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Managing the carnivore comeback : assessing the adaptive capacity of the Eurasian Lynx (*Lynx lynx*) to cohabit with humans in shared landscapes

Dissertation submitted for the degree of Doctor of Sciences

Yaëlle Bouyer

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“With public sentiment, nothing can fail. Without it, nothing can succeed”

Abraham Lincoln

"Conservation is not viewed as it should be…as an integral part of human survival."

Alan Rabinowitz

“Animals do matter to people, but on balance, they matter less than food, jobs, energy, money, and development. As long as we continue to view animals in ecosystems as irrelevant to these basic demands, animals will lose.”

Joshua J. Tewksbury & Haldre S. Rogers

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A thesis is generally considered as a personal production, where one person works on its subject to finally produce a document similar to this one. However, I consider that a thesis is a common work, an exchange between different people, different mentalities and sometimes different cultures. That was the case for my thesis, where I had the chance to meet people from so many different horizons that I am now professionally but also personally richer than I was at the beginning of this adventure.

Nothing would have been possible without the help of Pascal Poncin, who gave me the opportunity to realize this PhD project in the department of Behavioral Biology in Liège and to the Fonds National pour la Recherche Scientifique who funds me during the past 4 years.

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ABSTRACT

Conflicts between humans and large carnivores are one of the most visible examples of the challenges that arise when seeking to achieve coexistence between humans and wildlife. With their large spatial requirements and predatory behavior, large carnivores are among the most difficult species to preserve in our modern day landscapes. Although large carnivores are usually considered as the epitomes of wilderness, because of human population growth and habitat fragmentation they are inexorably and increasingly faced with the need to live in human-modified landscapes. As a direct consequence, conflicts over depredation on livestock, competition for game species and sometimes over human injury or death will only increase if clear management measures are not taken. This is particularly true in Europe, where, after many decades of absence, large carnivores are recolonizing areas where millions of people are present and where landscapes have been drastically modified. Two approaches to integrating wildlife into a human-dominated world have been proposed at an international scale. The first solution is called *land sparing,* in which wildlife lives exclusively in protected or wilderness areas where contact between animals and humans will be reduced to the minimum. The second solution, called *land sharing,* proposes to integrate human activities and wildlife in the same landscapes in non-protected interface zones in what is often called a coexistence approach. In a context of scarce true wilderness areas and a continuum of human-modified habitats, land sharing (*i.e.* the coexistence approach) is seen as the only possible approach valid for Europe. While a coexistence approach can be readily implemented with smaller species, it can represent a major challenge for species with large space requirements and with predatory behavior. To help manage these species in a long-term conservation vision and to predict where potential conflicts could arise between humans and carnivores, information on large carnivores and their habitat use in anthropogenic landscapes is a pre-requisite.

With the return of Eurasian lynx *Lynx lynx* in Western Europe, _the most densely populated areas of the continent_ information on the species tolerance to human land use will help predict where it is likely to occur in anthropogenic landscapes. Data collected in Scandinavia over 15 years were used to assess the use of landscape by lynx. In this study, we explored the effect of anthropogenic and environmental factors on Eurasian lynx habitat use in Scandinavia. The work was developed along two main axes.

The first axis aims to explore large scale potential patterns of lynx distribution through transferability of results obtained from habitat modelling to geographically different areas. Transferability of results was tested in two steps. Firstly, transferability success (i.e. predictive ability of the map) was tested at a regional scale using data on roe-deer, the main prey of lynx, to create a map of relative distribution and abundance of prey in southeastern Norway (Chapter 1). Secondly, transferability success was assessed at a larger extent and using data obtained from different sampling method (Chapter 2). A habitat suitability map for Eurasian lynx was produced to be used in management planning in geographically differentiated lynx management zones in Scandinavia. The results indicated that transferability of results from one region to an ecologically different region must be taken with caution. Nevertheless, the habitat suitability maps we constructed on the basis of extrapolation are a valuable asset to help management of the Scandinavian lynx population.

The second axis deals with lynx habitat use in relation to anthropogenic and environmental predictors. Lynx tolerance to human presence was first explored by looking at the orientation of home range in the landscape, taking into account proxies of human presence (Chapter 3). Values of these proxies were compared both inside home ranges and within a buffer surrounding the home ranges for several lynx inhabiting an anthropogenic gradient going from near-wilderness to urban periphery. Results showed a high diversity in the extent to which individual lynx are exposed to human influence, indicating that lynx are highly adaptable in terms of living space. Lynx seemed to be able to orientate their home range in order to avoid highest human impacts and select for areas of medium human impacts. Building on these results, finer scale information on lynx habitat use in an anthropogenic landscape were obtained taking into consideration different types of behavior (day-beds, moving and killing) displayed by adult lynx, as well as the effect of cumulative anthropogenic pressures on habitat selection (Chapter 4). Our results showed that lynx select for areas with medium levels of human modification, avoiding both the areas with highest and least modification. Females in general appear to be less tolerant to human modification than males, especially for day-beds.

Our study shows that Eurasian lynx can be considered as a species that is adaptable to human-induced changes in landscape even if its motivation to tolerate human presence is clearly linked to the presence and density level of its main prey, the roe deer. Our work shows that, contrary to much of the public and many conservation professionals' opinions, land sharing with large carnivores in Europe may be possible – even in the immediate proximity to urban centers. However, it is important to bear in mind that these results were obtained from countries with a relatively low human population density; even though some individuals observed lived in the periphery of large cities, the level of habitat fragmentation is less severe than in most of Western Europe. In order to properly assess the capacity of Eurasian lynx to live in highly populated areas, such as the Benelux, more detailed information on lynx distribution from continental European will be needed. However, our results underline the value of combining both correlational and mechanistic studies, and the need for caution in extrapolating data too far from its original context. As large carnivore recovery continues to progress in Europe we may not yet have seen the limits of these species' abilities to adapt.

RÉSUMÉ

La coexistence entre les hommes et la faune sauvage soulève de nombreux défis. Les conflits entre les humains et les grands carnivores en sont l'un des exemples les plus visibles. Les grands carnivores sont parmi les espèces les plus difficiles à conserver dans nos paysages modernes en raison de leurs besoins spatiaux importants et de leurs comportements de prédateurs. Les grands carnivores sont généralement considérés comme le parfait exemple de la nature sauvage. Cependant, en raison de la croissance démographique humaine et de la fragmentation de l'habitat, ils sont inexorablement confrontés à des paysages modifiés par l'homme. La cohabitation entre les hommes et les carnivores entraîne de nombreux conflits dus à la prédation sur le bétail, à la compétition avec les chasseurs pour le gibier et parfois à des blessures ou à la mort d’êtres humains. Ces conflits ne feront qu'augmenter si des mesures de gestion efficaces ne sont pas mises en place. Cela est particulièrement vrai en Europe, où, après plusieurs décennies d'absence, les grands carnivores recolonisent des zones densement peuplées où les paysages ont été considérablement modifiés. A l'échelle internationale, deux approches ont été proposées pour intégrer la faune dans un monde où l'homme est omniprésent. Dans la première solution, appelée *land sparing*, la faune serait présente exclusivement dans des zones protégées où le contact avec les humains serait réduit au minimum. La deuxième solution, appelée *land sharing*, propose d'intégrer les activités humaines et la faune dans les mêmes paysages au sein de zones non protégées. Cette deuxième option est souvent considérée comme une approche menant à la coexistence entre hommes et faune sauvage. Dans le continuum d'anthropisation de l’habitat, où les zones sauvages sont rares, le *land sharing* est considéré comme la seule approche concevable en Europe. Bien qu'une telle approche puisse être facilement mise en œuvre avec des espèces plus petites, elle peut représenter un défi majeur pour les espèces ayant de grandes exigences d'espace et un comportement prédateur. Dans une vision de conservation à long terme, la gestion des grands carnivores nécessite des informations sur leur utilisation de l’habitat dans des paysages anthropisés de façon à prévoir la présence de conflits potentiels entre les hommes et les carnivores.

Depuis quelques années, le lynx européen (*Lynx lynx*) recolonise l’Europe occidentale, la région la plus densément peuplée du continent. Afin d’anticiper la recolonisation de cette espèce, des informations sur son utilisation des paysages anthropisés sont nécessaires. Cette thèse de doctorat étudie l'utilisation de l’habitat par le lynx en explorant l'effet de divers facteurs anthropiques et environnementaux. Ce travail a été réalisé à partir de données récoltées pendant plus de 15 ans en Scandinavie et a été développé autour de deux axes principaux.

Le premier axe vise à explorer la distribution potentielle du lynx à large échelle grâce au transfert des résultats issus de la modélisation de l’habitat dans des zones géographiquement différentes. La transférabilité des résultats a été testée en deux étapes. Le succès de transférabilité (c’est-à-dire la capacité prédictive de la carte) a premièrement été testé à l'échelle régionale lors de la création d’une carte de distribution et d’abondance relative du chevreuil, la principale proie du lynx dans le sud de la Norvège (Chapitre 1). Deuxièmement, le succès de transférabilité a été évalué sur une plus grande étendue lors de la création d’une carte de qualité de l’habitat du lynx sur l’ensemble de la Scandinavie, à partir de données obtenues par différentes méthodes d'échantillonnage (Chapitre 2). Cette carte pourra être utilisée pour la gestion de cette espèce dans des zones géographiquement différenciées. Les résultats indiquent que la transférabilité des résultats d'une région à une région écologiquement différente doit être

considérée avec prudence. Néanmoins, les cartes de qualité de l'habitat que nous avons construit par transférabilité sont un atout précieux pour la gestion de la population scandinave de lynx.

Le second axe détermine l'importance de divers prédicteurs anthropiques et environnementaux sur l'utilisation de l'habitat par le lynx. La tolérance du lynx à la présence humaine a été étudiée en analysant l'orientation de domaines vitaux dans le paysage. Cette étude à été réalisée pour plusieurs lynx habitant un gradient anthropique allant de zones presques sauvages à la périphérie urbaine. (Chapitre 3). La quantification et la comparaison de variables représentatives de la présence humaine entre l'intérieur des domaines vitaux et une zone tampon adjacente montrent que cette espèce est en mesure d'orienter son domaine vital afin d'éviter les zones à impacts humains importantes et de sélectionnez les zones à impacts humains moyens. Ces résultats révèlent également une grande diversité de réponse entre les individus face à l'influence humaine, indiquant que le lynx est hautement adaptable. Parrallèlement, à une échelle plus fine, l'effet de différents comportements (repos, mouvements et prédation) a été déterminé sur la sélection de l'habitat par le lynx dans un paysage anthropisé (Chapitre 4). L'importance du cumul des pressions anthropiques sur la sélection de l'habitat a également été étudiée. Nos résultats montrent que le lynx sélectionne les zones ayant un niveau d'anthropisation moyen, en évitant à la fois les zones ayant un niveau d'anthropisation faible ou fort. En général, les femelles semblent être moins tolérantes que les males à la modification des paysages, particulièrement pour les sites de repos.

Notre étude montre que le lynx européen peut être considéré comme une espèce adaptable face aux paysages anthropisés. Cependant, il est clair que sa capacité à tolérer la présence humaine est liée à la présence et à la densité de sa proie principale, le chevreuil. Notre travail montre que, contrairement à l'opinion de la plupart des professionnels de la conservation et du grand public, la coexistence avec les grands carnivores, le *land sharing,* est envisageable en Europe - même dans la proximité immédiate de centres urbains. Cependant, il est important de garder à l'esprit que ces résultats ont été obtenus dans des pays ayant une densité de population humaine relativement faible. Même si certains individus observés dans notre étude vivent à la périphérie des grandes villes, le niveau de fragmentation de l'habitat reste moins important en Scandinavie que dans la plupart des pays d'Europe de l'Ouest. Afin d'évaluer correctement la capacité du lynx européen à vivre dans des zones densement peuplées comme le Benelux, des informations plus détaillées sur sa distribution en Europe continentale seront nécessaires. Cependant, nos résultats soulignent l'intérêt de combiner à la fois les études mécanistiques et les études de corrélation, et la prudence indispensable pour l'extrapolation de données vers des zones éloignées du contexte originel. Puisque les grands carnivores continuent de recoloniser l'Europe, il est possible que nous n'ayons pas encore idée de leurs capacités à s'adapter.

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INTRODUCTION

I. RECLAIMING A CONTINENT: LARGE CARNIVORES IN MODERN EUROPE

With their large spatial requirements and predatory behavior, large carnivores are among the most challenging species to conserve (Mech 1995; Linnell et al. 2001a). Accordingly, achieving coexistence between humans and wildlife is one of the biggest challenges facing conservation biology in this new millennium (Treves et al. 2006). Conflict between humans and large carnivores is one of the most obvious causes of these difficulties. Because of the massive loss of wilderness and wild spaces, the ongoing fragmentation of their habitats and the rapidly growing human population, large carnivores are now increasingly faced with human-modified landscapes where encounters with humans and livestock will obviously increase (Athreya et al. 2013). Information on the use of anthropogenic landscapes by large carnivores will be necessary to minimize conflicts and more generally for the conservation of this taxonomic group that is now recolonizing large areas of a continent from where it has been absent for decades: Europe (Kaczensky et al. 2013; Falcucci et al. 2013).

1.1 History of large carnivores in Europe

Large carnivores, i.e. the Wolf *Canis lupus*, the Brown Bear *Ursus arctos*, and the Eurasian lynx *Lynx lynx*, have been continuously present during the entire Holocene in most parts of European landscapes. However, as a result of continuous human-driven persecution and profound land transformation, populations dwindled to very small sizes and distributions were drastically reduced. Poisoning, trapping and shooting, reduction of natural prey and loss of habitat were at the root of large carnivore decline (Breitenmoser 1998; MacDonald & Loveridge 2010; Breitenmoser et al. 2000; Boitani et al. 1995; Swenson et al. 2000; Linnell et al. 2001a; Boitani 1992). Humans had always had an impact on wildlife distribution and the decline of European large mammals started very early. But the most radical changes in European carnivore distributions took place during the second part of 19th century, triggered by the industrial revolution and the associated growth in the exploitation of natural resources (Kaplan et al. 2009). Around 1850, large carnivores were discontinuously present in northern and eastern Europe and along forested mountain ranges in southeastern and central Europe (Breitenmoser 1998; Breitenmoser and Breitenmoser-Würsten 1990; Kaczenski et al. 2013; Figure 1).

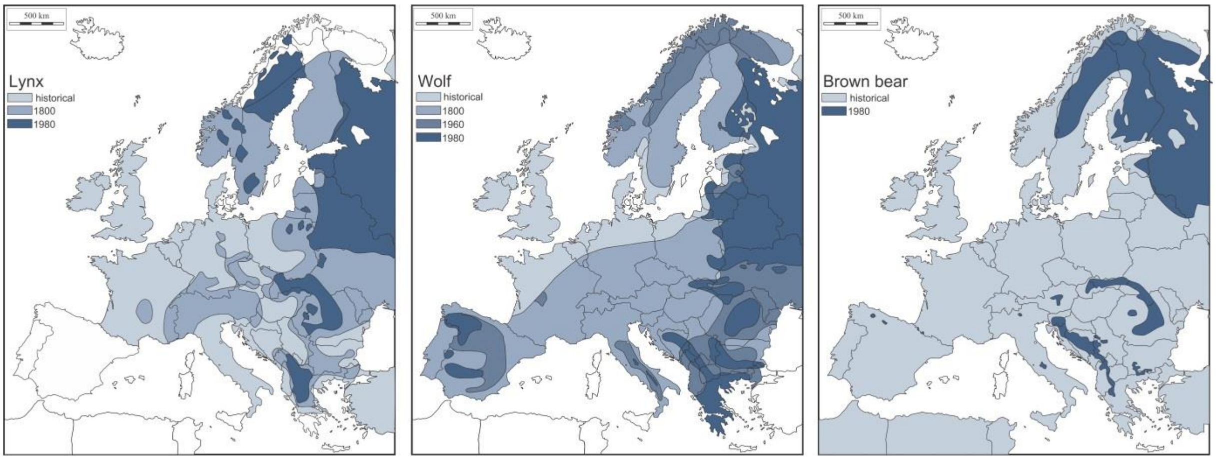

Figure 1: Historical distribution of Eurasian lynx (*Lynx lynx*), wolf (*Canis lupus*) and brown bear (*Ursus arctos*) in Europe. Adapted from Kaczensky et al. 2013.

Up until the mid-20th century, the future of large carnivores in Europe (and large mammals in general) looked bleak. The potential of losing many wildlife species that had such a strong iconic and heritage value first pushed hunters, naturalists and scientists to act in order to save the remaining wildlife diversity. The degradation of the environment and an increase in the number of natural disasters (e.g. flooding and avalanches) led to a growing public awareness of the need to maintain forests (Breitenmoser 1998). Many of the first nature reserves were thus created in the mid-19th century (e.g. the Fontainebleau forest in 1843; Ramade, 1989), often based around former Royal hunting estates (such as Gran Paradiso in the Italian Alps). The early steps towards wildlife conservation in the early 20th century were often led by hunters who feared for the loss of their prized game species. Hunters often promoted the introduction of new wildlife laws and actively conducted reintroductions. Additionally, laws were created to preserve forest habitats through the prohibition of grazing inside forests and, reforestation progressed throughout Europe. Hunting of large mammals was restricted, giving opportunity for species to return into European landscapes (Linnell et al. 2009). Some populations of wild ungulates, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, reindeer *Rangifer tarandus*, either naturally increased or were reintroduced and are now abundant in central and western Europe (Linnell et al. 2005a). Following World War 2 an interest in the status of wildlife spread from the world of foresters and hunters to a wider public. This general concern, both from conservationists and the public, led to the creation in 1948 of the International Union for the Conservation of Nature (IUCN) (Christoffersen 1997). The Stockholm Conference in 1972 amplified the movement: for the first time, the global scientific world acknowledged the amplitude of the degradation of nature, the *Declaration on human responsibility towards the environment* was drafted, and the United Nations Environment Programme (UNEP) was launched. In 1979, Europe took a step forward in protection of wildlife with the Convention on Conservation of European Wildlife and Natural Habitats (Bern) whose goal is to ensure the conservation of wild flora and fauna species and their habitats; and with the Convention on Migratory Species established in Bonn. Another step was taken in 1982 when the World Charter for Nature was signed by the member states of the United Nations. Its fundamental principles are that « Nature shall be respected and its essential processes shall not be impaired » and that « Ecosystems and organisms, as well as the land, marine and atmospheric resources that are utilized by man, shall be managed to achieve and maintain optimum sustainable productivity, but not in such a way as to endanger the integrity of those other ecosystems or species with which they coexist ». From that time on, many countries started their own national agencies for environment protection. Ecologists modified and adapted the direction of their research to make it directly usable for conservation. This led to the founding of a new discipline conceptually adapted to the biodiversity crisis, which became conservation biology (Devillers & Beudels, 1995). This new discipline has made essential contributions to wildlife conservation as it provides a conceptual and theoretical basis and expanded toolkit for the preservation and restoration of biological heritage in all its diversity (Devillers 2003). The implementation of the Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive) was a major step towards mainstreaming wildlife conservation into European policy. The sum of these changes to legislation and the environment during the 20th century implied that at the transition from the 20th to the 21st century, the general ecological situation was suitable and allowed for the maintenance and the recovery of large carnivore populations throughout Europe. Wolves, bears and lynx now have large populations in northern, western and central Europe and are expanding through their original range (Kaczensky et al. 2013, Figure 2).

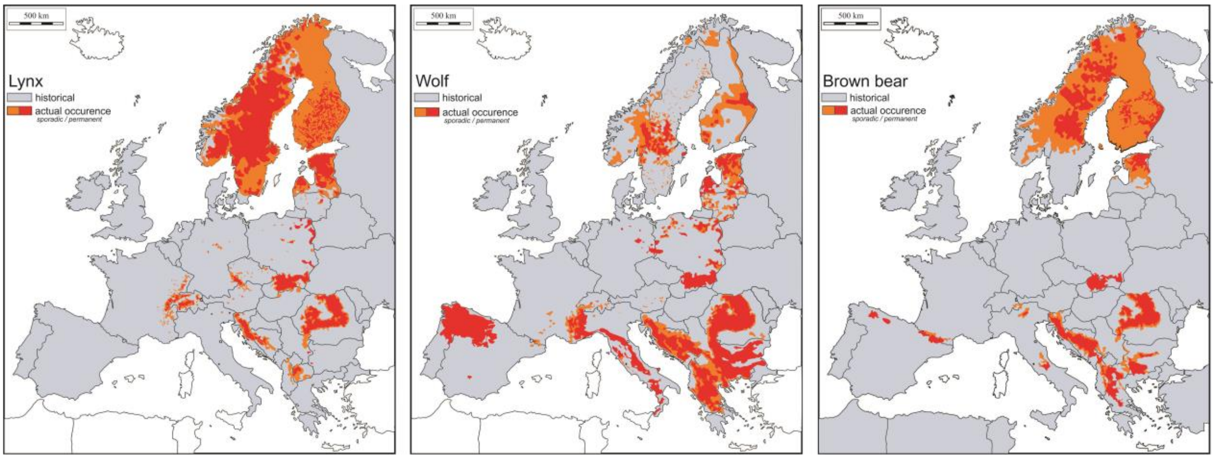

Figure 2: Current distribution (sporadic and permanent) of Eurasian lynx (*Lynx lynx*), wolf (*Canis lupus*) and brown bear (*Ursus arctos*) in Europe. Adapted from Kaczensky et al. 2013.

1.2 Conflicts arising from the presence of large carnivores

Large carnivores personify wilderness and attract public attention. This is why they are often used as flagships species for conservation programs (Linnell et al. 2000; Kruuk 2002; Fascione et al. 2004). But, despite the rising interest in their conservation, the rapid recovery of large carnivores through areas where they have been absent for decades has led to numerous problems. Their recovery in Europe has generated a re-emergence of ancient conflicts with human interests (Kaczensky 1996). Their predatory behaviour conflicts with local economic activity, such as livestock and game farming (Cozza et al. 1996; Boitani 2000). Human tolerance is still low toward predators, especially in countries where carnivores have been absent for a long time, and where the tradition of living closely with predators has been lost (Boitani 1992; Breitenmoser 2000). Conflicts can often be successfully mitigated through traditional techniques (guard dogs, presence of shepherds, small flocks and herds, electric fences) (Kaczensky et al.

1999; Mertens & Promberger 2001; Musiani et al. 2004). However, farmers are often not willing to modify their practices to favour the presence of large carnivores. In order to influence such behaviour, additional mitigation methods have been proposed to avoid an increase of conflicts and potential retaliation against predators. Most European governments currently give financial compensation for livestock killed by large carnivores; NGO's and conservationists propose other solutions such as guard dogs, and electric fences. Even with such mitigation practices, the presence of large carnivores still raises heated conflicts between farmers and the authorities (e.g. Enserink & Vogel 2006).

Farmers are not the only opponents to the return of large carnivores. Both real and perceived competition with hunters for game species is still an important obstacle for their return (Graham et al. 2005). Game species are economically important for people working in the commercial hunting business and game farming, but no financial compensation is given for loss. Sport hunters see large carnivores as competitors for prized ungulate trophies (Breitenmoser et al. 2010). Conflicts between hunters and large carnivores happen everywhere in Europe, but they are more heated in areas where predators have been reintroduced (Breitenmoser et al. 2010). Where hunters are allowed to sustainably hunt large carnivores, conflicts are apparently less acute.

