotland, are roads presenting considerable disturbance and acting as a barrier for connectivity between wildcat populations? Estimates indicate a very low wildcat population in Scotland and ecological corridors between wild populations can
be an essential measure to potentiate population recovery. However, the impact of human-made structures within these corridors should be investigated.

- It is also necessary to gather further information on the main requirements affecting wildcat distribution at different scales, particularly at finer scales. The preliminary study presented in this thesis, due to its small sample size, may be a useful starting point to delineate other research aiming to confirm or refute the results presented here, to search for further insights on wildcat key structures at this level and to develop accurate models to predict wildcat presence. Models should be produced with data from different areas of the country, in order to account for the heterogeneity between the East and West landscape in Scotland.

- At a broad-scale it is urgent to map suitable areas for focusing wildcat conservation efforts. The lack of recent prey data at broader scales in Scotland is a key obstacle to developing better predictive models for wildcat distribution at this level. The improvement of prey data is thus essential for wildcat conservation. The assessment of the overlap of wildcat suitable areas with those already legally designated to protect mammal biodiversity should be investigated. If those overlapping areas also sustain healthy wildcat populations, then they may be an important tool to act quick and actively on the survival of the endangered populations of the Scottish wildcat.

References