These types of conflicts have expanded along with the return of large carnivores in Europe. With the ongoing expansion of large predators, these conflicts are likely to increase. Because of the problems they represent and the costs involved in conflict mitigation, there is a current debate on the appropriate place of large carnivores in the current human-modified landscape that we know today, and their place in future landscapes (Packer et al. 2013a, b).

II. LAND SPARING VERSUS LAND SHARING

With the demand for space created by global human population growth and their increased consumption of resources, along with their associated infrastructure and habitat conversion, the negative impact on wildlife and biodiversity as a whole is likely to increase (Tilman et al. 2002). Two approaches have been proposed to reconcile the competing needs of humans vs biodiversity (Green et al. 2005; Phalan et al. 2011).

The first one, *land sparing*, consists of separating human-used lands and lands allocated to wildlife. The idea is that wildlife should be protected separately and away from human habitats to protected areas large enough to achieve long-term conservation of populations. Land sparing can be expressed through different ways. A common expression of the strategy is reflected in the focus on conservation of wilderness – areas where human activity is minimized. In Europe, where the amount of forests and scrubland is increasing after the land abandonment that began in the mid-twentieth century (FAO 2011), rewilding is seen as a possible embodiment of land sparing. Rewilding is defined as the passive management (i.e. no or low human interventions) of ecological succession with the goal to restore self-sustaining natural ecosystems processes and reduce human control of landscapes (Gillson et al. 2011). Currently, biodiversity efforts in Europe give priority to active management to maintain particular habitats or increase abundance of a specific taxa, inhibiting successional processes that could lead to forest regeneration (Navarro & Pereira 2012). Rewilding Europe through a process of passive management will most certainly change the current biodiversity, with some species increasing in abundance, and others decreasing. The species associated with High Nature Value Farmland (low-intensity farming systems) may decrease due to loss of management but other species now in decline or close to extinction in traditional agricultural landscapes will surely increase thanks to forest regeneration and reconnection of fragmented natural habitats (Keenleyside & Tucker 2010; Navarro & Pereira 2012). Rewilding will also have an effect on trophic interactions and cascading effects between species. For example, the presence of large carnivores can regulate the density of herbivores and thus influence herbivores' browsing impact on landscapes in some situations (Breitenmoser 1998). Rewilding can also bring benefits to people through ecosystem services. These benefits can be indirect (rewilded areas are habitats of conservation value as high or higher than other land management options, Navarro & Pereira 2012) or direct (presence of emblematic species such can increased tourism and hunting). For example, forest regeneration promotes carbon sequestration (Kuemmerle et al. 2008); allows soil recovery and nutrient availability (Pointereau et al. 2008) and regulates hydrological cycles (Körner et al. 2005). In Europe, a rewilding project of is occurring on a large scale; called Rewilding Europe (www.rewildingeurope.com). Its goal is to rewild one million hectares of land by 2022 by reintroducing or facilitating the return of species of interest such as grazers or large carnivores.

An extreme expression of the land sparing strategy calls for fencing wildlife. This widespread physical separation between humans and wildlife is only found in a handful of countries in southern Africa, where the human population is exploding and where conflicts with wildlife are longstanding, serious and diverse (*crop raiding* Gunn et al. 2014, Hsiao et al. 2013, Harich et al. 2013; *human death* Skuja 2002, Treves & Naughton-Treves 1999, Kruuk 2002; *livestock depredation* Kissui 2008, Hazzah et al. 2009, Ikanda & Packer 2008; poaching Becker et al. 2013; Gandiwa et al. 2014). Some go so as far as proposing to fence entire protected areas (Packer *et al.*, 2013a,b). There is an on-going debate on the costs and benefits of fencing animals for their conservation (Packer et al. 2013a,b; Creel et al. 2013). Those in favour argue that fences are the only variable having an impact on animal density. Fencing reduces edge effects and prevents predators from preying on livestock and people or prevents herbivores from raiding crops, inducing a decrease in retaliation killing. Fencing can also be a good tool in disease control between wildlife and livestock (Thomson et al. 2004; Grant et al. 2007) and reduces illegal extraction of natural resources by humans. Following these ideas, proponents would like to see huge areas fenced to protect wildlife. Several African countries have already followed this mitigation measure, with most wildlife in South Africa existing inside fenced reserves. Opponents, however, argue that fences could have more downsides than positive effects. Ill-conceived fences could exacerbate the impacts of global warming and prevent mammals finding food during hard times; the fencing of small parcels may reduce the carrying capacity of a landscape and cause habitat fragmentation; wildlife mortality could be caused by entanglement and electrocution; wires obtained from fences are often used as illegal snares for wildlife; genetic depletion will occur with time if there is no human intervention to translocate animals and fences would prevent migratory species from roaming freely (Ben-Shahar 1993; Newmark 1996, 2008; Cumming 2004; Western & Nightingale 2005; Beck 2007; Hayward et al. 2007; Shrader et al. 2010; Boone & Hobbs 2004; Becker et al. 2013).). One of the major problems with fences is that scientists do not know the long-term effects of these structures on wildlife and on ecosystems in general. Durant et al. (in press) identified six research areas where information on the effects of fences is needed to consider them as good conservation measures. First, the price of fencing and fence maintenance over long periods of time would certainly impede the use of such a conservation method by small reserves. It is not clear yet that the cost of fencing would be less than the cost of other conservation measures such as anti-poaching and community engagement which involve local populations in wildlife conservation. With the current budget limitations in conservation, money must be spent wisely to obtain sustainable results and maximize conservation impact, which may not be the case of fences. Second, fencing areas of conflict must be well thought out since conflicts are specific for certain species and contexts. Third, reserve design must be taken into consideration while fencing an area. Natural resources such as water are often shared between humans and wildlife. Fencing an area may prevent wildlife or human communities from having access to resources or may prevent a key habitat from playing a key role in ecosystems. Fourth, fencing runs the risk of disconnecting areas and preventing migratory species from having access to the full range of their habitat requirements. Connectivity must be taken into consideration in fencing design to evaluate its ecological impact. Fifth, the impact of fences on ecosystem services must be understood. Ecological processes often happen on a large scale and fencing may act upon these processes and indirectly have an effect on wildlife and human populations that are often dependent on them. Sixth, fencing could have an impact on local communities as it could limit access to natural resources. It also could exacerbate inequities within communities and marginalize the poorest members of societies. The difficulty with fencing is that the entire ecosystem must be taken into account before an area is fenced, even if the goal is to protect a single species. (Creel et al. 2013). Furthermore, many people just don’t want fences in their landscape and want to see wildlife moving free (Watson 2013).

European wildlife and ecosystem management is a good representative of the second approach uses to reconcile the needs of humans and wildlife. This second approach, *land sharing*, proposes to integrate human activities and wildlife on the same land in a coexistence approach (Carter et al. 2012). This involves both allowing wildlife to occupy human-dominated areas and allowing some human activity in protected areas. However, such approach could raise some problems in the case of large carnivores. Throughout the world, conflicts between humans and carnivores tend to occur the most in rangeland, where carnivores and their prey, and humans and their livestock occur in the same space and where their chance of encounters increases (Zimmermann et al. 2010). Although human-carnivores conflicts happen with different species and in different geographic and socio-economic contexts (e.g. wolves in North America; wild dogs *Lycaon pictus* in Africa; Dingos *Canis lupus dingo* in Australia; tigers *Panthera tigris* in Asia; lynx in Europe; Zimmermann et al. 2010), the consequence are similar between contentious situations. Most of the time, the presence of poorly guarded livestock predisposes large carnivores to livestock killing as they are easier to catch than the quicker and more alert wild ungulate. The resulting severity of conflicts may then be linked to the attitudes and beliefs of the local community (historical events, stories from other communities; Sillero-Zubiri & Laurenson 2001; Zimmermann et al. 2005) although the effect of different social, cultural and economic situations means that losses will not always accurately reflect the severity of the resulting conflict (Zimmerman et al. 2010). Recent studies on some large carnivores tend to show that land sharing and coexistence with humans is possible even at high human densities. One recent example of sympatry between large carnivores and humans is the presence of leopards *Panthera pardus* in agricultural areas in India (Athreya et al. 2013; Athreya et al. 2014). There, leopards have become established in areas of high human density (> 300 humans per km^2, Odden et al. 2014) and rely mainly on anthropogenic food (especially dogs; Athreya et al. 2014). The leopards observed in the recent studies showed some of the smallest home ranges reported until now, especially for individuals occupying the areas of highest human densities. Yet, size of home ranges generally varies with density and spatial distribution of food (Powell 2000). These home range sizes were only comparable to estimates from highly productive protected areas with a high density and diversity of wild prey (Odden & Wegge 2005 showing that areas of high human densities were providing enough food to sustain resident leopards. Reproduction even occurred during the study period (Odden et al. 2014). This sympatry between humans and leopards was possible thanks to temporal adaptations from the leopards. Even if differences between individuals were important, all leopards stayed further from human settlements during the day than at night. Similar results of temporal avoidance were also found for tigers in Nepal (Carter et al. 2012), indicating that large carnivores may be more adaptable to human-used landscapes and more prone to land sharing than what we fought. However, one could say that these examples of co-occurrence between humans and carnivores may not be representative of a worldwide future for carnivores since they happened in India and Nepal where traditional cultural, ethical and religious reverence towards life forms is surely important in contributing to the continued survival of large carnivores (Gadgil & Thapar 1990; Renugadevi 2012, Banerjee et al. 2014). Other examples of large carnivore adaptation to human presence exist throughout the world. For example, in Ethiopia where natural prey is getting scare, spotted hyenas *Crocuta crocuta* mainly get food from scavenging on urban and rural waste. In Transylvania, Romania, bears and people seem able to coexist relatively peacefully even if this coexistence is surely facilitate by the presence of large forest blocks connected to the source population in the Carpathian Mountains; by the use of traditional livestock husbandry techniques and some tolerance towards bears among shepherds (Dorresteijn et al. 2014). All these examples demonstrate the relative adaptability of carnivores towards humans. For some species, mainly small and medium carnivores, this adaptability was push so far that they are now considered as urban carnivores (Gehrt et al. 2010). In Europe, the main example of urban carnivore is surely the red fox *Vulpes vulpes* which has colonized urban areas such as London (Soulsbury et al. 2010), Oslo

(Christensen 1985), Rome (Cignini & Riga 1997), Vienna (Duscher et al. 2005), Geneva (Reperant et al. 2007), Berlin (Schöffel et al. 1991), Brussels (Van Gucht et al. 2010) etc. In Britain, populations of urban Eurasian badgers *Meles meles* can be found in Bristol and Brighton even if worldwide, badgers tend to stay most of the time in agricultural areas and wooded landscapes (Harris et al. 2010). In North America, coyotes *Canis latrans* are now colonizing metropolitan landscapes (Gehrt & Riley 2010) and can be observed in the Chicago and Los Angeles metropolitan areas. The bobcat *Lynx rufus*, even if not present directly in highly developed centers of metropolitan areas, is observed near major cities such as Los Angeles or San Francisco, sometimes in landscapes with a human population around 900 inhabitants per km^2 and with housing density > 350 houses per km^2 (Riley et al. 2010). Some of these species have been dwelling in urban areas for more than 80 years (e.g. red fox) and are still present in these landscapes. This doesn't mean that conflicts with humans are non-existent: urban wildlife can transmit disease, damage physical structures, steal food, attack pets etc. But, even if attitudes of humans towards urban carnivores are not identical between countries or even cities of the same country (Soulsbury et al. 2010), they are generally well accepted by local residents (Harris 1984; König 2008; Hunziker et al. 2001). Human attitudes towards larger carnivores in rural landscapes are generally not as positive as for urban carnivores. Even if large carnivores are able to adapt their behaviour to use anthropogenic landscapes in some places, conflicts with people are likely to occur due to predation on livestock, pets or in the extreme cases, human death.

In Europe, where wild land areas are sparse and where the landscape is mostly a continuum of human-modified areas, land sharing and the coexistence approach is seen as the most favourable (or indeed only possible) solution. Here, the mitigation of conflicts between humans and wildlife and environmental measures to improve biodiversity are seen as prerequisites to conserve wildlife (Farrell et al. 2000; Sutherland 2002). These environmental measures act mainly focused on agricultural interests since 1) agricultural lands represent an important part of European landscapes (more than 50 % of the European land surface is used for agricultural and forestry production, www.europe-fluxdata.eu) and 2) this indicates that the contribution of agricultural areas to biodiversity is critical for successful long-term conservation (Tallis et al. 2009). The intensification of agriculture has led to farmland biodiversity decline in Europe (Vickery et al. 2001; Stoate et al. 2009). To lessen the impact of agriculture and forestry on biodiversity and to try and create multi-functional landscapes, billions of euros are spent every year in Europe through agri-environment schemes (Bengtsson et al. 2000; Kleijn & Sutherland 2003; Habran 2014). These measures, including the promotion of extensive farming systems, a mosaic of landscapes, environmentally sound farming techniques adapted to region-specific needs, or extensive pasture systems that should meet society's demand for environmental outcomes provided by agriculture (www.ec.europa.eu). The potential for these land sharing approaches have been documented for a diversity of smaller species, such as insects (Attwood et al. 2008; Haaland et al. 2011; MacDonald et al. 2012; Woodcock et al. 2013), birds (Perkins et al. 2011; MacDonald et al. 2012; Meichtry-Stier et al. 2014) and mammals (Arlettaz et al. 2010; Petrovan et al. 2013; Meichtry-Stier et al. 2014).

Although solutions are proposed to help small wildlife species persist in European landscapes, there is still considerable scepticism among both the public and wildlife professionals concerning the potential for integrating large mammals, especially large carnivores, into these landscapes. Because these species only persisted in the wilderness areas of Europe in historical times there is a common perception that these are the only areas where they can survive. In order to get past these preconceived ideas there is a clear need to document, model, and visualize the ability of large carnivores to live in modern day, multi-use landscapes.

III. OBJECTIVES

The lynx, like the wolf and the brown bear, is returning to much of Europe after many decades of absence (Breitenmoser et al 2000). But the landscapes they are coming back to are different from those their kin knew decades ago. Most of the land has been profoundly modified by humans. Habitats are heavily fragmented, and continue to be, with the construction of roads, houses and other infrastructures; forests have been converted to agricultural areas. Such landscapes often result in high mortality rates for large carnivores, directly (road accidents; Kramer-Schadt 2005) or indirectly (conflicts with livestock owners, poaching; Andrén et al. 2006). For all these reasons, scientists have long considered that large carnivores avoid human-dominated landscapes (Niedziałkowska et al., 2006; May et al., 2008; Jedrzejewski et al., 2008; Güthlin et al., 2011). Several studies indeed reported the negative impact that such landscapes have on large carnivores through fragmentation by roads (Kaczensky et al. 2003; Bunnefeld et al. 2006; Güthlin et al. 2011; Basille et al. 2013).

However, in some cases, large carnivores have proven to be more tolerant and adaptable to human presence than many could have foreseen (Linnell, Swenson & Andersen, 2000; Treves & Karanth, 2003) and in some cases even profit from human-related features (e.g.: use of garbage, Swenson et al. 2000; Elfström et al. 2014, or the high densities of ungulate prey in fragmented habitats). The emerging picture from these studies is still not well documented and may suggest variations in the extent to which large carnivores may expand in a modern Europe. Information on how large carnivores respond to human-modified habitats on a fine scale is required to both predict where they can potentially live and where potential conflicts might arise between humans and large carnivores. This information will, in turn, help manage these species in a long-term conservation vision. Studies on large carnivore responses to human-modified habitats in Europe are relatively new (Basille et al. 2009; Martin et al. 2012; Basille et al. 2013; Frackowiak et al. 2014), and much information is still lacking. In this thesis, we explored the effect of anthropogenic and environmental factors on Eurasian lynx habitat use. The work has developed around two main axes.

The first axis explores large scale potential patterns of lynx distribution. One of the key methodological aspects concerns the transferability of results obtained from habitat modelling onto geographically different areas. We tested the transferability of results obtained from habitat modelling between regions in Norway. It was tested in two steps. The first chapter explores the transferability of results at a regional scale. We created a map of relative distribution and abundance of roe deer, the main prey of lynx, in southeastern Norway. This map was extrapolated over a larger area than the one used for the sampling of roe deer occurrences data. Transferability success (*i.e.* predictive ability of the map) was evaluated with internal and external data. The establishment of this map was also essential for the completion of the following chapters. The second chapter deals with transferability of results at a larger extent while considering different local predictors. The first goal was to explore the effect of using data obtained from different sampling methods in transferability accuracy. The second goal of this chapter was to obtain a suitability map for Eurasian lynx in Scandinavia to predict potential extension of populations in unoccupied areas.

The second axis of this thesis looks into much more detail about lynx habitat use in relation to anthropogenic and environmental predictors in order to provide insights into the mechanisms behind the patterns explored in the first axis. In the third chapter, we explore lynx tolerance to human presence by looking at the orientation of home ranges within a given landscape. We compared proxies of human disturbance within home ranges with the same proxies at the periphery of the home ranges. From the results of chapter 3, we sought to obtain information at finer scale on lynx habitat use in anthropogenic landscapes. To do that, we looked at lynx response to human-modified landscapes with respect to different behaviours. The disruption of a behaviour (of either anthropogenic or natural origin) can have important consequences on individual fitness. For this reason, information on habitat use for different behaviours expressed by an animal can have important effects on the management of a species. In this perspective, the goal of the fourth chapter is to examine lynx habitat selection for three behaviours (day-beds, moving and killing) at the within home range scale.

THE STUDY SPECIES – THE EURASIAN LYNX (*LYNX LYNX*)

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I. THE EURASIAN LYNX (*LYNX LYNX*)

1.1 Biology

The Eurasian lynx (*Lynx lynx*) is the largest member of genus *Lynx,* larger than the North American species (Bobcat *Lynx rufus* and Canadian lynx *Lynx canadensis*) and the Iberian species (Iberian lynx *Lynx pardinus*) (Wilson & Mittermeier 2009). Body weights can range from 12 to 35 kg with a high dimorphism between males and females. They reach between 70 and 130 cm long and 65 cm in height at the shoulder.

Considering the size of its European distribution, differences of habitat use occur between populations. In Europe and Siberia, the main habitat of the Eurasian lynx is forest. In Central Asia and at extreme northern latitudes, the lynx inhabits tundra, semi-arid habitats, open and sparsely wooded regions (Breitenmoser 2000). Although its range of prey species is quite vast, the Eurasian lynx preys mainly on the smallest available ungulates. In Europe this means the roe deer and the chamois (*Rupicapra rupicapra*) (Molinari-Jobin et al. 2004; Herfindal et al. 2005). In the northern part of its range, lynx also feed on semi-domestic reindeer (Nybakk et al. 2002). Sporadically, they can prey on the largest ungulates, red deer, moose (*Alce alces*) and wild boar (Breitenmoser et al. 2000; Odden et al. 2006). When ungulate densities are low, their diet can also be composed of lagomorphs, birds, and rodents (Nowell and Jackson 1996). Livestock can also be a part of the diet of lynx, particularly sheep, when they are left unsupervised (Sunde et al. 2000; Odden et al. 2002).

Lynx are solitary animals, except for females with young during the kitten rearing period. Home ranges are highly variable in size between the different populations, ranging from 100 to more than 1500 km^2 (Herfindal et al. 2005). This variation in range size between regions can be explained by the availability of prey, the habitat types and the composition of the prey community (Breitenmoser et al. 2000; Grigione et al. 2002). Usually, a male home range is overlapped by the home range of one or two females (Breitenmoser et al. 1993; Schmidt et al. 1997). Female ranges rarely overlap, except in Scandinavia where the ranges of some females can exceptionally overlap completely with those of their daughters. There is little variation in home range size, except for reproductive females which have a smaller home range during the breeding period (Schmidt 1998; Linnell et al. 2001b). Lynx travel at night but the distance travelled can be highly different between individuals of different age, social status, sex and between the differences in hunting success and prey density (Schmidt 1999; Breitenmoser et al. 2000; Bunnefeld et al. 2006).

During the reproductive period, males follow the females to check their reproductive status. Mating takes place between February and mid-April and birth takes place after 67-74 days, usually in late May. Most often, the litter size consists of 2-3 cubs but it can vary between 1 and 4 (Gaillard et al. 2014). The mortality rate of the cubs is very high, with 50% of the offspring dying before adulthood (Breitenmoser et al. 1993). Cubs stay with their mother until they are 10 months old, when they are able to feed by themselves, and before the next mating season (Samelius et al. 2012). Males are sexually mature around the age of three years while females are sexually mature at the age of two.

The only known enemy of lynx is humans, but some confrontation events with wolves and wolverine can cause lynx death (Breitenmoser et al. 2000). The main cause of lynx mortality is anthropogenic, with starvation, intra and interspecific killing and disease having a minor role

(Andrén et al. 2006). Human-caused mortality can be either indirect or accidental (e.g. road traffic accidents, change of habitat; Huck et al. 2010; Kramer-Schadt et al. 2004, 2005; Basille et al. 2013) or direct (e.g.: hunting, poaching; Andrén et al. 2006).

1.2 Past and Present Lynx distribution

Lynx were present everywhere throughout Europe until the mid-Holocene. They suffered a great reduction in range of distribution by the end of the 19th century (Breitenmoser et al. 2001; Linnell et al. 2009). By the middle of the 20th century, only some small relicts remained, and the total European lynx population reached its lowest with the Scandinavian population extremely reduced and divided. The only other remaining populations were in the Carpathian, in the eastern Baltic and in the Balkan regions (Breitenmoser et al. 2001; Linnell et al. 2009, Figure 5).

Compared to the other two large carnivores (wolf and brown bear), lynx access to food is limited since they do not scavenge but feed only on what they kill themselves. Ungulate densities were particularly low in most European countries in the 19th and early 20th centuries and lynx were forced to prey on domestic livestock, which caused conflicts and led to persecution (Breitenmoser et al. 2001). Low prey density, human persecution and destruction of their main habitats (forests) led to the diminution and/or extermination of lynx populations in many areas of Europe. Even if loss of habitat and reduction of prey species were important drivers of lynx decline, human induced mortality (enhanced through the payment of bounties) must have been the main driver for the diminution of an ecologically stressed species. Improvements of ecological conditions (reforestation, increase in prey density) and new legislation in the mid-20th century stopped the decline of Eurasian lynx in Europe and favoured its return (Breitenmoser 1998; Breitenmoser & Breitenmoser-Würsten, 2008).

The subsequent recolonization of Europe by lynx was also favoured by several reintroduction programs. The first reintroduction project took place in Germany in 1970, in the Bavarian Forest, and was followed by 14 other reintroduction projects in eight countries. A total of 175 lynx were reintroduced between 1970 and 2007 (Linnell et al. 2009). Currently, the lynx is strictly protected within all EU Member States (except Estonia) under the Habitats Directive. However, to reduce conflicts, the culling of lynx by hunters is authorized in Sweden, Finland and Latvia (Kaczensky et al. 2013). In Norway, the lynx is protected under the Bern Convention although it is managed as a game species with an annual quota for hunters.

Currently, eleven populations of Eurasian lynx have been identified in Europe (Breitenmoser et al. 2001; Kaczensky et al. 2013), dispersed over 23 countries. Only five of these populations are autochthonous while the others originate from reintroduction programs from the 1970s and 1980s (Kaczensky et al. 2013; Table 1).

Table 1: Estimations of the numbers of lynx for each European population (except Ukraine, Russia and Belarus) based on Kaczensky et al. 2013.

Population	Minimum Number of lynx	Autochthonous/ Reintroduced population
Scandinavian population	± 400 in Norway and 1400-1900 in Sweden	Autochthonous
Karelian population	± 2500	Autochthonous
Baltic Population	± 1600	Autochthonous
Carpathian population	±2300	Autochthonous
Bohemian-Bavarian population	± 50	Reintroduced
Harz Mountain population	10	Reintroduced
Balkan population	Less than 50	Autochthonous
Dinaric population	Between 120 and 130	Reintroduced
Alps population	Between 130 and 160	Reintroduced
Jura population	> 100	Reintroduced
Vosges population	19 (?)	Reintroduced

In total, between 9000 and 10000 lynx are currently present in Europe (excluding Ukraine, Russia and Belarus). Most of these populations are stable even if some decrease may be occurring in the Bohemian-Bavarian population, the Vosges and the Dinaric populations. There is at present an apparent increase in the Karelian and the Jura populations (Kaczenski et al. 2013; von Arx et al. 2004). Non-confirmed sightings of lynx have recently been made in Belgium and Luxembourg (http://observations.be/).

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STUDY SITE & GENERAL METHODS

I. STUDY SITE

1.1 Overview of Scandinavia

The Scandinavian Peninsula is made up of Norway and Sweden (Figure 3) of 775 300 km^2 has a resident population of nearly 15 million of people living at an average density of 19 humans/km^2.

Figure 3: Map of Scandinavia (from Google Earth)

Scandinavia covers nearly 775 000 km^2 (with 58% inside Sweden). The peninsula is characterized by complex environmental gradients of latitude and altitude. In general, with increasing latitude and altitude boreal forest (Norwegian spruce *Picea abies* and Scots pine *Pinus sylvestris*) gives way to a thin belt of birch (*Pinus* sp.) forest before reaching alpine tundra. The Gulf Stream excerpts a strong influence in Norway, greatly moderating the effects of latitude. Topography is highly varied, ranging from flat and rolling terrain to steep mountains (the Scandes Mountains run the length of the peninsula), deep valleys and fjords. Densities of human habitation and infrastructure, as well as the extent of forest conversion to agriculture, are greatest in the south, and in a few coastal areas towards the north. Although most of the area is still covered by semi-natural habitats (forest, bogs, alpine-tundra) these are intensively exploited for forestry, livestock grazing, hunting and recreation.

1.2 Study site

Most analyses in this thesis were realized from data collected across a series of study sites in southern Norway (Figure 4). Scandinavia has one of the most important populations of Eurasian lynx in Europe (around 2000 individuals) and has been conducting research and monitoring lynx since the 1990's. Data have been collected in the framework of a multifaceted project on lynx ecology called Scandlynx (http://scandlynx.nina.no/scandlynxeng/Home.aspx) and the Large Predator Monitoring Program (www.rovdata.no). The data used throughout the articles were mainly telemetry data (both Very High Frequency VHF and Global Positioning System GPS location data). Counts of lynx tracks in the snow (family group data); pellet-group counts for roe deer were also used to infer habitat selection. These data were collected by the public (family group data), researchers (telemetry and pellet-counts data) and national wildlife management agencies (count of road accidents) since 1994.

The main study site was located in southern Norway centered on the capital city of Oslo (Figure 4). The north-western part of the area is dominated by steep elevation gradients from valleys and up to mountains > 1000 m above sea level. This area is forested with a domination of Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. The south-eastern part of the study area included patches of deciduous forest within a more human-modified landscape. The forest is fragmented by cultivated land. It is the most human-dominated part of Norway with a mean density of 59 (±349 SD) inhabitant/km^2. In both parts, lynx have access to roe deer, red deer and sheep.

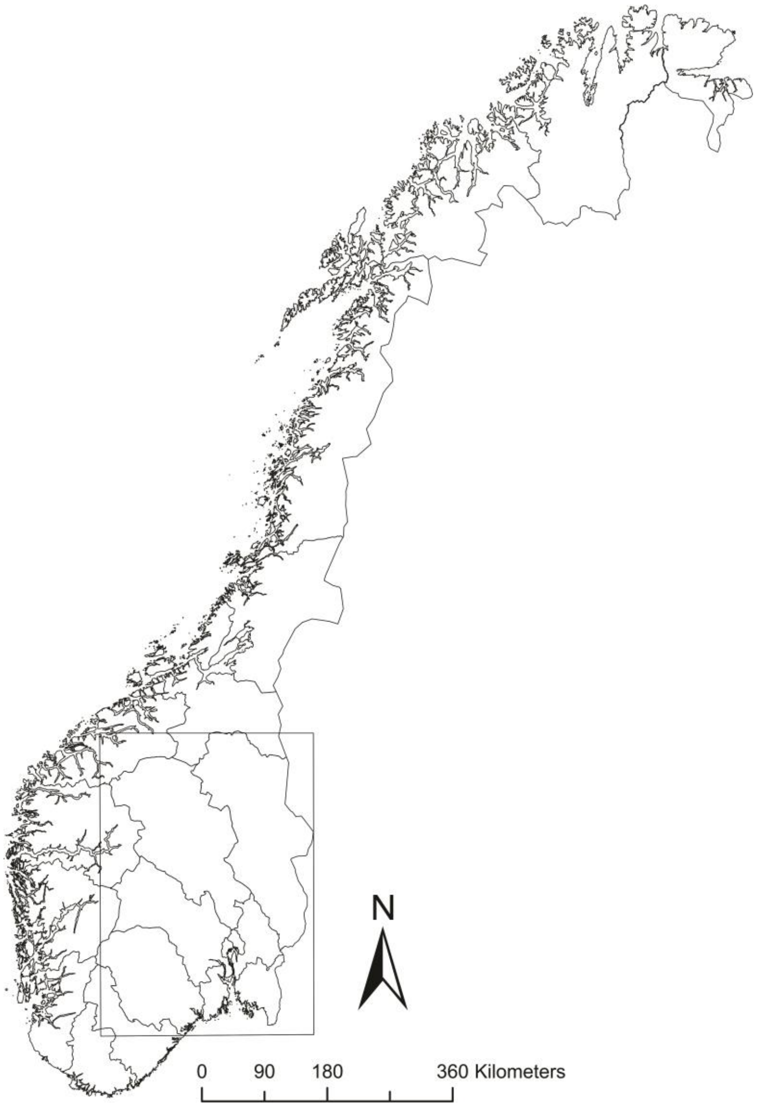


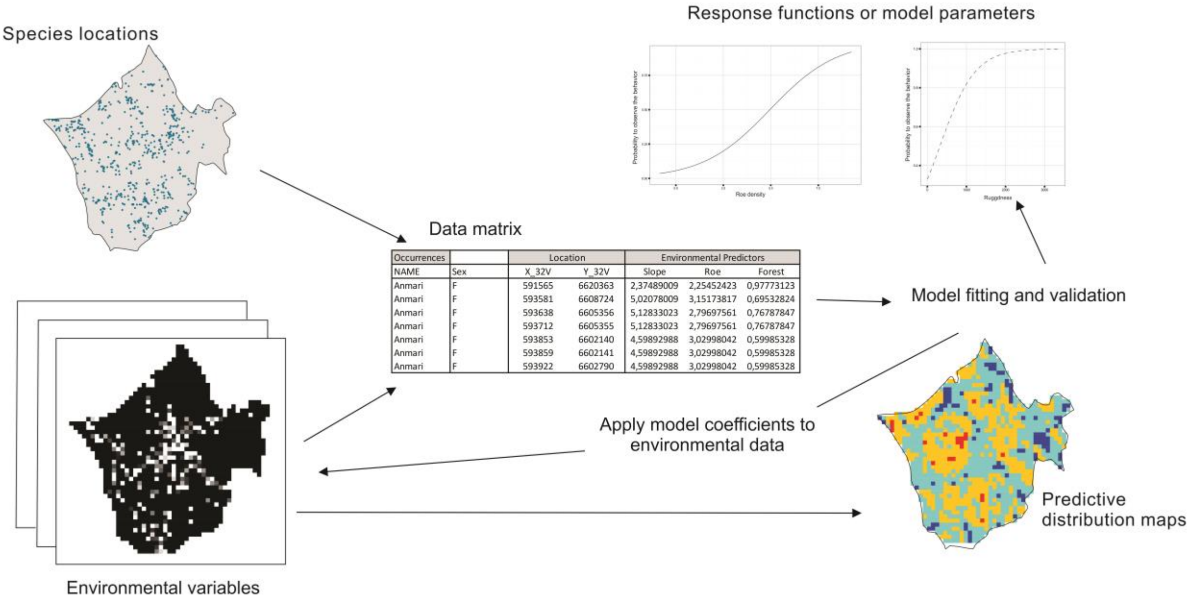
Figure 4: Localization of the study site in Norway

II. GENERAL METHODS: MODELLING HABITAT USE OF RECOLONIZING POPULATIONS

2.1 Ecological understanding of species distribution models

As large carnivores progressively re-occupy some of their original range in modern Europe, they are now confronted with totally different landscapes than the ones they roamed decades ago. The wider European landscape has been profoundly modified; from the presence of large forested areas to a mosaic of human-dominated landscapes (*i.e.* agricultural fields, large network of roads, infrastructure, urban and peri-urban areas, etc…). Large carnivores were originally reintroduced to the wildest areas of Europe during the 1970s and 1980s (Alps, Jura, Vosges…; Linnell et al. 2009; Kaczensky et al. 2013), but they are now recolonizing some of the most human impacted landscapes. Sightings of wolves and lynx are recorded closer and closer to cities (Enserink & Vogel, 2006). In this part of Europe where habitat fragmentation, roads and human density are among the most important of the continent and where natural habitats and true wilderness are sparse, persistence of large carnivores is not an easy target. In such area, large carnivores will have to use mostly human-modified landscapes to meet their ecological requirements.

The ecological requirements of species are shaped by several factors such as the distribution and availability of food, human activities and landscape features (Zimmerman 2004). These factors determine species occurrence within geographic landscapes. Based on statistical approaches, species distribution models (SDMs) relate species occurrence data to environmental factors thought to influence species distribution (Franklin 2009; Figure 5).



Occurrences		Location		Environmental Predictors		
NAME	Sex	X_32V	Y_32V	Slope	Roe	Forest
Anmari	F	591565	6620363	2,37489009	2,25452423	0,97773123
Anmari	F	593581	6608724	5,02078009	3,15173817	0,69532824
Anmari	F	593638	6605356	5,12833023	2,79697561	0,76787847
Anmari	F	593712	6605355	5,12833023	2,79697561	0,76787847
Anmari	F	593853	6602140	4,59892988	3,02998042	0,59985328
Anmari	F	593859	6602141	4,59892988	3,02998042	0,59985328
Anmari	F	593922	6602790	4,59892988	3,02998042	0,59985328

Figure 5: The different steps in species distribution modelling and predictive mapping. Spatially explicit (georeferenced) species occurrence data are linked with digital maps of environmental predictors and values of environmental predictors for species locations are extracted. A statistical model describing the relationship between species occurrence and environmental data is developed. The parameters or response functions are evaluated and these coefficients or decision rules are applied to environmental maps yielding spatial predictions of species distribution or habitat suitability (adapted from Franklin 2009).

SDMs are linked to the species niche concept (Austin 2002; Guisan & Thuiller 2005; Soberón 2007; Hirzel & Le Lay 2008). Species niche is characterized as "the hypervolume defined by the environmental dimensions within which a species can survive and reproduce" (Hutchinson 1987). Two types of niches are further considered: the *fundamental* niche (potential) which is the response of a species to environmental variables with no biotic interactions (such as competition, predation…); and the *realized* niche (actual) that considers the effects of biotic interactions (Austin & Smith 1989; Austin 2002). Since actual species occurrences are used to create SDM, it is considered that the outcome of the model is a description of the *realized* niche in the environmental dimensions (Guisan & Thuiller 2005; Austin 2002). The SDM outcome is then mapped in geographical space to obtain a map representing the probable distribution or habitat suitability of the species (Araújo & Guisan 2006; Soberón 2007; Figure 6). These maps are commonly used to infer species distribution and habitat suitability, to target priority zones of conservation, to assess threats toward those zones, to manage invasive species or design reserves (Franklin 2009; Jimenez-Valverde et al. 2011). SDMs may also be used to (*i*) spatially predict a species distribution across others regions and (*ii*) to provide insights into species tolerance and habitat requirements.

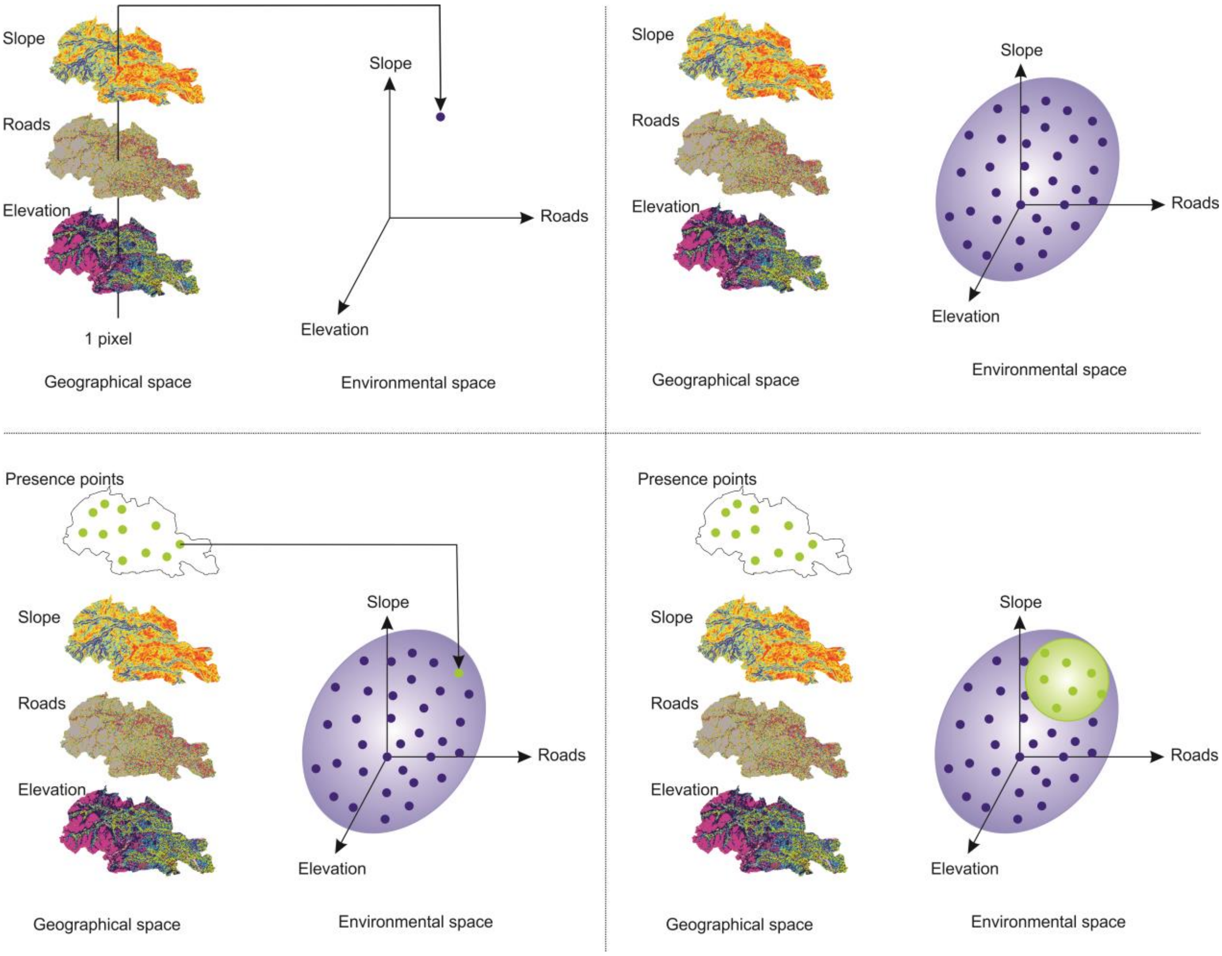


Figure 6: Representation of the relationship between the geographical and the environmental space. A) Value of one pixel in the geographical space is represented in the environmental space. B) The group of pixels from the geographical space forms the hypervolume of the niche (blue). C and D) If we take into consideration the location of the presence of a species then it forms the realized niche (green).

2.2 Interpolation and extrapolation abilities of Species Distribution Models

SDMs not only used to infer habitat use of a species in one focal region, but also to generalize these results to other regions (Fielding & Haworth 1995). SDM are widely used to spatially predict (or geographically extrapolate) species occurrence across regions. The procedure yields predictive maps used to generalize species occurrence for areas where survey data are lacking (interpolation) or areas expected to be colonized (extrapolation). Interpolation enables the prediction of results in the same area as the one used for training the model, i.e. to fill gaps in an already known species distribution (Araújo & Williams 2000; Segurado & Araújo 2004; Fortin et al. 2005). This process may be useful for species with large space requirements; for which it is time and money consuming to obtain data on daily habitat use on a large geographic scale. Although collection improvement (e.g. use of GPS collars, snow tracking) allows precise data to be obtained on intensive study sites, these techniques often represent only a subset of a population. Predictive habitat models are used to generalize results obtained from some parts of the area to the entire area, and hence to create distribution maps across whole populations to ensure efficient management plans (Guisan et al. 2013). The second type of generalization, called extrapolation or transferability, permits the building of a model in one area and exporting it to another area (Dobrowski et al. 2010). Such methods have been particularly useful for resource management and conservation planning including dealing with invasive species or ecological restoration (Guisan et al. 2013; Barnes et al. 2014). However, transferability can lead to serious errors in model outputs (Brown et al. 1998; Osborne & Suárez-Seoane 2002). Indeed, models are applied on abiotic environmental predictors that most often reflect resources that have no physiological importance for the species (e.g.: elevation, slope…) (Guisan & Zimmerman 2000). But these abiotic predictors are expected to differ increasingly from the model designed, as one draws further away from the area where the model was generated. Even if quality and type of predictors can have an effect, the difference in range values of predictors between sites can lead to spurious results (Randin et al. 2006). This question of transferability of results is particularly important for large carnivores since meaningful habitat suitability maps have to be created over very large areas where the environment and its underlying ecology can vary significantly from one part of the range to another.

2.3 Tolerance and requirements - Resource Selection Functions

It is generally considered that in static (statistical) species distribution models the species are in equilibrium with the environmental conditions. The observed distribution is then representative of environmental tolerances and resource requirements (Franklin 2009). An ecological concept relating species to their resource requirements in SDM studies is "resource selection". Resource selection describes selection of resources (i.e., environmental variables such as habitat, food) by animals. Different statistical methods can be used in resource selection functions (RSFs) but all predict the probability of use of a resource unit by a species (Boyce et al 2002; Manly et al. 2002; Boyce 2006). RSFs are usually represented graphically as response curves, which depict a function describing the relationship between species occurrence and the values of an environmental variable. The concepts of niche and resource selection can be seen as similar. RSFs represent the probability of resource use relative to resource availability and can be used for example to define the selection of home range by a species. RSFs are proportional to probability of use, while SDMs represent the likelihood that a species occurs at a given location, or, in other words, the probability of species presence (Franklin 2009).

These different methods have been used throughout the thesis, with Chapters 1 & 2 dealing with transferability and Chapters 3 & 4 with lynx habitat selection. Generalized Linear Models analyses were used in Chapter 1 to determine where roe deer, the main prey of lynx, were distributed in southeastern Norway and how well the model was able to transfer results to the regional scale. In Chapter 2, Maximum Entropy Modeling (Maxent) approaches were used to develop maps of lynx habitat suitability at the Scandinavian scale and to test the effect of sampling designs on transferability of results at large scale. Tolerance and habitat selection of Eurasian lynx towards human-modified landscapes are described in Chapters 3 & 4. Two hypotheses were tested: (1) that lynx orientate their home ranges to avoid high human presence and (2) that, at finer scale, lynx selection of human-modified landscapes (tested by RSFs) varies with behaviours. Each chapter of the present thesis represents an independent scientific paper.

CHAPTER 1 – USING ZERO – INFLATED MODELS TO PREDICT THE RELATIVE DISTRIBUTION AND ABUNDANCE OF ROE DEER OVER VERY LARGE SPATIAL SCALES

Using zero-inflated models to predict the relative distribution and abundance of roe deer over very large spatial scales

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Using zero-inflated models to predict the relative distribution and abundance of roe deer over very large spatial scales

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In Norway, recovering populations of large carnivores commonly prey on roe deer (*Capreolus capreolus*). Understanding predator habitat use and ecology requires fine-scaled information on prey distribution and abundance. However, the massive spatial scales at which large carnivores use the landscape presents many practical and statistical challenges for developing functional prey distribution models. Pellet-count data from > 1000 km of transects gathered across southeastern Norway between 2005 and 2011 were used to derive a map of the relative prey abundance for roe deer. These data were modeled using zero-inflated hurdle models using both environmental and anthropogenic variables. Snow depth and agricultural fields were the most significant variables in explaining both presence and abundance. Internal *k*-cross validation of the model showed medium accuracy (Spearman's $r = 0.35$), whereas external evaluation carried out on the basis of independently collected snow-tracking data (Spearman's $r = 0.37$) and hunting statistics (Spearman's $r = 0.88$) showed higher accuracy. The map generated can facilitate both the study of broad scale processes linking predators and prey as well as roe deer management in southeastern Norway.

Introduction

Large carnivores, like Eurasian lynx (*Lynx lynx*) and wolves (*Canis lupus*), are returning to many areas of Europe from which they have been absent for decades (Linnell *et al*. 2009, Linnell & Boitani 2012). Managing their recovery in the heavily human-modified landscapes of Europe requires a detailed understanding of how they relate to a range of habitat and landscape features. Several studies have focused on issues like effects of human infrastructure and broad scale habitat availability (e.g. Schadt *et al.* 2002). However, knowledge of prey distribution and abundance is an important precondition to gain a better mechanistic understanding of carnivore demography, movements and habitat use (Karanth *et al.* 2004, Herfindal *et al.* 2005). Eurasian lynx and wolves have very large annual home ranges [100–1500 km^2 for lynx (Linnell *et al.* 2001, Mattisson *et al.* 2011), and 100–2000 km^2 for wolves (Mech & Boitani 2003, Matisson *et al.* 2013)] as compared with their prey's home ranges [e.g. roe deer (*Capreolus capreolus*): 1 km^2 (Jeppesen 1989, Cederlund & Liberg 1995, Morellet *et al.* 2013)], and carnivore population processes occur over even larger areas. Models of prey habitat selection are often built at much smaller scales than the areas over which they need to be utilized for large carnivore research. Due to logistical reasons (lack of funds, time etc.) it is rarely feasible to intensively map ungulate abundance over very large areas. Such surveys will also only reflect a snapshot of animal distribution. When working with large carnivores, the use of predictive prey distribution models are therefore needed to extend the models to larger scales. When modeling issues related to lynx and wolves, this can imply study areas in the order of several tens of thousands of square kilometers (e.g. Basille *et al.* 2009, 2013). The logistical and financial constraints of all research projects impose limitations on how much sampling is possible. An additional challenge with sampling is imposed in study areas with low prey densities, which tends to give zero inflated data.

Species distribution models (SDMs) are empirical models relating species occurrences to eco-climatic variables on a correlative basis (Guisan & Thuiller 2005, Fitzpatrick & Hargrove 2009). They are mostly produced to map the potential geographic range of species within study regions, according to the hypothesis that their distribution is actually influenced by the factors investigated. While SDMs are commonly used for conservation purposes, few have used zero-inflated models. Zero-inflated models are useful tools when data sets exhibit more zeroes than acceptable for a Poisson or negative binomial model (Zeileis *et al.* 2008), which is not unusual with ecological data sets such as counts of abundance or presence/absence. Statistically ignoring the existence of zero inflation can cause bias in parameter estimates as well as overdispersion (Zuur *et al.* 2009). When assessing the relationship between the abundance of a species and its environment, it has been shown that hurdle models performed better than Poisson or negative binomial models (Potts & Elith 2006), which justified their uses in this study.

Southeastern Norway has recently been recolonized by the Eurasian lynx and the wolf, two large carnivores regularly involved in conflicts with humans due to their predation on wild and domestic animals. For management programs to be effective, information on large-carnivore behavior and future abundance are needed. Roe deer are the main prey of lynx as well as a very common prey of wolf in this region (Wikenros 2001, Müller 2006, Odden *et al.* 2006). We mapped roe deer distribution and abundance in regions where lynx and wolf are present. Even though roe deer are known to be widely distributed throughout much of the country (Andersen *et al.* 2004), and their fine scale (habitat patch level) pattern of habitat use is well documented and understood (e.g. Torres *et al.* 2011), no abundance maps are currently available for any scale. For this reason, we used hurdle models based on pellet count data to investigate the importance of ecological and anthropogenic factors related to the species' abundance. In Norway, snow has a high impact on roe deer occurrence as it can affect both access to food and mobility, for example when escaping from predators (Jędrzejewski *et al.* 1992). Based on this, we expected roe deer to be negatively associated with increasing snow depth (Prediction 1). We also expected a selection for agricultural lands (Prediction 2) since human-dominated landscapes are known to provide high-quality ecotones and important forage resources (Panzacchi *et al.* 2010, Torres *et al.* 2012). Other variables that describe habitat, climatic and human disturbance characteristics were also included in an attempt to improve model predictions.

We created a large-scale abundance map that will then be available as a map layer to

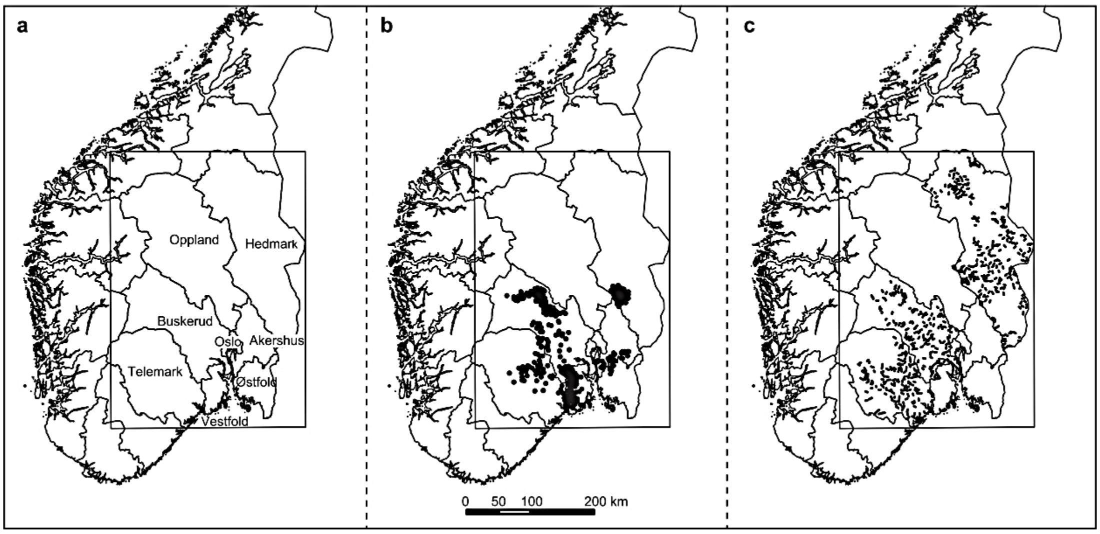

Fig. 1. (**a**) The five regions of the study area are situated in southeastern of Norway, (**b**) pellet group transects are represented by grey dots, and (**c**) snow-tracking transects are shown with black lines. The frame represents the extent of the predictive maps.

study large carnivore ecology (e.g. Gervasi *et al.* 2014). As the area to which the map was extrapolated was very large, the evaluation process was particularly important, and was conducted in two ways: firstly, using a spatial *k*-fold cross validation procedure and, secondly, by comparing the model results to two independent abundance indices. Based on the predictive map generated, we briefly discuss the implications for predator population distribution and dynamics.

Material and methods

Study site

The study took place in southeastern Norway across six counties (Telemark, Vestfold, Østfold, Buskerud, Hedmark and Akershus) (Fig. 1, extent area: 15 550 km^2). The area spans a wide range of environmental conditions: from highly fragmented agricultural areas in the southeast (Østfold and Akershus) to forest dominated areas in the north (Hedmark). The topography is also highly variable: from flat or hilly areas in the east to higher altitudes with steep slopes in the west and north (elevation [mean ± SD]: 1020 ± 593 m). Overall, the forests are intensively exploited, and are mainly composed of Norwegian spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), hoary alder (*Alnus incana*) and birch (*Betula pubescens*). The study site is described in greater detail in other papers (Basille *et al.* 2009).

Sampling of pellet data

Data on roe deer pellet groups were accumulated for the whole study area during the years 2005, 2007, 2008 and 2011. Pellets were counted along 346 transects by different observers who all received the same training in pellet identification. Transects were stratified by altitude and distributed randomly inside and adjacent to the areas surrounding polygons representing the home-ranges of lynx that were equipped during the same period with GPS collars (Fig. 1). Each transect consisted of a 1 km × 1 km × 1 km triangle. A total of 30 circular 10-m^2 plots were surveyed for pellets, with one plot located at 100-m intervals along each triangle (Wahlstrom & Liberg 1995). This is logistically a very efficient field design with the starting point coinciding with the final point (Lindén *et al.* 1996). Each transect was chosen to fit within one 1 × 1 km square on the UTM grid. If a transect fell on areas that could not be surveyed, such as a lake, urban area, or an area totally dominated by agricultural fields, it was moved to the nearest 1 × 1 km square containing sufficient natural or semi-natural habitats. Within a transect, individual plots were only counted if they fell on natural or semi-natural habitats (e.g. forest, bogs, alpine tundra, moorland, rough meadows). Agricultural fields under cultivation were not counted since it was not possible to walk on fields during spring due to young crops growing and because many fields were ploughed in spring, which destroys the ability to count pellets accumulated during the autumn/winter. Although we can expect roe deer to be frequent users of fields when foraging, they rarely bed on fields and did not use them much during daylight, usually retreating to the surrounding forests to rest. Therefore, we did not expect the failure to count pellets on fields to greatly bias our results considering the spatial scale (1 km^2) of our analysis.

Following Mayle *et al.* (2000) a pellet group was counted when it contained six or more pellets, when it was considered to have been produced during the same defecation event (same color, texture, size, shape) and when the group center was within the plot. Other herbivorous species are present in the same area such as moose and red deer but assigning pellet group to the right species was possible due to differences in size and shape.

Data were collected in spring (mainly May and early June) to avoid high vegetation in summer and snow cover in winter. The pellets accumulated thus mainly reflected the habitat use for a period extending from autumn, through winter, to spring. However, pellets decompose slowly in this northern environment, such that it is also possible that some summer pellets were counted as well. Given that the accumulation period covers periods when roe deer are in both winter and summer ranges (for the proportion of the population that migrates) the results should be viewed as reflecting year round distribution.

Explanatory variables for relative roe deer distribution and abundance

Explanatory data used to create the roe deer map were classified into two categories, relating to habitat (i.e. environmental data) and to human activity (Table 1). These data were chosen based on previous fine-scale studies of roe deer habitat selection (Torres *et al.* 2011, Torres *et al.* 2012) and on the availability of digital maps at the scale of the study area. The data were recoded into raster layers of 1 km^2 spatial resolution using a geographic information system (ArcGIS 9.3.1). In order to account for the broader landscape effect of each variable, we computed their respective average value around the center of each sampling plot (i.e. focal cell). This computation was carried out using moving windows of 3 × 3 km, 7 × 7 km and 11 × 11 km pixels, which approximately correspond to buffers of 1.5, 3.5 and 5.5 km radii around the focal cell.

Table 1. Explanatory variables used in the analysis. All covariates were at a 1 km^2 scale.

Variables	Explanation
Habitat	
Forest	Proportion of forest within each pixel
Bogs	Proportion of bogs within each pixel
Snow	Mean snow depth (mm) during winter within each pixel
Slope	Mean of the slope (degrees) within each pixel
Hillshade	Index of the combination of the slope and aspect of the terrain in relationship to the azimuth and aspect of the sun within each pixel
Climatic gradient	Regional variation (gradient) from coast to inland and from oceanic/humid to continental each areas within pixel
Human activity	
Field	Proportion of agricultural fields within each pixel
Public roads	Total length (km) within each pixel
Private roads	Total length (km) within each pixel
Human density	Number of individuals within each pixel

The Global Land Cover 2000 database was used to calculate the amount of forest, fields and bogs within each pixel. Layers for slope and hillshade were obtained from the Norwegian Mapping Authority and interpolated snow depth maps were obtained from the Norwegian Meteorological Institute. Hillshade is a measure of the incoming solar radiation for the pixel at 12:00 on 20 June. The values ranged from 0 to 255, where pixels with the value 0 are in complete shadow whereas pixels with the value 255 are facing directly (perpendicular) towards the sun. Accordingly, it is an index representing a combination of the slope and aspect of the terrain in relationship to the azimuth and aspect of the sun. An additional environmental variable, called Climatic Gradient, was obtained from Bakkestuen *et al.* (2008). This variable is a principal component extracted from a set of 54 environmental variables and represents regional variation (a gradient) from coast to inland and from oceanic/humid to continental areas. This axis corresponds to one of the bioclimatic gradients used in expert classification of Norway into biogeographical regions (Bakkestuen *et al.* 2008). Data on public and private roads were obtained from the Norwegian Mapping Authority. Data describing human density came from Takle (2002). All the processed explanatory variables were checked for collinearity prior to analyses (filter = 0.7, Zuur *et al.* 2009). From this, collinear variables, such as snow, temperature and elevation, were filtered. Thereby, the most significant variables that remained may not be the ones with the more direct or intuitive mechanistic influence (e.g., if an animal does not occur at high elevation, it is more likely because of temperature-influenced vegetation than elevation itself). Instead, it is those with the highest statistical power that were retained, even if they may only reflect other factors that have a more direct mechanistic influence.

Statistical analysis

Because of the low densities at which boreal forest mammals like roe deer occur, many transects gave zero-count values (53% of the total number of transects for roe deer). This obvious zero-inflation was instrumental in our analytical approach. Zero-inflated models, like hurdle models, are used when the response variable contains more zeroes than expected based on a Poisson or negative binomial distribution (Zuur *et al.* 2009). Developed by Cragg (1971), hurdle models consist of two parts. The first part uses a binomial distribution to model the presence and absence of a species. The second part is a count model with a Poisson, negative binomial or geometric distribution that can either accommodate zero observations or not (Barry & Welsh 2002) and models species abundance. The positive observations arise from crossing the zero-hurdle or probability threshold (Potts & Elith 2006, Zuur *et al.* 2009). This approach therefore recognizes the possibility that the mechanisms that determine presence/absence can be different from those that determine abundance (Ridout *et al.* 1998). The presence of over-dispersion appeared in the dataset thus justifying the use of negative binomial distributions instead of Poisson distributions (Zuur *et al.* 2009).

To initialize the model, the same set of environmental and human-related covariates were included in both parts of the hurdle (i.e. the presence/absence part and the abundance part). This was achieved in parallel, and independently for the covariates computed within the 3 × 3 km, 7 × 7 km and 11 × 11 km moving windows. To select which buffer size was more accurate, three hurdle models with the same covariates, but collected at different scales were applied. The model with the more accurate buffer size was evaluated using the stepAIC function in R (package MASS, Venables and Ripley, 1999) and $AIC_c < 2$. Finally, the best model was constructed with the covariates that explained a significant ($p < 0.05$) amount of variation of roe deer data. In addition, in order to account for spatial autocorrelation, we computed and added a residual autocovariate (RAC) to our best model based on the method provided in Crase *et al.* (2012). In essence, this approach consists of constructing an autocovariate based on the spatial autocorrelation found in model residuals. In addition, the method has been shown to increase the accuracy of parameter estimates and therefore further limits the potential bias in parameter estimation linked to spatial autocorrelation (Dormann *et al.* 2007).

In order to evaluate the distribution map, two different approaches were used. In the first approach, a spatial *k*-fold cross-validation (Nilsen *et al.* 2009b) was applied as an internal evaluation, with a *k*-fold partition of five groups representing sub-regions within the study area (Fig. 1). The model was trained iteratively on four of the five areas using the hurdle procedure. The remaining testing set was used as a validation set. As a second approach, external evaluations were carried out based on two independent datasets representative of relative prey densities. These datasets were compared with prey abundances predicted by the distribution map. The first dataset represents the number of snow tracks recorded along a total of 587 transects, each 3 km in length, collected during winters 2008–2011 in our study area. The correlation between the average number of tracks for all years and per transect (corrected for the number of days since snowfall) and the average abundance of animals predicted by the map in a 3 km buffer zone (diameter equivalent to the length of the snow tracks transects) from the center of each transect was assessed using Spearman's rank correlation. The second dataset consisted of hunting statistics (hunting bag) at the municipal level (Statistics Norway, www.ssb.no), which recorded the number of shot roe deer during the period 2009–2011 in each municipality of the whole study area. It is expected that hunting statistics give only a coarse representation of species abundance, but previous studies have shown that a very good concordance was present between hunting statistics and other independent indices of roe deer abundance (Grøtan *et al.* 2005, Nilsen *et al.* 2009a). The fact that harvest abundances varied by several orders of magnitudes across the study area also reflects the fact that abundance differences are dramatic.

All analyses were carried out using R (R Development Core Team 2011) and the package *pscl* (Zeileis *et al.* 2008). The package *raster* (Hijmans & van Etten 2011) was used to generate the predictive maps. The spatial extent of the predictive map was selected in order to include the area of lynx and wolf distribution in southeastern Norway (Basille *et al.* 2009). Spatial autocorrelation was investigated using Moran's *I* statistic from the package *spdep* (Bivand *et al.* 2008).

Results

Hurdle models

The most parsimonious hurdle model (i.e. which minimized AIC values) is presented in Table 2. The best model was obtained with the 3 × 3 km (1.5 km radius) buffer and identifies factors associated with both roe deer presence (binomial part), and roe deer abundance (negative binomial part) within this area of presence.

Agricultural fields and snow depth were the only variables retained by the model. Presence and abundance of roe deer were positively asso-

Table 2. Response variables retained after hurdle models selection for roe deer: parameter estimation, standard error (SE) and level of significance. The left part of the table represents the best model (buffer scale: 1.5 km) without the autocovariate (RAC). The right part represents the best model with the autocovariate. The model in the right part of the table was kept to predict the map.

	Without RAC			With RAC		
	Estimate	SE	*p*	Estimate	SE	*p*
Negative binomial part						
Fields	2.613	0.540	< 0.001	2.209	0.393	< 0.001
Log(Snow)	–0.674	0.164	< 0.001	–0.510	0.147	< 0.001
RAC	–	–	–	0.178	0.039	< 0.001
Binomial part						
Fields	5.242	1.542	< 0.001	5.050	1.561	0.001
Log(Snow)	–0.823	0.191	< 0.001	–0.833	0.193	< 0.001
RAC	–	–	–	0.316	0.180	0.079

ciated with the area of fields within the buffer but negatively associated with snow depth.

Model evaluation

On average, Spearman's correlation for the internal evaluation was $r_S = 0.35$ but there were differences between the regions (Buskerud: $r = 0.19, p < 0.05$; Telemark: $r_S = 0.27, p < 0.001$; Hedmark: $r_S = 0.66, p < 0.0001$; Vestfold: $r_S = 0.31, p < 0.0001$; Ostfold/Akershus: $r_S = 0.34, p < 0.05$). The resulting map indicated that roe deer reach the highest abundances in the southeastern part of the investigated area. The range of predictions for the pellet-counts was between 0 and 15.3 pellets. The predictive map (Fig. 2) was compared with external independent datasets. The Spearman's correlation between snow-tracking transects and model prediction values was significant ($r_S = 0.37, p < 0.001$) and at a coarser spatial scale (i.e. municipality level), the correlation between model predictions and the hunting bags was highly significant ($r_S = 0.888, p < 0.001$) (Appendices 1 and 2).

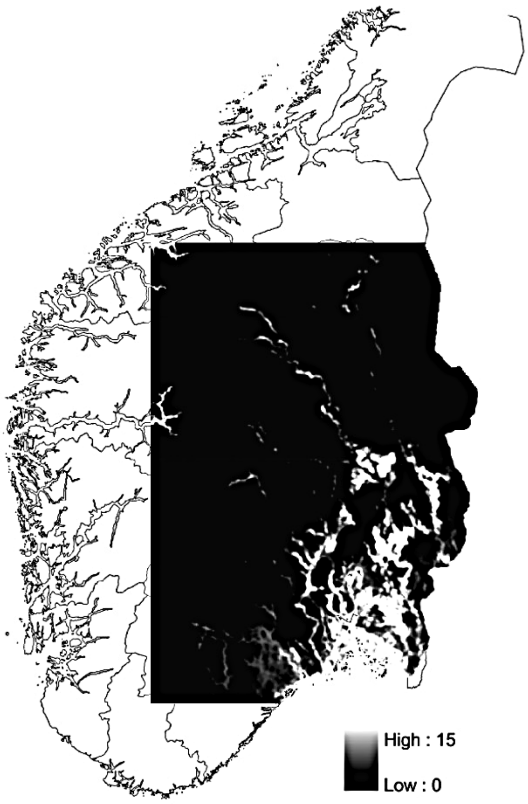

Fig. 2. Roe deer distribution and pellet-count abundance in southeastern Norway.

Discussion

Habitat preferences

The factors that were retained from the model selection procedure to explain the observed variation in pellet density are generally consistent with what is known about the species' ecology. The spatial and temporal impact of snow depth on roe deer distribution (Holand *et al.* 1998), habitat use (Mysterud *et al.* 1997, Ratikainen *et al.* 2007) and dynamics (Grøtan *et al.* 2005, Nilsen *et al.* 2009a) is well documented, as is their preference for edge habitats at the forest–field interface (Kjøstvedt *et al.* 1998, Torres *et al.* 2011). In Norway, roe deer harvest is subject to only fairly loose management protocols and harvest quotas are rarely filled. This implies that the broad scale species abundance reported in this study is mainly influenced by biological drivers, rather than specific management decisions. Therefore, variables that were found to influence roe deer abundance (snow and fields) very likely depict natural ecological factors influencing roe deer.

Pellet counts, zero inflation and data resolution

When pellets were counted, the observer error was likely to be small because of the small size of the plots which facilitated careful searching and the fact that pellets from roe deer could be readily discriminated. Young red deer pellets can be similar to roe deer pellets but red deer are present only in a small part of the study area which limited the possible error and in the event of doubt, pellets were brought in from the forest for comparison with a reference collection.

Pellet group counts have been shown to be effective for other habitat selection studies (*see* Kurki *et al.* 2000, Shorrocks *et al.* 1998) and have been a technique widely used to assess ungulate habitat use and density since the 1940s (Neff 1968, Tsaparis *et al.* 2008). Although pellet group surveys are an established method, criticism has been made concerning their use in the estimation of population densities, distribution and habitat use (Neff 1968, Collins & Urness 1981, Rowland *et al.* 1984). With pellet group counts, major concerns come from spatial variation of pellet decay rates (e.g. between moist and dry habitats, Harestad & Bunnell 1987) and from the sensitivity of defecation rates to seasonal variation (Mitchell *et al.* 1985, Rogers 1987). However, use of such indirect count methods are often favored to direct count methods in ungulate research as they demand less effort, cost less and are sometimes more adapted for some habitats such as forest (Marques *et al.* 2001, Laing *et al.* 2003). Also, results from pellet group counts on broad scale habitat use have been shown to be comparable to those obtain by other methods such as radio-tracking (Guillet *et al.* 1995, Månsson *et al.* 2011). Defecation rate was not an issue in this analysis as we did not use it to estimate absolute roe deer abundance.

Hurdle models were used to gain information on the distribution and abundance of roe deer pellet groups, which can be interpreted as a relative distribution and abundance of roe deer. No test was made on decay rates of roe deer pellet groups in the different habitat types in the study area prior to analysis and this could have biased the results. However, in Norway, pellet groups can persist for many months because of the temperate climate, cold winters and general lack of dung beetles. Even if the decay rate is higher in some habitats than others, the difference is likely to be small and impact on pellet group counts should be limited.

Another difficulty we were confronted with in our analysis was the coarse spatial scale of the environmental variables to which we had access. Most of the variables available to use as covariates in the model were only available at the scale of a roe deer's home range (1 km^2) and did not differentiate between types or age classes of forest habitats which have been shown to be important for explaining fine-scaled herbivore distribution and density (Torres *et al.* 2011). If the map data had allowed us to work at the individual habitat patch scale instead of the transect scale we would probably have been better able to make predictions of roe deer distribution and relative abundance. However, such fine scale data are rarely available for large spatial scales.

Model evaluation

Our predictions were evaluated using both snow track transects and hunting bags. These internal evaluations supported our results, although there was much unexplained variation. Species Distribution Models never explicitly incorporate underlying processes, and this constitutes the first important limitation of our study. For instance, this could strongly limit the extrapolative ability of SDMs out of the training area and further explains why the accuracy of spatial *k*-fold cross-validations herein constructed are weak (roe deer, on average $r_S = 0.35$).

On the contrary, the external evaluation carried out with the hunting bag data showed good accuracy ($r_S = 0.88$, for hunting data on roe deer), although our predictions were made for an area 8 times larger than the initial area used for training (although the training areas were scattered throughout the prediction area and covered all parts of the ecological gradient). The higher accuracy of the coarse scale (external evaluation) as compared with that of the local scale (internal evaluation) is surprising since model extrapolation at large scales may potentially lead to significant errors (Guisan & Zimmermann 2000). However, a similar effect has been reported in studies using climate variables at different scales in which coarse scale data (such as NDVI) outperformed local scale climate variables (such as weather station data) when explaining variation in performance traits of large herbivores (Post & Stenseth 1999, Nielsen *et al.* 2012). Thereby, we can assume that the hurdle SDM built in the present study on the pellet-counts data was well suited for mapping broad scale roe deer distribution across southeastern Norway.

Previous studies emphasized the fact that roe deer distribution and density are important drivers for lynx habitat selection in Norway (Basille *et al.* 2009), most likely explained by the importance of this ungulate on lynx diet (more than 80% in winter, Odden *et al.* 2006).

Although there were a number of challenging issues, we believe that the map that we have generated is sufficient for the study of broad scale processes linking predators and prey, including the investigation of the impacts of predators through an increased ability to explain spatial patterns in predator density, movement and kill rates. This map gives information relevant for roe deer management in the face of lynx predation at a regional scale because it will allow a more accurate prediction of relative predator impact as well as a more detailed understanding of the mechanisms of lynx predation behavior. Concerning the external validation of our map with hunting bags, we believed that this roe deer map could be a good asset for roe deer management in Norway at a regional scale. While one could wish for more confident predictions and fine scaled resolutions, the realities (concerning the abundance of training data and the resolution of map data) of large scale studies imply that it is unlikely that it will be possible to improve on the level of accuracy that we obtained for similar species with broad distributions and generalist habits.

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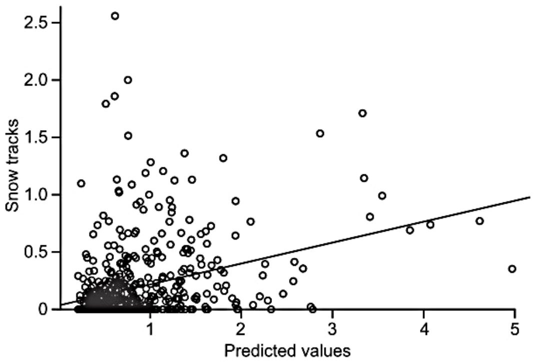
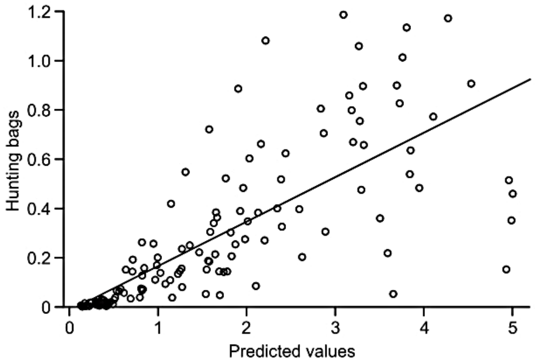


Appendix 1. Graphical representation of the correlation between the predicted values of pellet groups in a 3 km buffer around the snow track transects and the density of snow tracks observed in the transects. r_S = 0.37, $p < 0.001$.



Appendix 2. Graphical representation of the correlation between the predicted values of pellet groups in the different municipalities and the density of roe deer observed in each municipality. r_S = 0.88, $p < 0.001$.

CHAPTER 2 – THE DANGERS OF EXTRAPOLATION: THE EFFECT OF DIFFERENT TRAINING DATA ON HABITAT MODEL TRANSFERABILITY FOR EURASIAN LYNX IN SCANDINAVIA

The dangers of extrapolation: the effect of different training data on habitat model ransferability for Eurasian lynx in Scandinavia.

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Abstract

In species distribution models, model extrapolation (or transferability) and sampling bias are areas of active research. Sampling bias can affect model predictions while extrapolation from one region to another ecologically different region can be problematic in terms of performance of models. Here, we explored the effect of using different sampling designs on model transferability using Eurasian lynx occurrence data in Scandinavia. Scandinavian lynx populations have been monitored and studied for the past 20 years, providing us with a huge amount of data. To test the effect of sampling design on model transferability, radio-telemetry data and snow-tracking records were used to build respective models of female lynx suitability, while data on harvested animals were used to evaluate the models. We tested model transferability by dividing Scandinavia into three ecologically distinct regions that were separated by qualitative differences in prey species availability. In addition, a best possible habitat suitability map for Scandinavian lynx was produced to be used in management planning with respect to geographically differentiated lynx management zones. The analyses revealed that models based on telemetry data gave slightly different results concerning estimates of lynx habitat suitability than models trained on snow-track observations. Transferability between eco-regions was difficult even if maps extrapolated from models trained on snow-tracking records performed better than maps obtained from models trained on telemetry data. Models developed at the Scandinavian scale indicate that almost the entire peninsula constitutes lynx habitat with elevation (-), presence of forest (+), and steepness (+) explaining most of the variation.

Introduction

Knowledge about where species can occur, either in a region where species are already present, or in areas of potential spread, is fundamental for conservation planning of native species and for the management of invasive species [1, 2, 3, 4]. Since the 2000's, species distribution models (SDMs) have assisted conservation planning [5, 6]. These models correlate environmental attributes to species locations in order to characterize the ecological niche of a species or to predict the potential suitability of a landscape [7]. SDMs are used by conservationists to estimate suitable areas for a species in regions where it is already present or to assess probability of presence in regions where the species is known to not occur yet or where no surveys have been conducted and to plan population recovery and reintroductions [8].

One of major traits of ecological science is to identify relationships and patterns that can be generalized and repeatable [9]. This is especially important with distribution and suitability maps derived from SDMs since they are often used to extrapolate information obtained from one region to another that may have different environmental conditions. This ability to give reliable predictions of species distribution from one region to another (or from one time to another) is referred to as model generality [10] or model transferability [11] and is an area of active research [12-14]. The ability to transfer a model in space (or in time) is dependent on the predictor variables [15]. Three kinds of environmental predictors exist: (i) resource predictors that are consumed by the species; (ii) direct predictors which have physiological importance but are not consumed (e.g. temperature) and (iii) indirect predictors which have no direct physiological relevance (e.g. elevation, slope, vegetation type) but which are assumed to reflect resource or direct predictors [16]. Since direct predictors have more direct mechanistic effects and are supposed to remain stable between regions, they should be more transferable in space [12]. Inversely, indirect predictors might reflect different habitat properties in different regions. By their nature, indirect predictors are easily measured and maps of many parameters are currently available for large parts of the planet thanks to remote sensing technologies (e.g. Corine vegetation map; Landsat images). For these reasons, they are widely used in distribution modelling. But the preferential use of indirect predictors can have negative consequences for model transferability since indirect predictors are expected to differ increasingly with distance in space or in time [12]. Previous studies have tested the relevance of model transferability for several parameters such as effect of predictor variables [17], effect of modelling methods, effect of species [18, 14, 19, 20] and effect of sampling design [13, 21, 22].

In SDMs, sampling design (i.e. the sample of presence only or presence-absence data that is used to build the model) should not be biased or model predictions can be affected [23, 24, 25]. For example, previous studies found that systematic survey designs give better accuracy than random sampling [23, 26, 27] and that the number of observations was less important than a well-dispersed distribution throughout the species' environmental space [28, 29]. However, occurrence data will often have been collected for other purposes than the estimation of distribution which may lead to sub-optimal data distribution. To develop reliable species distribution models for conservation planning, it is of critical importance to evaluate the potential differences in results induced by using different sampling designs and data sources.

To explore the effect of sampling bias on model transferability, occurrence data from Eurasian lynx (*Lynx lynx*) in Scandinavia (Norway and Sweden) were used. Three reasons justified the use of Scandinavia as a regional model. Firstly, the lynx populations in Norway and Sweden have been subject to very intensive research and monitoring over a period of 20 years, providing huge amounts of data on which to build and validate models. Data on harvested animals, snow-tracking records and radio-telemetry all provide different types of data, with different distributions and biases, providing an ideal basis for testing methodological issues. Secondly, the Scandinavian peninsula can be considered as a single biogeographic region such that it might be expected that models would have a high degree of internal transferability. Thirdly, Scandinavia hosts one of the largest lynx populations in Europe making it an important area for the conservation of this species. The chronic nature of conflicts between lynx and livestock (semi-domestic reindeer and sheep) and with hunters is leading to many discussions concerning zoning of lynx management areas. For this it is essential to have an idea as to how much of the peninsula represents potential habitat.

Availing of the large amount of data available from Scandinavia, we predicted female lynx habitat suitability using the commonly-utilized presence-only method Maxent [30]. We focused only on adult female lynx so as to assess the availability of habitat suitable for a reproductive population, to avoid potentially including areas that were only suitable for dispersal or for males, who are known to adopt a riskier behavior [31]. To test for the effect of sampling design, we conducted statistical analyses on two different datasets (telemetry data vs. snow-tracking data). To test for model transferability between regions, we compared the models derived from three ecologically distinct regions in Scandinavia, which can be separated by qualitative differences in prey species availability. Evaluation of model fit was made using the Area Under the Curve (AUC) approach and an independent dataset of lynx occurrence (shot lynx). In addition to the insights into methodology, we aimed to produce a best possible habitat suitability map for Scandinavian lynx that can be used in management planning with respect to geographically differentiated lynx management zones [32, 33].

Material and methods

Study area

Scandinavia covers nearly 775 000 km^2 (with 58% inside Sweden). The peninsula is characterized by complex environmental gradients of latitude and altitude. In general, with increasing latitude and altitude boreal forest (Norwegian spruce *Picea abies* and Scots pine *Pinus sylvestris*) gives way to a thin belt of birch (*Pinus* sp.) forest before reaching alpine tundra. The Gulf Stream excerpts a strong influence in Norway, greatly moderating the effects of latitude. Topography is highly varied, ranging from flat and rolling terrain to steep mountains (the Scandes Mountains run the length of the peninsula), deep valleys and fjords. Densities of human habitation and infrastructure, as well as the extent of forest conversion to agriculture, are greatest in the south, and in a few coastal areas towards the north. Although most of the area is still covered by semi-natural habitats (forest, bogs, alpine-tundra) these are intensively exploited for forestry, livestock grazing, hunting and recreation.

The study area can be divided into three ecologically distinct regions based on the distribution of the main lynx prey species; roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and reindeer (*Rangifer tanrandus*) [34, 35, 36] (Figure 1):

- South: This covers the area up to the southern edge of the semi-domestic reindeer herding area (the border is formally designated as it reflects legal access to grazing rights). Roe deer are the main prey of lynx and are found in all forested areas with the exception of some of the fjord coastline of southwest Norway. Red deer are also abundant in all of southwestern Norway, and are also present at lower densities in most forested areas of the Norwegian part of the region, as well as in some pockets of Sweden. Wild mountain reindeer are present in the areas above treeline on the Norwegian mountains in this region.
- Central: This covers the area north from the southern limit of the semi-domestic reindeer herding area to the biogeographic limit of roe deer distribution. In this area, roe deer are present in all forest areas (although their density decreases dramatically towards the north). Red deer only have a sporadic occurrence in the Norwegian sector. Semi-domestic reindeer (grazed by Sami communities) are present in all the alpine tundra areas (above treeline) and also seasonally graze in most of the forest areas.
- North: This corresponds to the area north of the biogeographic limit of roe deer (only sporadic occurrences occur to the north). Semi-domestic reindeer herding is widespread, with reindeer being common in most alpine-tundra and forested areas, although long migrations cause dramatic seasonal fluctuations in their availability.

Occurrence dataset

Our occurrence dataset was composed of a total of 35 013 points of presence (Figure 1) collected from two different sampling methods; telemetry and snow-tracking (Table 1).

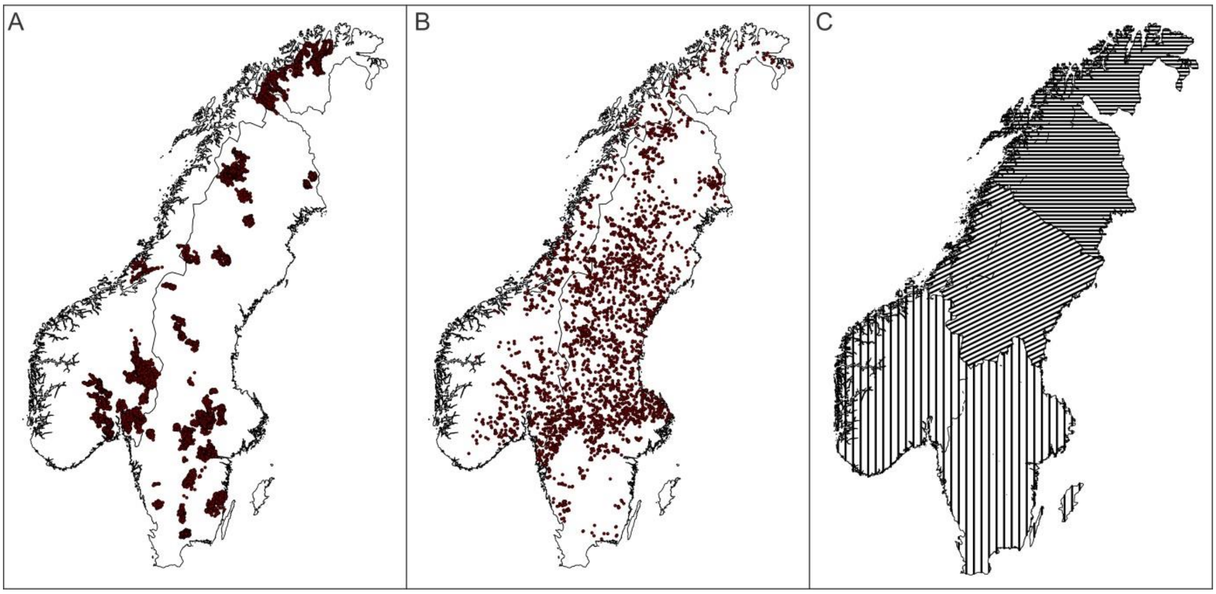

Figure 1. Distribution of lynx occurrences for the two datasets. A) Telemetry data (n = 31967 locations from 133 individuals); B) Snow-tracking observations of family groups (n = 3046 observations) and C) the three ecoregions (south, central, north) used in the analysis.

Table 1. Number of occurrence data observed for each sampling design and for each ecologically distinct parts of Scandinavia.

	Global	**South**	**Central**	**North**
Nb. of telemetry locations (nb. of individuals)	31967 (133)	16200 (91)	1863 (12)	13903 (30)
Nb. of family group track observations	3046	1497	1094	452

Telemetry data

The first group of data consisted of 31 967 VHF and GPS locations (with only one point selected per day per animal to reduce autocorrelation) collected from study areas covering most of the peninsula, with 41% collected from Sweden. Telemetry data were collected between 1995 and 2014 on 133 adult females. Lynx were equipped with VHF (mainly before 2005) and GPS collars. They were captured using a range of methods, including box-traps, foot-snares, darting from helicopters, or being treed by trained hounds. Lynx were immobilised using a mixture of ketamine (100 mg) and medetomidine (4 mg) reversed with atipamezole (5 mg) [37]. All procedures were approved by the Norwegian Experimental Animal Ethics Committee and by the Animal Ethics Committee for Sweden.

Snow-tracking (Family group count data)

Counting lynx family groups is the main monitoring method used for lynx in both Norway and Sweden national monitoring programs [38, 39]. Since kittens stay with their mother until they are 10 months old, tracks in the snow of more than one individual during early winter indicate a family group (mating does not take place before late March and the sexes largely remain separate before then). In this analysis we have used 3046 records (76% from Sweden) of snow-tracking observations from family groups (reproductive females with dependent young; [40]). These observations were mainly reported by the public, but all were verified by trained personnel who have followed the tracks for more than 1 km. The family group locations are non-replicated, and represent the geographical mean of separate observations of each family group each year. Family groups were clustered based on a set of rules developed from telemetry data. We used lynx family-group data from the winters 2004-2012, corresponding to reproductive events during the summers 2003-2011.

Independent dataset

To obtain a measure of performance for the models, we used an independent dataset of lynx occurrences. This dataset is composed of 1237 locations of legally shot female lynx in Norway and Sweden compiled between 1994 and 2014.

Distribution and bias

The data sets all have slightly different potential biases associated with their distribution. Telemetry data is widely used to build habitat suitability models as it involves very detailed data with no fine scale location bias (animals are located irrespective of how they use the landscape). However, this data tends to come from a limited sample of individuals, producing data with a higher degree of dependence, and tends to be dominated by data from one or a few study sites that are rarely chosen randomly. Our data reduces this by having an unusually large sample size of 133 adult females, with data collected from 8 very large study sites that cover most of the landscape variation found within Scandinavia. The monitoring data on family group track observations is collected by a wide public from across Scandinavia, so there is no study site selection bias on the broad scale. However, there is a potential fine scale bias caused by the increased probability of people finding tracks close to houses and roads. The independent dataset from shot lynx lies somewhere between. Although lynx tend to be shot close to roads, the fine scale bias is not so extreme as family group observations as it involves active snow-tracking and pursuit. Lynx are also shot over very large parts of Scandinavia, especially in Norway, removing any study site selection bias.

Environmental variables

A range of environmental variables were used as predictor variables including information on habitat type, topography, environmental productivity and human presence. Multicollinearity between model variables was investigated through Pearson's correlation tests with the software ENMtools (version 1.4.4.; [41, 42]), and no significant correlation was detected between variables ($P < 0.5$). The variables were chosen according to previous established knowledge regarding lynx habitat preferences in Scandinavia [43-48].

Habitat type was obtained from the a 30 x 30m NORUT map (Norway) and a 25 x 25 m Swedish Land Cover (SDM; National Land Survey of Sweden) map (Sweden), which were reclassified into a 1 x 1 km scale with 5 aggregated classes that were defined in a manner that we, a priori, considered to be meaningful to lynx based on our existing knowledge of their habitat use and the factors that affect their demography [43, 44, 47]. It was designed to reflect the way that the Scandinavian landscape is structured. Because of the overall low degrees of habitat conversion, low human population density and low degree of infrastructure development we had to use low thresholds for the presence of these variables for them to be present at all in aggregated classes. This was based on the idea that human influence extends beyond the area of urbanized or agricultural land. These classes were, (1) *Urban areas*: when at least 10% of the area in a 1 km^2 pixel was urban area, then the whole pixel was classified as urban areas; (2) *Agriculture*: when at least 25% of the area in a 1 km^2 pixel was cultivated farmland, then the pixel was classified as agricultural areas; (3) *Forest*: if the majority of the area in a 1 km^2 pixel was forest, then the pixel was classified as forest, this includes both coniferous and deciduous forest and bogs; (4) *Open area below treeline*: if the majority of the area in a 1 km^2 pixel was open area below treeline, then the pixel was classified as open area below treeline, which includes moorlands and heaths; (5) *Open area above treeline*: if the majority of the area in a 1 km^2 pixel was open area below treeline, then the pixel was classified as open area above treeline, including alpine tundra, snowbed vegetation, rock, ice and permanent snow. We began to classify starting with class 1, with subsequent classes only being used if they were not already classified by a previous class. To separate open areas above and below treeline, we used a layer representative of the existing climatic forest treeline created from Digital Elevation Model (DEM) provided by the Norwegian Mapping Authority.

Topography was defined by 50 x 50m DEM (from the Norwegian Mapping Authority and National Land Survey of Sweden) and slope (calculated from the DEMs by the Vector Ruggedness Measure (VRM), [49]). Environmental productivity was obtained from the normalized difference vegetation index (NDVI; [50]). Human presence was expressed through human density and road density.

Model fitting

We used the machine learning method of maximum entropy implemented in the Maxent software (version 3.3.3k) to develop the models [30]. Maxent is a freely released software that has been developed explicitly for modelling presence-only data, and which is able to handle complex interactions between responses and predictors [30, 51, 52]. Comparisons with other modelling techniques have demonstrated that Maxent performs well [51, 53]. Maxent defines the unknown probability distribution of maximum entropy (i.e. the most spread out) of the known occurrences of a species constrained by environmental conditions. The expected mean value of each environmental variable is close to the average value for the pixels with known species occurrences [30, 54]. Since our goal was to illustrate the potential impact of different input data on model transferability, Maxent was parameterized with the default settings [55], but using a 10-fold cross-validation procedure, and 5000 instead of 500 iterations. While overfitted (i.e. overly complex) models are likely to limit transferability [42], Maxent handles overfitting by regularization mechanisms. The regularization parameter defines an error bound around the average value of the occurrences, and it regulates the model to fit the data correctly without being too complex [55]. To explore if higher regularization parameters increased the predictive ability and transferability of the models, we ran models with regularization parameters equal to 1,2,3,4 and 5 [19]. The default regularization parameter (i.e. 1) was the most appropriate for our dataset, based on the Area Under the Curve (AUC).

We first trained the model over all Scandinavia and then trained models for each of the three eco-regions. Each of the regional models were also extrapolated to the two remaining regions (e.g. the models were trained on region A, then transferred on region B and C).

Measures of models performance

To estimate the effect of different data sets and model transferability, trained model performance was assessed using the Maxent AUC calculation from the randomly withheld test (hereafter AUC_{PO}). In this case, AUC represents the probability that a presence site is ranked higher than a background site, the sites being randomly chosen. According to [56], an AUC value > 0.9 is excellent, 0.80-0.90 is good, 0.70-0.80 is fair, 0.60-0.70 is poor and 0.50-0.60 is failed. However, AUC does not give information on the calibration precision of the model but only measures the capacity of the model to discriminate between presence and background [57, 58].

For this reason, we used the occurrence data from the independent dataset (shot lynx) to obtain an evaluation of the models' predictions using a presence/pseudo-absence design. In each eco-region, we generated the same number of pseudo-absence locations as the number of shot lynx locations. The pseudo-absences were generated outside of known lynx home ranges (kernel home ranges estimated from the telemetry data). These shot lynx occurrence (presence) and pseudo-absence data were used to calculate different measures of model performance. Firstly, an AUC based on presence/pseudo-absences (hereafter AUC_{PA}) was calculated for each extrapolated map (North extrapolated from the South model; North extrapolated from the Central model; Central extrapolated from the North model; Central extrapolated from the South model; South extrapolated from the North model and South extrapolated from the Central model). Secondly, we calculated Cohen's kappa coefficient (hereafter kappa; [59]) for each map. Kappa uses data from a confusion matrix to measure agreement between presence/pseudo-absence [60]. Kappa values range from -1 to 1. And thirdly, we used the Spearman correlation and the Schoener's D index [61] to calculate the correlation and agreement in probability of suitability for each pixel between maps. Schoener's D index measures similarity between predictions of habitat suitability and is suggested to be best suited for SDM outputs [62]. It considers the probability distributions across space of the difference in the probability of presence of two species. This D index ranges from 0 (no overlap) to 1 (total overlap).

Results

Effect of sampling design

Trained models obtained from occurrence data collected from different sampling designs showed differences in their suitability scores (Table 2; Spearman correlation and Schoener's D index). Global models obtained from the two different occurrence datasets showed medium levels of correlation and overlap (Figure 2). The South models produced from the two different datasets are the most similar, while the North models showed the greatest differences. Based on visual inspection, three major areas showed the greatest discrepancies between maps generated from the different data sets: (1) the Stockholm – Uppsala area of Sweden, (2) the greater Oslo area around Oslo fjord in Norway, and (3) the far North of Norway (Figure 3).

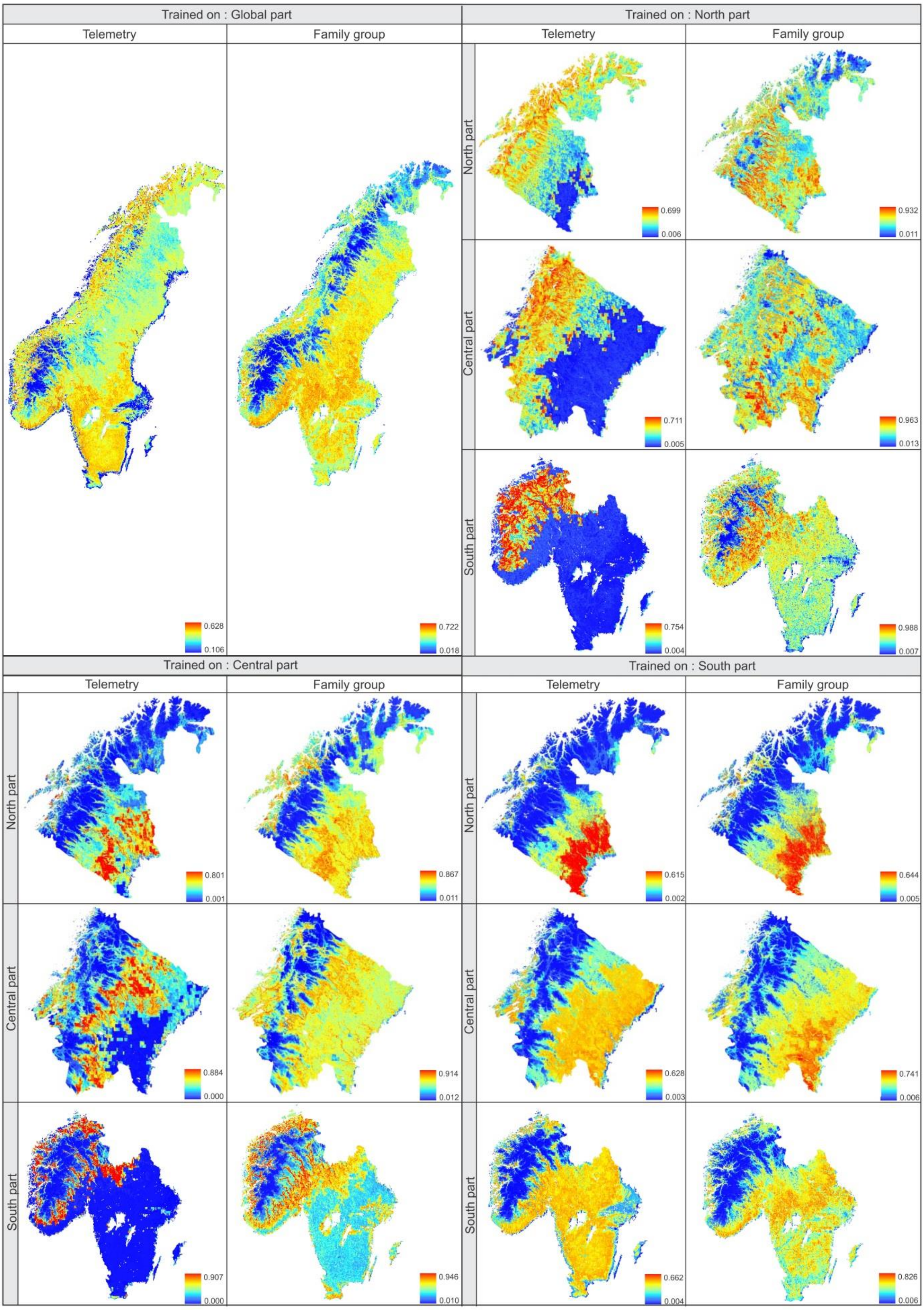

Figure 2. Suitability maps obtained for the different eco-regions of Scandinavia. Top left: map obtained using occurrence data for all Scandinavia. Top-right: the model was trained on the North data and extrapolated to the two other regions. Bottom-left: the model was trained on the Central data and extrapolated to the two other regions. Bottom-right: the model was trained on the South data and extrapolated to the two other regions.

SDMs in our study indicated fair to good predictive power (Table 2; AUCs and Kappa). Statistically, global models obtained from telemetry occurrence data performed slightly better than global models obtained from the family group snow-tracking dataset. Models for the North and South eco-regions trained on telemetry data performed better than the same eco-regions trained on the family group data. In contrast, models for the Central eco-region trained on telemetry data performed worse than the same eco-region trained on family group data.

Overall, models based on telemetry occurrence data perform slightly better (AUC_{PO} (mean ± SD) = 0.82 ± 0.05; Kappa (mean ± SD) = 0.26 ± 0.13; AUC_{PA} (mean ± SD) = 0.72 ± 0.08) than models based on family group observation data (AUC_{PO} (mean ± SD) = 0.72 ± 0.07; Kappa (mean ± SD) = 0.28 ± 0.04; AUC_{PA} (mean ± SD) = 0.71 ± 0.02). However, visual inspection showed that the maps based on family group data looked closer to our expectations (based on 20 years of field research and monitoring) than maps obtained from telemetry data.

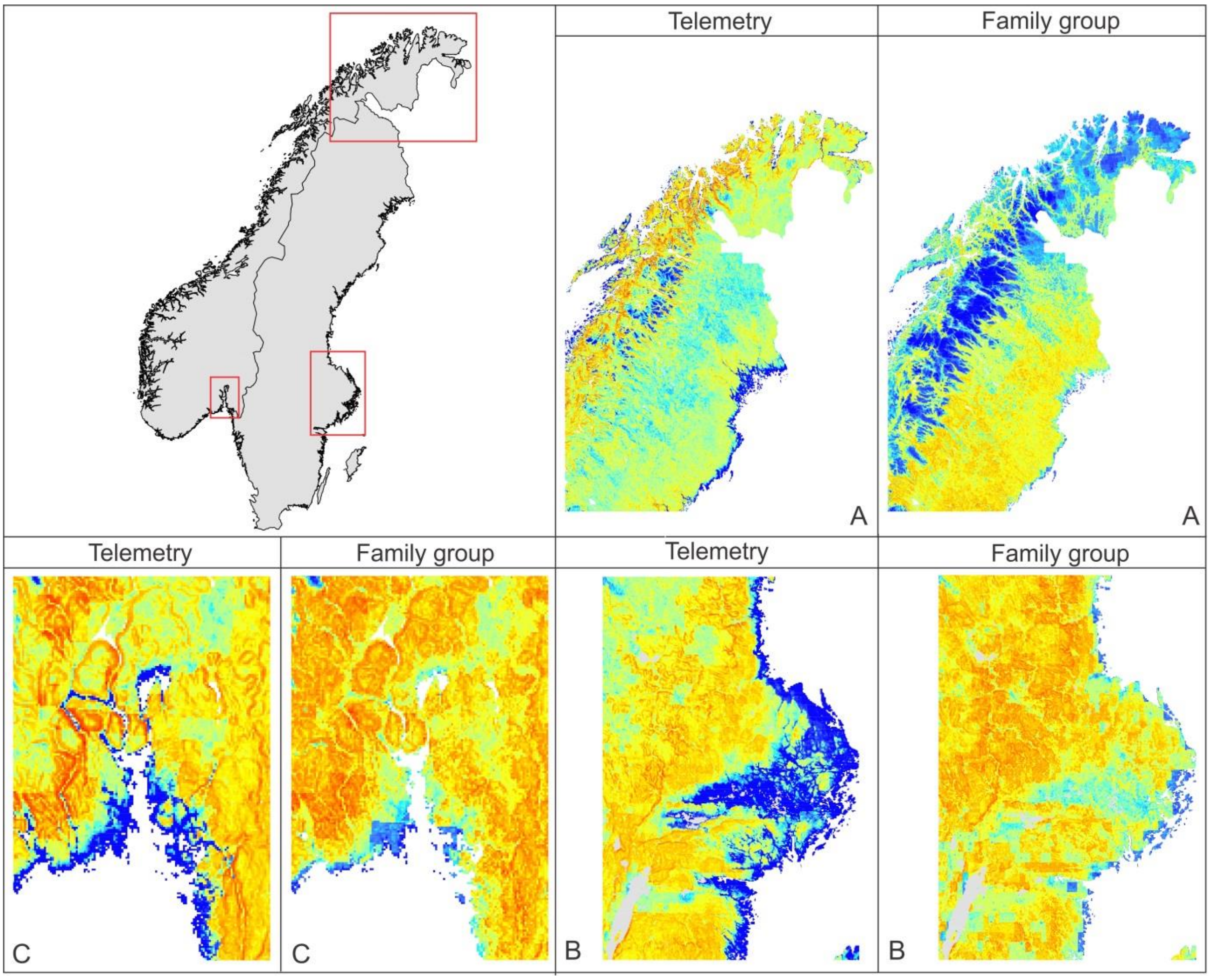

Figure 3. Presentation of 3 areas from the Global model presenting major differences between models obtained from Telemetry data and models obtained from Family group data. A) the far North of Norway; B) the Stockholm – Uppsala area of Sweden C) the greater Oslo area around Oslo fjord in Norway.

Model transferability

Results obtained from extrapolated models indicated a failed or poor performance (Table 2). AUCs and Kappa showed that maps extrapolated from models trained on family group data (AUC_{PO} (mean ± SD) = 0.58 ± 0.03; Kappa (mean± SD) = 0.13 ± 0.12; AUC_{PA} (mean ± SD) = 0.62 ± 0.05) performed better than maps obtained from models trained on telemetry data (AUC_{PO} (mean ± SD) = 0.53 ± 0.03; Kappa (mean ± SD) = 0.03 ± 0.05; AUC_{PA} (mean ± SD) = 0.56 ± 0.04). Differences were observed when comparing maps from the same eco-region but based on different training datasets. Maps extrapolated from the North to a different eco-region were highly dissimilar between the two occurrence datasets. In contrast, maps extrapolated from the South and Central parts to the North were quite similar between the two occurrence datasets.

Comparison of models trained on one eco-region and models extrapolated on that same eco-region showed substantial divergence between the two occurrence datasets for Schoener's D index (Table 3). Family group data produced more similar maps between trained models and extrapolated models (Spearman rho (mean ± SD) = 0.45 ± 0.2; Schoener's D index = 0.77 ± 0.05) than maps produced from telemetry dataset (Spearman rho (mean ± SD) = 0.008 ± 0.45; Schoener's D index = 0.45 ± 0.16). There was no general agreement between the overlaps of regional and extrapolated maps and the overlap between two extrapolated maps in the same region.

Table 2. Results obtained from the different evaluation methods for the trained models and for the extrapolated models between eco-regions.

	AUC_{PO}		**Kappa**		**AUC_{PA}**		**Spearman rho**	**Schoener's D index**
	Telemetry	Family group	Telemetry	Family group	Telemetry	Family group	Telemetry vs. Family group	Telemetry vs. Family group
Trained maps								
Global map	0.77 ± 0.003	0.71 ± 0.005	0.26 ± 0.01	0.28 ± 0.02	0.71 ± 0.01	0.71 ± 0.01	0.56	0.861
North map	0.85 ± 0.002	0.76 ± 0.01	0.40 ± 0.05	0.27 ± 0.06	0.82 ± 0.02	0.68 ± 0.03	0.34	0.770
Central map	0.88 ± 0.003	0.70 ± 0.007	0.08 ± 0.02	0.34 ± 0.03	0.63 ± 0.02	0.74 ± 0.01	0.60	0.713
South map	0.79 ± 0.003	0.74 ± 0.006	0.32 ± 0.02	0.24 ± 0.03	0.74 ±0.01	0.71 ± 0.01	0.77	0.886
Extrapolated maps								
North from South	0.51 ± 0.004	0.59 ± 0.013	0.001 ± 0.001	-0.008 ± 0.008	0.53 ± 0.04	0.58 ± 0.04	0.95	0.863
North from Central	0.51 ± 0.004	0.60 ± 0.014	-0.04 ± 0.02	0.18 ± 0.05	0.51 ± 0.04	0.61 ± 0.03	0.87	0.773
Central from South	0.58 ± 0.006	0.60 ± 0.007	0.11 ± 0.02	-0.01 ± 0.01	0.61 ± 0.02	0.59 ± 0.02	0.92	0.918
Central from North	0.55 ± 0.006	0.56 ± 0.009	0.03 ± 0.01	0.13 ± 0.03	0.55 ± 0.02	0.58 ± 0.02	0.31	0.612
South from North	0.55 ± 0.004	0.61 ± 0.007	-0.01 ± 0.01	0.24 ± 0.02	0.57 ± 0.02	0.69 ± 0.01	0.21	0.410
South from Central	0.52 ± 0.004	0.53 ± 0.007	0.08 ± 0.01	0.27 ± 0.02	0.60 ± 0.01	0.69 ± 0.01	0.51	0.412

When comparing maps of the same area (the trained map and the two extrapolated ones), substantial divergence appeared between maps produced from the telemetry data and maps produced from the family group data (Table 3). Similarity between the trained and extrapolated maps of one area are more important for maps produced from family group data (Spearman rho (mean ± SD) = 0.45 ± 0.2; Schoener's D index = 0.77 ± 0.05) than for telemetry data (Spearman rho (mean ± SD) = 0.008 ± 0.45; Schoener's D index = 0.45 ± 0.16).

Table 3: Results of Spearman correlation and Schoener's D index for the extrapolated models. For the name composed of two parts (e.g. CentralNorth), the first name indicates the part where the model has been extrapolated to and the second name corresponds to the part used to train the model (i.e. CentralNorth means "extrapolated to Central from North training data").

	Spearman rho		**Schoener's D index**	
	Telemetry	Family group	Telemetry	Family group
Central vs. CentralNorth	0.04	0.28	0.474	0.811
Central vs. CentralSouth	0.23	0.60	0.641	0.835
CentralNorth vs. CentralSouth	-0.62	0.27	0.371	0.738
North vs. NorthCentral	-0.22	0.48	0.487	0.763
North vs. NorthSouth	-0.34	0.46	0.414	0.660
NorthCentral vs. NorthSouth	0.86	0.89	0.754	0.815
South vs. SouthCentral	0.02	0.26	0.271	0.730
South vs. SouthNorth	-0.36	0.43	0.251	0.791
SouthCentral vs. SouthNorth	0.47	0.42	0.402	0.787

Lynx habitat associations

For all the trained models (i.e. global and the three eco-regions), habitat type, topography and environmental productivity had the most important effects, contributing between 87% and 99% of the model performance, while human presence had a minor impact. In general, the most informative variable on its own was habitat type, whereas the variable containing the most unique information was NDVI (productivity). However, differences in the effects of these variables are present between models based on different training data. At a Scandinavian (global) scale, lynx appear to avoid high elevation but select for high productivity and steep areas for both types of occurrence data. However, open areas were avoided by the family group model but not for the telemetry model. Habitat type contributed the most to the model based on the family group data while it had a slight contribution for the model based on the telemetry data. For the North eco-region models, habitat type also contributed the most to the model based on family group data but not for the model based on telemetry data. In this area, lynx selected high elevation, high productivity, high road density, steep areas, farmlands and forested areas for the family group data. They avoided medium and high population density, urban areas and open areas. Results from telemetry data did not show the same pattern since lynx selected for low to medium elevation, high productivity and steep areas. Population density, roads density and habitat type did not have a large effect in this last model. Results for the Central area were similar between the family group model and the telemetry model. Lynx selected low elevation, high productivity, steep areas, human settlements, farmlands, forested areas and open areas below the treeline. Differences between models based on different input data were minor in the South eco-region models. Based on the family group data, lynx avoided medium and high elevation, high road density, open areas, urban areas and farmlands. They selected for high productivity and steep areas. The model trained on the telemetry data showed that lynx selected for low elevation and avoided medium and high elevation and open areas. They selected for high productivity and steep areas. Here, urban areas and farmlands had a stronger negative effect than for the family group model.

Discussion

The overall aim of this study was to avail of the enormous datasets that have accumulated in Scandinavia during the last 20 years of Eurasian lynx research and monitoring to examine methodological issues related to assessing large scale habitat suitability. Our first aim was to study the effect of using different types of input data on model transferability. We found that models trained on telemetry data gave slightly different results concerning estimates of lynx habitat suitability than models trained on snow-track observations. Our second aim was to assess the extent to which models generated on data from one part of Scandinavia could be used to assess habitat suitability in a different part of the peninsula. Our results show that transferability was difficult and clearly dependent on the nature of the training datasets. Finally, when using datasets from all Scandinavia we were able to visualize the fact that almost the entire peninsula constitutes lynx habitat, with an intuitively logical suite of factors like elevation, presence of forest, and steepness explaining most of the variation.

Effect of sampling design on model transferability

The way in which data is collected is of critical importance to generate accurate species distribution models [63]. It is generally suggested that completeness (wide areas covered) of sampling is more important than sample size [29, 64]. Here, we show that data collection does not necessarily have a high statistical impact on SDM measures of prediction power [29]. Although the family group data used in this study only had a tenth of the number of locations as the telemetry data, it covered a greater proportion of Scandinavia (Figure 1). For this reason, it was expected that models based on family group data should outperform models based on telemetry data. However, maps trained on telemetry data yielded models with similar predictive accuracy than maps trained from the family group dataset. The similarity in model accuracy may be due to the fact that both datasets used in this study can be considered as exceptionally good quality data. It is then unlikely that biases in the resulting distribution data have been generated. The restricted range of each eco-region allowed SDMs to capture the environmental-distribution relationship for both sampling designs, even if family group data were less numerous than telemetry data [65, 66]. Indeed, the three eco-region specific models were better at describing lynx distribution than the global models for both training datasets. While regional models can easily incorporate local specificities, global models have to detect a far greater heterogeneity in the species-environment relationship. These results are consistent with previous studies which have highlighted the importance of local variations in species 'responses to their environment [67, 68].

However, visual inspection of the maps indicates that there may be some crucial differences that are not detected when using SDM as an evaluation tool. The telemetry training data underestimated the suitability of the habitats close to the major urban conurbations around the capital cities. This was probably due to the relatively few animals that had been collared and tracked in these exact areas. The model based on family group snow-tracking data indicated that these areas were more suitable, and a simple visual plot of the training data indicates that many family groups were actually detected in these very regions that the telemetry based model predicted would be unsuitable. This presence of reproducing lynx in the area would indicate that the family group model was more realistic than the telemetry model. In contrast, in northern Norway the family group model predicted that the higher elevation areas were less suitable habitat than the predictions from the telemetry data model. A visual plot of the telemetry data in this region shows that lynx heavily utilized the high elevation areas that the family group model indicated were unsuitable. This indicates that the telemetry model was probably more realistic. The discrepancy is probably due to both the relative few family group observations in the north, and the expectation that there will be a severe elevation bias in the areas where they are found (close to roads) compared to where the lynx actually spend their time. Apart from these areas, the two training datasets gave broadly comparable results for most of the landscape.

In contrast, the extrapolated maps showed far greater sensitivity to the origin of the data, supporting the idea that transferring models to unsampled regions can be more problematic than simply interpolating (i.e. filling gaps) in a sampled region [13]. However, transferable models are necessary with species that have not been sampled in all their occurrence distribution (e.g. [18, 69]). It is often argued that extrapolation of a model must be done in the same environmental conditions as the ones used to train the model to obtain good modelling success [67, 70]. Our study is consistent with this recommendation as we showed that the predictive ability of the extrapolated SDMs was limited and that all models were the bests at explaining lynx distribution in their own eco-region. There is a cautionary tale here, however, as the environmental differences between the eco-regions were subtle.

Extrapolated maps obtained from family group data gave better results than extrapolated maps obtained from telemetry data. Better coverage of the trained area must have allowed a broader representation of lynx response to their environment [24, 28] and thus gave a more accurate predictive description of species-environment relationships in the other eco-regions. It is certainly for the same reason that family group based models (trained and extrapolated) appeared more realistic when examined visually.

Some authors argued that a model with a good fit to the starting data (verified with good intrinsic evaluation) may be effective when extrapolated outside its range [71, 72]. Here, we showed that this conclusion may not be generalized to all situations. Even the best trained models (e.g. Central model based on family group) gave inaccurate extrapolated maps for a region.Maps extrapolated from the best-trained models even gave similar performance results than maps extrapolated from the worst trained models. Similar results have been obtain in [68], emphasizing the fact that good descriptive ability of a model is not enough to obtain good extrapolated maps.

One of the most obvious discrepancies concerns the extent to which lynx can be expected to utilize the alpine tundra zone of the southern Norwegian mountains. Maps generated from southern data classify these high altitude habitats as being unsuitable. This finding is supported by detailed telemetry studies that show lynx rarely cross the treeline in this area and rarely kill wild reindeer [73]. However, the maps generated from northern data indicate that these mountain areas should be suitable, and telemetry studies from the north do show that lynx regularly move and kill semi-domestic reindeer above treeline in the northern area [74]. The potential difference is probably due to two co-varying differences. Although reindeer are present in both areas, those in the north are semi-domestic (with presumably less anti-predator behaviour) while those in the south are wild. Secondly, roe deer which are the preferred prey of lynx, are available at lower altitudes in the south, but are functionally absent in the north. This shows how relatively subtle differences in prey identity and community composition can have dramatic impacts on models that would have been ignored, if for example, all cervid prey had been condensed into a biomass variable.

Lynx habitat

Results obtained in this study about lynx habitat agreed with previous studies conducted on finer scales [44, 47, 75]. Elevation, steepness, habitat type and productivity appeared as the most important factors for lynx presence even if their relative effects varied within Scandinavia. Previous studies conducted at a smaller scale in southern Norway [44, 46, 47, 48] have already highlighted the importance of these environmental variables for lynx in multi-use landscapes. But contrary to other studies carried out at finer scales, human presence does not seem to have an important impact on lynx habitat suitability, especially for telemetry based models. Lynx are generally considered as a forest-dwelling species [76], and this is confirmed by our results. The fact that human presence was not considered as an important factor in lynx habitat suitability is surely due to the broad scale used in this study as well as the large number of individual lynx used. Due to the low human density in Scandinavia, many individual lynx are still able to avoid human presence, especially in the Central and North parts. The fact that family group models displayed a more important effect of human presence than telemetry models can be explained by the sampling designs. While our data indicates that most family groups are detected by the monitoring program, the location within their home ranges where they are detected is probably biased towards areas close to roads and habitation.

Lynx are generally considered as a specialist species since they predate on a small range of specific species and rarely scavenge [77]. In this study, the ecoregions were separated based on prey distribution. For each eco-region, prey was thus considered as being universally available, and only the environmental variables were taken into account. Any potential spatial variation in prey density was indirectly represented by the productivity and the different habitat types, although the different species will react in different ways. Indeed, roe deer and red deer are known to occur in forests and farmland-forest mosaics [31, 78] while reindeer are more associated with alpine tundra and high altitude areas [35]. Differences of model outputs between North, South and Central parts showed that lynx can adapt to a broad range of conditions in terms of habitat type. Hence, when prey is considered as available everywhere, lynx can be considered as a habitat generalist species. Due to their tolerance toward a broad range of conditions, it was not surprising that the global maps gave predictions barely better than random (from a statistical point of view). Even if the evaluation methods indicated medium accuracy between predicted and observed occurrences, visual inspection of the final maps indicated a good representation of the actual lynx distribution in Scandinavia, especially for the map based on family group data.

Conservation implications

Even if the evaluation methods only indicated fair to good predictive accuracy for the different models, we argue that the global maps produced here can be a valuable asset to help management of lynx populations in Scandinavia. Conflicts with lynx are recurrent with livestock producers and hunters throughout Scandinavia. In the South (Norway only), lynx predate on unguarded domestic sheep during summer, causing thousands of deaths every year [79]. In the Central and the North (both countries), lynx kill free-ranging semi-domestic reindeer which are herded by the Sami ethnic group [80]. In addition, many roe deer hunters both perceive and experience lynx as a competitor for roe deer [81]. As a response, lynx are subject to a geographically differentiated population management (keeping low population density in high conflict areas, and vice versa) through hunter harvest [33]. Planning for this geographic differentiation requires allocating lynx population targets to different regions. The results of our modelling exercise identify the areas where lynx populations can potentially persist, which aids in concrete management planning. The maps clearly show that managers have a great deal of freedom as most of the peninsula comes across as suitable lynx habitat. Another more diffuse benefit likes in the visualization of the massive potential that exists in Scandinavia for allowing a potential further recovery of the lynx population to just about all parts of the peninsula. The communication value of this finding should not be underestimated as there is still a widespread perception among the public that large carnivores, like lynx, can only persist in the wilderness. However, the extent to which lynx will be permitted to utilize this potential remains to be seen given the chronic nature of many of the conflicts.

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CHAPTER 3- TOLERANCE TO ANTHROPOGENIC DISTURBANCE BY A LARGE CARNIVORE: THE CASE OF EURASIAN LYNX IN SOUTH-EASTERN NORWAY

Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway

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Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway

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Abstract

The relative merits of land sparing versus land sharing are being debated within conservation biology. While the debate is multifaceted, a central issue concerns the ability of biodiversity to actually persist in 'shared' human-dominated landscapes. There is a widespread perception that large predators are synonymous with wilderness and have a low tolerance for human-modified landscapes. However, there is an increasing body of evidence that is questioning this paradigm. In order to explore the tolerance levels of Eurasian lynx to human activity, we have analysed data on 49 lynx home ranges in south-eastern Norway occupying a gradient of landscapes from near wilderness to the urban–forest interface. Our results indicate that lynx have the ability to tolerate relatively high levels of human presence both within their home ranges and within the immediate surroundings of their home ranges. Home-range orientations reflect preference for areas associated with low levels of human-induced habitat modification, and avoidance of the more heavily disturbed areas. The results show that lynx have a large potential to exist in shared landscapes if their presence is tolerated by people.

Introduction

Because of their charismatic nature, large carnivores are often used as flagship species (Linnell, Swenson & Andersen, 2000). They are often considered as keystones species because as top predators, they can have a role in regulating their prey species, which in turn can potentially have significant impacts on habitats and other species via trophic cascades (Terborgh & Estes, 2010; Ripple & Beschta, 2012). It is also widely recognized that large carnivores are a challenging group of species to conserve in the modern world. There is currently an ongoing debate in the conservation literature about how best to go about conserving them, which can be viewed within the wider debate about land-sparing versus land-sharing strategies (Phalan *et al.*, 2011). One line of argument argues for a heavy focus on protected areas as the mainstay of their conservation, even extending to calls to fence these reserves (Packer *et al.*, 2013). The other line of argument focuses on the potential to integrate large carnivores into human-modified landscapes in a coexistence approach (Carter *et al.*, 2012). In Europe, where the landscape is a continuum of human-modified areas and where wild areas are sparse, the coexistence approach is viewed as the only possible solution. But the viability of the coexistence approach depends on the ability of large carnivores to live in human-modified landscapes. Many studies haves documented a statistical avoidance of human infrastructure and modified habitats by several species. On a fine scale, this concerns an avoidance of such areas by individuals within their home ranges (*Puma concolor coryi*, Cox, Maehr & Larkin, 2006; *Gulo gulo*, May *et al.*, 2006; *Canis lupus*, Hebblewhite & Merrill, 2008; *Ursus arctos*, Güthlin *et al.*, 2011; *Lynx lynx*, Basille *et al.*, 2013; *U. arctos*, Coleman *et al.*, 2013), while on a larger scale, it concerns how human habitat modification influences distributions (*Canis lupus lycaon*, Mladenoff *et al.*, 1995; *L. lynx*, Niedziałkowska *et al.*, 2006; *C. lupus*, Jedrzejewski *et al.*, 2008). However, a range of other studies have shown that these species are able to persist in often heavily human-modified landscapes (Gehrt, Riley & Cypher, 2010; *Panthera tigris*, Carter *et al.*, 2012; *Panthera pardus*, *Hyaena hyaena*, Athreya *et al.*, 2013), even in the proximity of urban areas (*Puma concolor*, Beier, Riley & Sauvajot, 2010). Some extreme examples concern species that have shown an ability to fully adapt to urban environments (McKinney, 2006; Bateman & Fleming, 2012; *Martes foina* and *Vulpes vulpes*, Duduś *et al.*, 2014).

While most of these studies have looked at what large carnivores prefer (in a statistical sense), in a world where human density and anthropogenic impact are increasing every year (United Nations Population Fund, 2007), it is interesting to explore the issue of tolerance as opposed to preference, and focus more on defining the limits of human disturbance that can be tolerated by large carnivores in order to plan for their conservation. This is particularly relevant for areas such as Europe, which lacks wilderness areas without human activities as an alternative arena for conservation.

The range of Eurasian lynx *L. lynx* has expanded in Europe during the last 40 years because of both reintroduction and natural recolonization (Linnell *et al.*, 2009). However, the Eurasian lynx is often regarded as having a limited ability to tolerate fragmented habitats (Schadt *et al.*, 2002; Niedziałkowska *et al.*, 2006; Breitenmoser-Würsten *et al.*, 2007). Scandinavia has one of the biggest lynx populations in Europe (Linnell *et al.*, 2005). Although much of Scandinavia is sparsely populated, there is very little true wilderness as most of the landscape is exploited in some manner and the southern parts are relatively densely populated (http//:www.ssb.no). In order to explore the tolerance of lynx to human disturbance, we compared established lynx home ranges and their immediate surroundings with respect to a number of proxies of human disturbance. In contrast to previous studies (Basille *et al.*, 2009) that have looked at lynx distribution at a population level, our goal was to look at lynx tolerance at an individual level, and above all, to consider the actual configuration of individual home ranges. To better evaluate lynx tolerance to humans, we addressed the following questions: (1) What are the range of values of various proxies of disturbance that lynx can tolerate both within the home ranges and within a surrounding buffer? (2) Does the magnitude of disturbance have an effect on the way lynx configure the shape of their home ranges? (3) Is there a potential trade-off between avoidance of people and access to areas of high prey density?

Based on results of previous studies (e.g. Basille *et al.*, 2009; Basille *et al.*, 2013), we expected lynx to place their home range in order to avoid areas of high human disturbance, but still included areas of low to medium human disturbance to have access to prey.

Methods

Study area

The study was conducted across 90 000 km^2 of south-eastern Norway, between 58°N and 63°N, covering eight counties (Fig. 1). These comprise the most populated areas in Norway, including the urban conglomeration around the capital city, Oslo. The area spans a wide range of environmental conditions: from highly fragmented agricultural areas in the south-east (Østfold and Akershus) to forest-

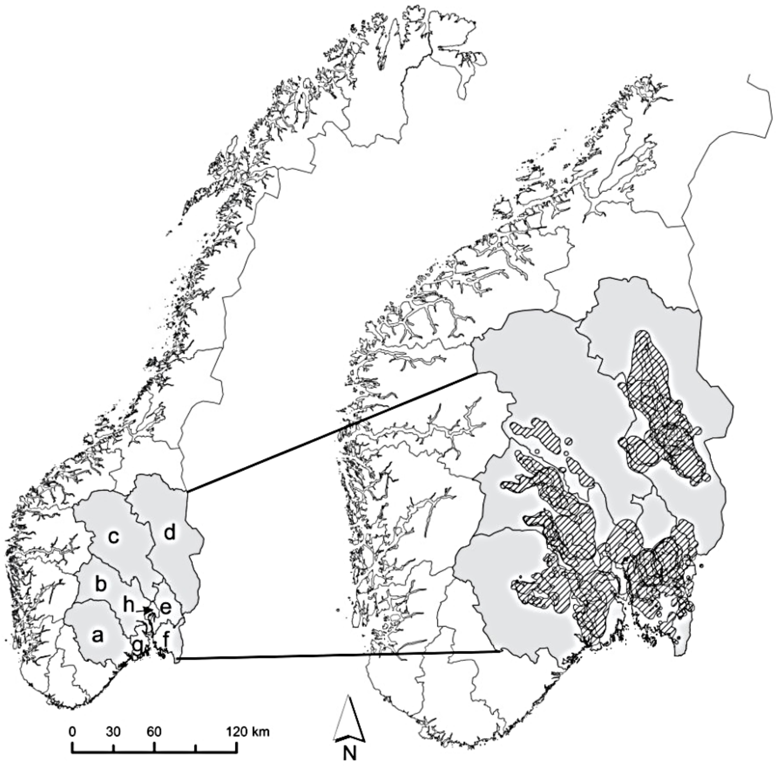

Figure 1 Location of the study area in south-eastern Norway (in grey shading), and location of home ranges of all 49 lynx. Names of the counties: (a) Telemark; (b) Buskerud; (c): Oppland; (d) Hedmark; (e) Akershus; (f) Ostfold; (g) Vestfold; (h) Oslo.

dominated areas in the north (Hedmark). Agriculture mainly consists of growing grass for livestock, and grain for animal food. Fields tend to be small and mainly located in lowlands and along valley bottoms. All forests are commercially exploited, which has led to the creation of an extensive network of forest roads. Forests consist of a mosaic of even aged stands following clear-cutting and replanting/ regeneration. Forests are also utilized by hunters (from August to April), grazing sheep flocks (June to September) and year-round for a diversity of recreational activities such as picking berries and mushrooms, picnics, fishing, hiking, jogging and cross-country skiing. Further details are provided in Basille *et al.* (2009).

Lynx data and home-range estimation

Between 1995 and 2012, 49 lynx (25 females and 24 males) were live-captured and equipped with radio collars (see Arnemo *et al.*, 2012; Basille *et al.*, 2013). During this period, the study adapted to changes in available technology; the early years involved very high-frequency (VHF) telemetry, while the later years availed of global positioning system (GPS) collars. VHF-equipped animals were located from both the ground and the air (reducing location bias). Tracking schedules varied widely during the study.

We estimated year-round (1 April to 31 March) home ranges for 49 lynx using a total of 5723 VHF locations from 22 individuals and 7402 GPS locations from 27 individuals. To minimize autocorrelation from periods of more intensive positioning, we randomly chose one location per day when several fixes were available. Individuals were only included if they had a minimum of 90 locations and at least 6 months of tracking data. The mean number of locations was 266 [±104 standard error (SE)] per individuals with a range of 94 locations to 503 locations among individuals. Duration of tracking varied between 8 and 83 months with a mean of 24 months (±18 SE). Only resident adults with stable home ranges were used for the analysis.

To characterize lynx home ranges, we constructed a utilization distribution using 95% kernel estimation (Worton, 1989; Seaman & Powell, 1996). To select the bandwidth parameter *h* for each individual, we used the R package adehabitatHR (Calenge, 2006) and applied them in a geographic information system using Hawth's Tools (ArcView 9.3.1, Environmental Systems Research Institute, 2009). In order to compare home ranges with their immediate surroundings, we created 5-km buffers around each home range using ArcGIS 9.3.1. The size of the buffer was chosen so as to create an area of similar size to the home ranges. It was also on a scale small enough to consider only the human disturbance, which is more likely to cross these borders and use lynx home range for different activities.

Environmental variables

A set of proxies for human disturbance were quantified at a 1-km^2 resolution. These included forest road density, public road density and human density. Data on public and forest roads were obtained from the Norwegian Mapping Authority, and data on human density came from Takle (2002). All these maps are based on data collected in the early 2000's – and are thus associated with the midpoint of the 17 years of gathering lynx data. During these 17 years, no dramatic large-scale landscape changes have been observed. An index of relative prey (roe deer *Capreolus capreolus*) density was obtained from a map based on extrapolation from pellet count data (Gervasi *et al.*, 2014). We used roe deer to take into account the importance of prey as roe deer are the main prey of lynx in the study area and represent 83% of the biomass consumed by lynx in winter (Bunnefeld *et al.*, 2006; Odden, Linnell & Andersen, 2006; Gervasi *et al.*, 2014). ArcGIS 9.3.1 was used to derive the data from digital maps.

Statistical analyses

To test if lynx place their home range to reduce the impacts of human disturbance, we compared the regression slopes of each of the human disturbance proxies (human density, forest and public road density) and roe deer density for the home range versus its respective buffer with a *no preference slope*. This *no preference slope*, of intercept 0 and slope 1, indicated that for a given density value inside the home range, the corresponding point within the surroundings would hold the same density value. A regression slope for one of the proxies of human disturbance less than the *no preference slope* indicated that the density was relatively higher within the buffer than within the home range. Inversely, a regression slope steeper than the *no preference slope* indicated that the density was relatively higher within the home range than within the buffer. Using the linearHypothesis function in the *car* package, we first tested whether proxies of human disturbance differentially affected male and female lynx. We then tested if the regression slope of each human disturbance proxy was significantly different from the *no preference slope*. All analyses were performed using R version 2.13 (R Development Core Team, 2011).

Results

Annual home ranges varied in size from 429 to 4130 km^2 for male lynx [mean = 1496 km^2 standard deviation (SD) = 814 km^2, $n = 24$] and 428 to 1978 km^2 for female lynx (mean = 930 km^2 SD = 388 km^2, $n = 25$). Because there were no differences in the values of any human disturbance proxies between male and female lynx (Mann–Whitney *U*-tests, $P > 0.05$), the genders were pooled for all further analyses.

The values of the various human disturbance proxies varied greatly among individuals, both within home ranges and within the surrounding buffers (Table 1). The largest variation was in human population density, as some individuals included small towns within their home ranges, or else lived immediately adjacent to larger urban conglomerations. This included some animals bordering directly onto the edge of the city of Oslo, whereas some other animals

Table 1 The values (minimum, maximum, mean and SD) for all parameters within 49 lynx home ranges and associated buffers in south-eastern Norway

	Home range			Buffer		
	Minimum	Maximum	Average (mean ± SD)	Minimum	Maximum	Average (mean ± SD)
Human density (habitants per km^2)	1.61	314	41 ± 70	0.62	647	67 ± 129
Public roads density (km km^{-2})	0.15	1.54	0.53 ± 0.31	0.06	2.45	0.56 ± 0.54
Forest roads density (km km^{-2})	0.57	1.31	0.99 ± 0.19	0.32	1.30	0.86 ± 0.26
Roe deer density (pellets per km^2)	0.29	3.11	1.24 ± 0.85	0.22	3.43	1.3 ± 0.99

SD, standard deviation.

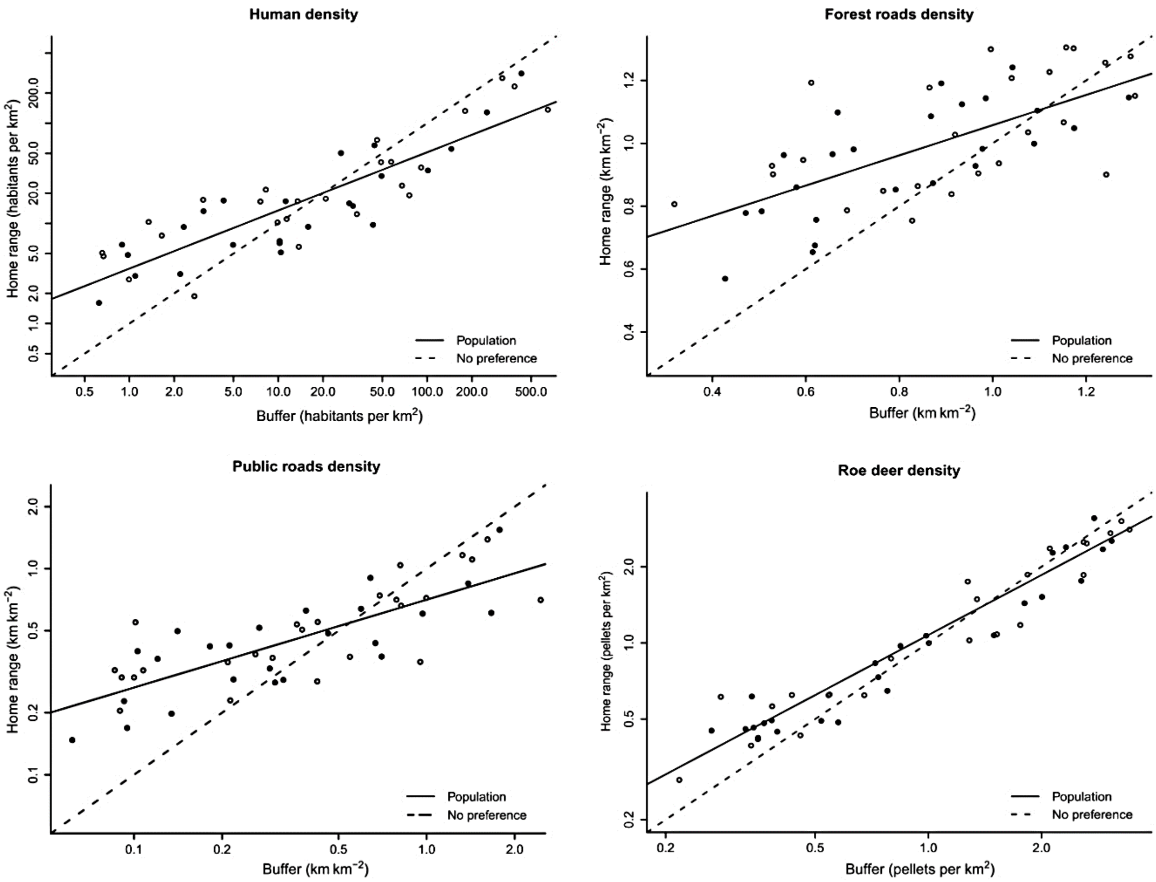

Figure 2 Regressions of parameter values of proxies of human disturbance and prey density for lynx home ranges against associated buffers (solid line) and a *no preference slope* (dotted line).

lived in near-wilderness settings. There was also a high degree of variation in the other parameters. There were no dramatic overall differences between mean values for the home ranges and the buffers. However, when comparing the regression slopes of buffer area versus home range for the different parameters to the *no preference* slopes a consistent pattern emerged.

For all parameters, the results of the linear regressions revealed differences between the parameter regression slopes and the *no preference* slopes ($F_{[2,\ 47]} = 39.11$, $P < 0.001$ for human density; $F_{[2,\ 47]} = 41.83$, $P < 0.001$ for forest road density; $F_{[2,\ 47]} = 80.92$, $P < 0.001$ for public road density; and $F_{[2,\ 47]} = 23.24$, $P < 0.001$ for roe deer density). All of these parameters showed the same pattern (Fig. 2); at low-density values, the densities for the parameters were higher within the home ranges than within the buffers. But the regression lines all crossed such that at high densities, the values for the home ranges were lower than for the buffer. The intersection of the two regressions can be interpreted as a critical point beyond which preference switches to avoidance. These thresholds were of 20 habitants per km^2 for human density, 1.1 km km^{-2} for forest roads, 0.54 km km^{-2} for public roads and 1.4 pellets per km^2 for roe deer density. Overall, these results indicate that lynx only orientate their home ranges to reduce their exposure to human disturbance in the most disturbed areas. Results of the linear regression showed no differences between male and female lynxs for all the human disturbance proxies ($F_{[2,\ 23]} = 0.88$, $P < 0.43$ for human density; $F_{[2,\ 23]} = 1.04$, $P < 0.36$ for forest roads density; $F_{[2,\ 23]} = 0.75$, $P < 0.48$ for public roads density; and $F_{[2,\ 23]} = 0.50$, $P < 0.61$ for roe deer density), further justifying the pooling of sexes.

Discussion

As a compliment to previous works related to the effect of human presence on lynx distribution in the same study area (Bunnefeld *et al.*, 2006; Basille *et al.*, 2009, 2013), we worked at the home-range scale and took into account the shape of home ranges to describe the actual areas used by the animals. Being a forest species, most of the home range of a Eurasian lynx is expected to be placed in and around forests and exclude areas with high human presence (Sunde, Stener & Kvam, 1998; Niedziałkowska *et al.*, 2006; Basille *et al.*, 2009). However, in the very human-modified landscape that we know today, even if large carnivores managed to place a home range in an area with a low human density, the surroundings of this range will most likely be populated by humans. Hence, because of the high mobility of humans (for both work and leisure activities), home ranges are influenced by people living both within and around a home range. In our analysis, we considered the buffer to be an important zone with two main functions. The first function is to show the buffer's area of influence, which represents people who can potentially access a lynx's home range, and the second function is to serve as a comparison between buffer and home range in order to show how lynx orientate their home ranges in order to minimize the impacts of human presence at a fine scale.

Studies on tolerance to humans are context dependant as human behaviour and human disturbance patterns are likely to influence carnivore responses to human disturbance. In contrast, to most parts of west Europe, lynx are managed as a game species in Norway (Linnell *et al.*, 2010) where they are subject to an annual quota-limited hunt during a short season (Bischof *et al.*, 2012). This forces lynx to adopt a shy behaviour, especially as Basille *et al.* (2013) have shown that road density has a consequence for lynx survival, and humans are the dominant cause of lynx mortality (Andrén *et al.*, 2006). In addition to direct hunting, people use the habitats where lynx live for a diversity of recreational (moose and roe deer hunting, hiking, cross-country skiing, and picking of mushrooms and berries) and commercial (forestry) activities. While these activities do not directly threaten lynx, they vary greatly in the extent to which they are limited to certain times and places (such as trails) or not, making it challenging for lynx to differentiate between threatening and non-threatening activities. Disturbance also includes human 'kleptoparasitism' of lynx killed prey (Krofel *et al.*, 2008).

Our results show that there is a massive variation among individuals regarding the extent to which they are exposed to human presence. At the individual level, we observed individuals living in areas than can be classified as wild (with less than two inhabitants per km^2) and others living in sub-urban or peri-urban areas [with more than 300 habitants per km^2 (average human density in Norway being 14 habitants per km^2)]. It is important to consider that these results have been found in Norway, one of the least urbanized countries in Europe, although some of the individuals used for the study settled in areas touching the Oslo urban area, the most densely populated area in Norway. For example, a female lynx living in Oslo's periphery had an average human density of 647.2 habitants per km^2 in her buffer. However, our study only looked at where our sample of lynx lived, and it is probable that we have not yet found the critical limits of tolerance of lynx to human presence.

When we look across individuals at how they orientate the placement of their home ranges with respect to the surrounding buffer area, a clear pattern appeared for all the human disturbance proxies. At low overall human proxy densities, lynx had a higher density of human proxies inside their home range than in the buffer, but this pattern was reversed when the density of the human proxies increased, such that they appeared to orientate the home range shape to minimize the density of disturbance proxies.

Our results suggested that in some situations, lynx occurrence is associated with human presence and human habitat modifications. This relationship is almost certainly because of the distribution of roe deer. Multiple previous studies have shown that roe deer, the lynx's main prey, tend to be close to human-modified landscapes (crops, edges, early successional stage habitats) and artificial feeding sites, as well as responding to human land use practices – especially during winter (Gill *et al.*, 1996; Kjøstvedt, Mysterud & Østbye, 1998; Mysterud, Lian & Hjermann, 1999; Moa *et al.*, 2006; Odden *et al.*, 2006; Torres *et al.*, 2011, 2012). Results of another study that we have conducted (not published yet), based on the roe deer density map layer that we used in this study, also indicate that roe deer density is higher in areas with higher human impacts than in areas with very few human impacts. Previous studies conducted at a larger scale (Basille *et al.*, 2009, 2013) have shown that lynx displayed a trade-off between abundance of prey and avoidance of human activity – a trade-off that seems also to be present at the finer scale shown in this study. Our results indicate that as human disturbance increases, lynx are forced to adjust their home-range configuration to minimize their exposure to the most disturbed areas.

Bateman & Fleming (2012) indicated that large body size, hypercarnivory diet (more than 70% of meat), hunting behaviour (vs. scavenging behaviour) leads felids to be poor urban adapter. Large body size in a fragmented habitat may lower the viability of individuals as the necessary requirements in terms of habitat and food may be lacking (Crooks, 2002). Hunting behaviours often lead to conflicts with humans who then see carnivores as a threat to their own security, preventing carnivores from coexisting with humans (Bateman & Fleming, 2012). However, our results contradict these findings for the Eurasian lynx. Eurasian lynx are a large felid (±15 kg), highly carnivorous and only scavenge occasionally. Our study animals showed an ability to include villages and towns within their home ranges and lived right up to the edge of cities, but almost never ventured into built up areas. So while they appear to be well adapted to often densely populated and modified rural landscapes (as long as there is some forest), they could not be called urban dwellers. Similar traits have been reported for wolves (Promberger *et al.*, 1998; Musiani *et al.*, 2003; Wydeven *et al.*, 2004), black bears (Beckmann & Lackey, 2008) and brown bears (Kaczensky *et al.*, 2003).

Implications

Despite the fact that some regions of Europe are associated with rural–urban migration and the subsequent abandonment of agricultural lands (Navarro & Pereira, 2012; Alcantara *et al.*, 2013), the overall European landscape is going to remain dominated by human land use and be increasingly fragmented by human infrastructure. As long-term large carnivore conservation in Europe requires the adoption of large-scale approaches where carnivore populations must naturally connect across large parts of the continent (Linnell & Boitani, 2012), it is important to understand the tolerance levels different species have for residing in the modern landscape. Our study has shown that lynx can occupy areas with high densities of humans and human infrastructure, actively preferring more modified areas in some cases at low density, and then adjusting home-range orientation to avoid the highest densities when these disturbances pass certain thresholds. This implies that we can consider lynx to be an adaptable species. Therefore, the bottom line for their conservation is not going to lie with the lynx's tolerance of humans, but with the willingness of humans to tolerate lynx. Given the dominance of human-caused mortality (Andrén *et al.*, 2006), the imperative for management is to ensure that mortality levels (from hunting and poaching) can be kept below critical levels, and this will be even more important in areas with higher human presence (Basille *et al.*, 2013).

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CHAPTER 4 - EURASIAN LYNX HABITAT SELECTION IN HUMAN-MODIFIED LANDSCAPE: EFFECTS OF DIFFERENT HUMAN HABITAT MODIFICATIONS AND BEHAVIOR

Eurasian lynx habitat selection in human-modified landscape: effects of different human habitat modifications and behavior

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Abstract

Eurasian lynx are often regarded as being particularly sensitive to human land-use. However, in the European context where human influence is pervasive, the conservation of lynx requires that they be integrated into the human-dominated landscape. Although previous studies have looked at how lynx respond to human land-use in a broad sense, they have failed to examine the details of how different types of human activity (forest fragmentation, human density, different types of transport infrastructure) differentially influence lynx behaviour. Furthermore, they have not examined the extent to which lynx modify their fine scaled avoidance of anthropogenic landscape features according to the specific behaviours (day-beds, kill sites, movement) in which they are engaged, how these relationships are modified by prey density or the sex of the lynx. We examined how 19 GPS-marked lynx in southeastern Norway respond to an index of cumulative human habitat modification while engaged in different activities. We found that lynx select for areas with medium levels of human modification, avoiding both the very highly modified and the areas with low degrees of modification. Females in general appear to be less tolerant of human modification than males, especially when it comes to day-beds. Terrain (ruggedness and altitude) appear to be important in permitting lynx to exploit heavily modified areas. Our study demonstrates that lynx show a nuanced response to human infrastructure and habitat modification which offers hope for their conservation in Europe.

Introduction

Most of the planet is now impacted by human activities (Sanderson et al. 2002), with an ever increasing conversion and fragmentation of natural habitats. The impact of anthropogenic development is a major concern in conservation biology since it can have important consequences for biodiversity. Transport infrastructure, forest-related activities and forest conversion to agriculture continually fragment and disturb habitats, and can affect species behavior, abundance and survival (Vos & Chardon 1998; Kramer-Schadt 2004; Northrup et al. 2012; Fahrig & Rytwinski 2009; Trombulak & Frissel 2000; Baldwin et al. 2004). Human density and related infrastructures, above some threshold, are often linked to avoidance behavior (Basille et al. 2009). Of all the species negatively affected by human developments, large carnivores are generally considered as particularly sensitive because of their large space requirements and low densities (Fahrig & Rytwinski 2009; Cohen & Newman 1991; Crooks 2002). These spatial requirements imply that their conservation, especially in crowded areas like some parts of Western Europe, require their integration into human-dominated landscapes. In addition to their indirect effects (habitat fragmentation, development of road networks, loss of prey availability, Huck et al. 2010; Putman & Staines 2004; Milner et al. 2007), humans are considered as the most dangerous intra-guild predators for large carnivores (Woodroffe & Ginsberg 1998; Treves & Karanth 2003) directly causing mortality through hunting, poaching, vehicle collisions (Lindsey et al. 2007; Packer et al. 2009; Andrén et al. 2006; Kaczensky et al. 2003).

The response of large carnivores to human activity is conceptually similar to a prey response to predation risk (Frid et al. 2002). For example, large carnivores have been shown to adjust their habitat use to avoid human hunting (Ordiz et al. 2012; Theuerkauf et al. 2003) or human encounters (Ordiz et al. 2013; Wam et al. 2012; Valeix et al. 2012). To reduce mortality risk, large carnivores should then avoid areas with high densities of humans and select areas with perceived low mortality risk. However, in Europe, the ungulates that are the main prey of large carnivores occur at higher densities close to feeding sites and human modified landscapes (Mysterud et al. 1997; Bunnefeld et al. 2006; Torres et al. 2011). This distribution of prey can induce potential trade-offs between risk avoidance and prey access (Bunnefeld et al. 2006). Therefore, individuals should balance between access to resources and mortality risks induced by human proximity (Valeix et al. 2012). However, complex species like large carnivores should have the ability to make these trade-offs in a very fine-scaled and differentiated manner. To date, there have been many broad scale studies of how a diversity of large carnivores respond to human habitat modification, activities and structures (e.g. Jedrzejewski et al. 2004; Blanco et al. 2005; Niedzialkowska et al. 2006; Ordiz et al. 2013). However, these studies have not been able to explore the details of the way the species adapt to human-modified landscapes.

Quantification of species-habitat relationships can be done through habitat selection modelling. Habitat selection can vary depending on the behavior since access to a diversity of resources is essential for survival and reproduction. Finding, killing and consuming prey, territory defense, mating, raising offspring and avoiding mortality are necessary parts of an individual's daily or annual life cycle. Spatial segregation of the resources for different behaviors can in theory induce specific behavioral differences in habitat selection (Owen-Smith et al. 2010; Roever et al. 2014). Quantifying habitat selection from pooled data can have important implication for conservation and management (Roever et al. 2014). Indeed, one major effect of pooling data is the risk to reduce the inference obtained from statistical models used to understand species ecology and habitat selection. Roever et al. (2014) identified pitfalls in the statistical quantification of habitat selection when behaviors are pooled: (1) Opposite patterns of habitat selection between behaviors may lead to a failure to detect selection; (2) An underestimation of the strength of selection and failure to recognize the importance of some habitats, and (3) The shape of the selection curve is likely to be sensitive to behavior and thus can express different shapes from one behavior to another.

Our previous studies of Eurasian lynx (Lynx lynx) habitat selection in Norway have focused on a coarse spatial scale – approximately related to the distribution and alignment of lynx home ranges (Basille et al. 2009; Basille et al. 2013; Bouyer et al. 2015). A home range necessarily contains all the diverse resources needed for individual survival and reproduction. These studies have shown that lynx can live in relative close proximity to human-modified areas, often selecting for areas with medium levels of human modification. However, these studies have not explored the behavioral mechanisms by which lynx manage to integrate themselves into these landscapes. In this study we use GPS telemetry data on lynx in southeastern Norway to explore lynx's habitat selection in a human-dominated landscape. We differentiate between the sexes and between three broad behaviors (day-beds, kill sites, movement) in our attempt to understand how lynx respond to different degrees of human habitat modification / infrastructure development (Riffell et al. 1996). In addition, we examine how prey density and topography modulate these patterns.

Contrary to previous studies, we were interested in the cumulative effects of different types of human modifications to the landscape. We considered that effects were cumulated when the joint effects of features in close proximity were greater or lesser than the influence of the features alone (Riffell et al. 1996). An animal's response may depend on the intensity of human pressure. For example, a field surrounded by forest areas may not represent an area of high human pressure for a carnivore and may even have a positive effect as it can attract prey such as large herbivores. But a field surrounded by houses and a road may represent too great a risk of mortality and disturbance to be worth the potential benefits.

For this reason, we expected that areas with both low and high cumulative land uses should be avoided and areas with medium cumulative land use should be selected. Taking into consideration the evolutionary weights of the different behaviors (Krebs & Davies 1981), we predicted resting sites to show stronger selection for less disturbed areas and kill sites to occur in areas with higher human pressures due to the presence of prey (Basille et al. 2009). We also expected that females would show a stronger avoidance of human dominated landscapes than males. Finally, we predicted that topography (ruggedness and slope) would influence lynx's tolerance of human land uses because of the variability in cover and security provided.

Material and Methods

Study site

The study was conducted in southeastern Norway across seven counties (Telemark, Vestfold, Østfold, Buskerud, Oslo, Akershus and Oppland) between 58°N and 63°N. This includes the most populated areas in Norway, including the urban conglomeration around the capital city, Oslo. The area follow a gradient of environmental conditions with highly fragmented urban, suburban and agricultural areas in the southeast (Oslo, Østfold, Akershus) and southwest (Vestfold) to forest dominated areas in the north (Oppland) and northwest (Telemark, Buskerud). The topography goes from flat or hilly areas in the south and east to higher altitudes with steep slopes in the north and west. Overall, the forests are intensively exploited through clear cutting and regrowth, and are mainly composed of Norwegian spruce (Picea abies), Scots pine (Pinus sylvestris), hoary alder (Alnus incana) and birch (Betula pubescens). Agriculture mainly consists of the production of grass and grain, with some production of crops like potatoes, turnips and strawberries. For more information on the study site see Basille et al. (2009).

Animal capture

Between 2008 and 2013, we captured 19 individual lynx (8 females and 11 males) following pre-established protocols. We used GPS-collars which transferred data via the GSM network (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). Adult lynx were trapped in wooden walk-through box-traps and foot snares. Box traps were equipped with two SMS-alarms that permitted reaction with in average 5 hours and foot snares were continually monitored using radio-alarms which permitted a reaction time always less than 15 min. Adults (males 18-28 kg, females 14-19 kg) were darted with an initial dose of 4 mg medetomidine + 100 mg ketamine per animal using a remote drug delivery system (Dan-Inject). In adults captured in box traps (calm animals) and in juveniles (6-12 months 9-16 kg, yearlings 12-21 kg), the doses were reduced to 2 mg medetomidine + 50 mg ketamine. For reversal of immobilization, 5 mg of atipamezole (Antisedan®) per mg of medetomidine was administered. All procedures were approved by the Norwegian Experimental Animal Ethics Committee, and permits for wild animal capture were obtained from the Norwegian Environment Agency. No complications were ever detected as a result of collaring among these animals.

Behaviour identification

We selected data collected during periods of intensive location collection (510 lynx days; 7-19 locations per day) in order to identify the behaviour related to each GPS point. Only resident individuals with fixed home range were selected for this analysis. For reproductive females, we removed GPS locations obtained between beginning of June and end of August, which correspond to the three first months of offspring. Differentiation between behaviours was first made based on travel speed, and reinforced by field visits to locations. Field data were collected between November and April in winter, and between May and September in summer. Animals were fitted with GPS-GSM collars that allowed us to visit potential kill sites / day-beds directly after the animal had left the area. Potential kill sites were defined as a set of at least two locations within 100m and visited to search for prey remains (Matisson et al. 2011b). The prey species and, whenever possible, its sex and age class was identified when a carcass was found. Such visits also helped confirm some locations as day-beds (based on signs in snow during winter and compressed vegetation in summer). A threshold of 135m/h was obtained by calculating the mean speed between two consecutive confirmed day-beds and two consecutive confirmed kill sites. When the speed between two consecutives locations was less than 135m/hour and no kill was recorded at this location, the location was considered as a resting site. Kills were defined as a location with a speed less than 135 m/hour and when the presence of prey was confirmed. Movements were defined when the speed between two points was more than 135 m/hour and when no kill was recorded.

To reduce autocorrelation, we systematically selected points with at least 2h differences for the movements. Since points of resting and killing sites tended to be clustered over several days, only one point representative of the cluster was kept for the analysis and considered as a kill or day-bed.

Statistical analysis

Habitat covariates

We included environmental, topographic and anthropogenic covariates in our models. All these covariates were available in a raster format at a 1km^2 spatial resolution. Topographic variables included elevation and ruggedness as a previous study showed that these variables may have an important effect on lynx habitat selection (White et al. submitted). An index representative of roe deer abundance (Bouyer et al. 2015) and proportion of forest were also included as predictor variables. In addition, sex was taken into consideration to test for potential differences in lynx habitat selection between males and females.

Anthropogenic covariates were represented as an anthropogenic index. Our interest was in the additive effect of the main anthropogenic variables expected to have an impact on lynx habitat selection. To create this index, we used digital maps representative of the density of fields, forest roads, public roads and humans inside 1km^{2}pixels in an area large enough to include the home ranges of all our study lynx. The default situation (index value 1) consists of semi-natural habitats (mainly exploited boreal forest, bogs, or rarely alpine tundra) but without habitat conversion (to fields or built-up areas), infrastructure (roads) or resident people. We then ranked other pixels according to extent to which this situation was modified (Table 1).

Table 1: Presentation of the classes of human habitat modification. The index is intended to represent increasing levels of human habitat modification and increasing levels of infrastructure. The map-based criteria that we used to classify the 1x 1 km pixels are presented, along with an interpretation of what landscape type this represents. The column "% of presence" quantifies the percentage of pixels of the related index value present in the study area.

Class	**Classification criteria**	**Interpretation**	**% of presence**
1	Semi-natural habitats with no fields and no roads	"Forested" areas of semi-natural habitat with no infrastructure or habitat conversion (although all forest is exploited)	59%
2	Presence of agricultural fields and / or forest road	Rural landscape (low human modification)	20%
3	Presence of both forest roads and public roads, but no fields	Rural landscape (Low human modification but with public road access)	9%
4	Presence of fields, forest roads and public roads	Rural landscape (Medium human modification)	7%
5	Human density ≥ 20 and < 100 inhabitants per km^2	Rural landscape (High human modification and substantial number of residents)	3%
6	> 100 inhabitants per km^2	Rural – urban interface (periurban / suburban / urban)	2%

Use of Resource Selection Functions

We used resource selection functions (RSFs) to assess habitat selection under a use-availability design (Manly et al. 2002) for the three different behavior types. RSFs compare habitats that are used (animal points) with those that are available (or unused) to predict a relative probability of use. RSFs equations often take the form:

$$w(x) = \exp(\beta 1x1 + \ldots + \beta nxn),$$

were w (x) is the relative probability of use, exp is the base of the natural logarithm, βn are the estimated coefficients, and xn are habitat variables.

To define available habitat characteristics, we generated random 'available' locations within home ranges. For each individual lynx we used a different number of random locations equal to the number of locations of the most common behavior.

To account for different responses between different animals to similar availabilities of habitat, we added individual identity as a random effect to our model (Hebblewhite et al. 2008). It allowed for conditional inferences about individuals lynx as well as marginal inferences about the population and accounted for different sample sizes between individuals (Gillies et al. 2006; Wilmers et al. 2013). To obtain individual estimates of selection on the Index covariate, we added random coefficient to the model. The generalized linear two-level mixed-effects binomial model for location i and lynx j, with a random coefficient is given by:

$$\text{Logit}(yij) = \beta 0 + \beta 1x1ij + \beta 2x2ij + \ldots + \beta nxnij + \gamma 1jx1j + \gamma 0j,$$

where β0 is the fixed-effect intercept, γ0j is the random intercept (i.e., the difference between the mean intercept β0 for all lynx and the intercept for lynx j), and γ1j is the random coefficient of covariate x1 for lynx j (i.e., the difference between the mean coefficient β1 for all lynx and the coefficient for lynx j)(Mabille et al. 2012).

To improve model convergence and to facilitate comparison of model coefficients among covariates, we z-transformed all the covariates such as $(\frac{x-\bar{x}}{std\,(x)})$. For each behavior, models were fitted with multiple combinations of covariates and the best models retained were the ones minimizing the AIC.

All analyses were conducted using the package lme4 in R. We checked for correlation among variables using the Variance Inflation Factor (VIF; realized on GLMs) in the package car and made sure than no variables had a VIF higher than 3. GLMMs did not exhibit any sign of spatial autocorrelation based on the semi-variograms.

Results

Average home range size using the 95% kernel method was 912 km^2 (±485 km^2) for males and 535 km^2 (±481 km^2) for females. We recorded 709 day-bed locations for 19 individuals (a mean of 30 (±30 SE) day-beds per individual), 194 kill-sites for 16 individuals (a mean of 11 (±4) kill-sites per individual) and 3905 movement locations for 19 individuals (mean of 205 (±70) movement locations per individual).

Table 2: Results for the best RSFs presented for each behavior. Binomial mixed models with z-transformed explanatory variables.

	Resting sites		*Kill sites*		*Movements*	
Fixed effects	Coeffcients	SE	Coefficients	SE	Coefficients	SE
Roe density	0.528	0.087	-13.303	2.455	-2.468	0.336
SexM	-0.096	0.496	1.148	1.467	0.016	0.161
Index2	0.581	0.259	5.779	1.790	1.066	0.195
Index3	1.015	0.449	5.294	2.158	1.271	0.273
Index4	1.301	0.336	7.086	1.845	1.785	0.216
Index5	1.116	0.467	6.162	1.943	1.981	0.232
Index6	-2.525	0.844	-30.182	1289.505	2.044	0.407
Forest density	0.731	0.112	-0.023	0.365	0.419	0.055
Ruggedness	0.685	0.054	0.283	0.071	0.579	0.064
Elevation	0.919	0.097	-4.860	0.770	-1.264	0.109
SexM x Elevation	-2.241	0.165	-0.611	0.251	-0.106	0.070
SexM x Index2	-0.824	0.345	-1.474	1.373	/	/
SexM x Index3	-0.719	0.572	0.288	1.878	/	/
SexM x Index4	-0.797	0.461	-0.704	1.585	/	/
SexM x Index5	-0.334	0.637	-0.234	1.757	/	/
SexM x Index6	2.910	1.278	29.065	1289.222	/	/
SexM x Forest density	0.399	0.186			0.122	0.071
SexM x Roe density	-1.394	0.293	/	/	/	/
SexM x Ruggedness	/	/	/	/	0.227	0.083
Index2 x Forest	/	/	0.983	0.584	/	/
Index3 x Forest	/	/	0.629	0.551	/	/
Index4 x Forest	/	/	0.724	0.452	/	/
Index5 x Forest	/	/	1.146	0.681	/	/

Index6 x Forest	/	/	14.309	18.681	/	/
Index2 x Elevation	/		4.189	0.785	0.830	0.117
Index3 x Elevation	/	/	5.082	0.902	1.505	0.156
Index4 x Elevation	/	/	5.446	0.788	1.787	0.115
Index5 x Elevation	/	/	6.086	0.863	2.151	0.142
Index6 x Elevation	/	/	9.797	4.804	4.037	0.372
Index2 x Roe	/	/	10.915	2.520	2.372	0.355
Index3 x Roe	/	/	12.195	2.816	2.052	0.470
Index4 x Roe	/	/	13.046	2.486	2.885	0.344
Index5 x Roe	/	/	13.071	2.563	2.718	0.340
Index6 x Roe	/	/	23.936	14.283	2.723	0.378

	Resting sites	***Kill sites***	***Movements***
Random effects	Variance	Variance	Variance
Index2	0.027	3.641	0.155
Index3	0.538	8.311	0.463
Index4	0.365	6.207	0.330
Index5	0.973	6.971	0.344
Index6	3.396	11.316	0.882

The RSFs analysis results revealed that lynx selection of landscape was dependent on the degree of human modification (Table 2). Plots of the relative sensitivities of each behavior to human modification revealed that the pattern of response to human impact is similar between the behaviors (Figure 1). For the three behaviors, lynx seem to select rural areas of medium to high human modification and avoid forested and rural-urban interface areas.

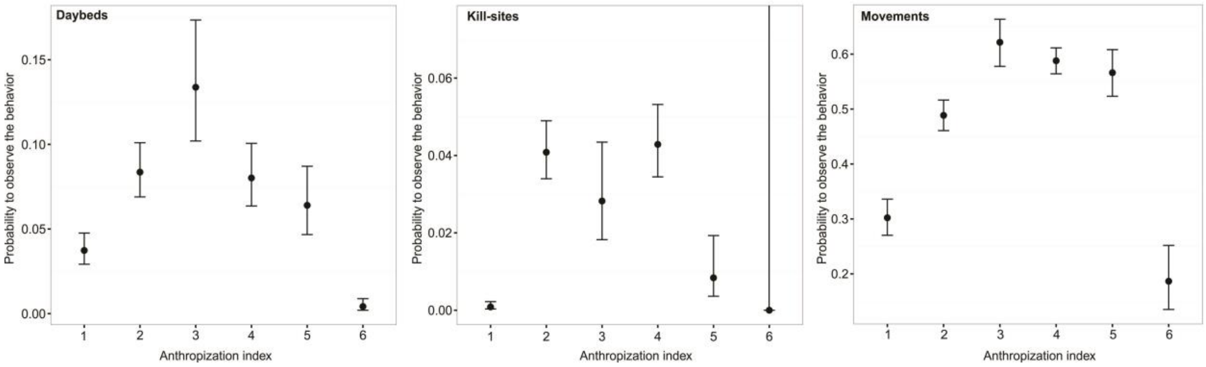

Figure 1. Lynx selection for the three behaviors (resting, killing and moving) presented for six levels of increasing habitat modification (with the other covariates maintained at their mean for each classes of the index). The standard error of the prediction is very high for kill-sites and anthropization index 6 because of the very few observations of this behavior in these conditions (N = 2)

For all the three behaviors considered, lynx select rugged areas. Daybeds and kill-sites are present in rugged areas for all the classes of human habitat modification except for the rural-urban interface both for daybeds and kill-sites and not in forested areas for kill-sites (Figure 2). Lynx clearly select for and move in rugged areas for all the different classes of human habitat modification.

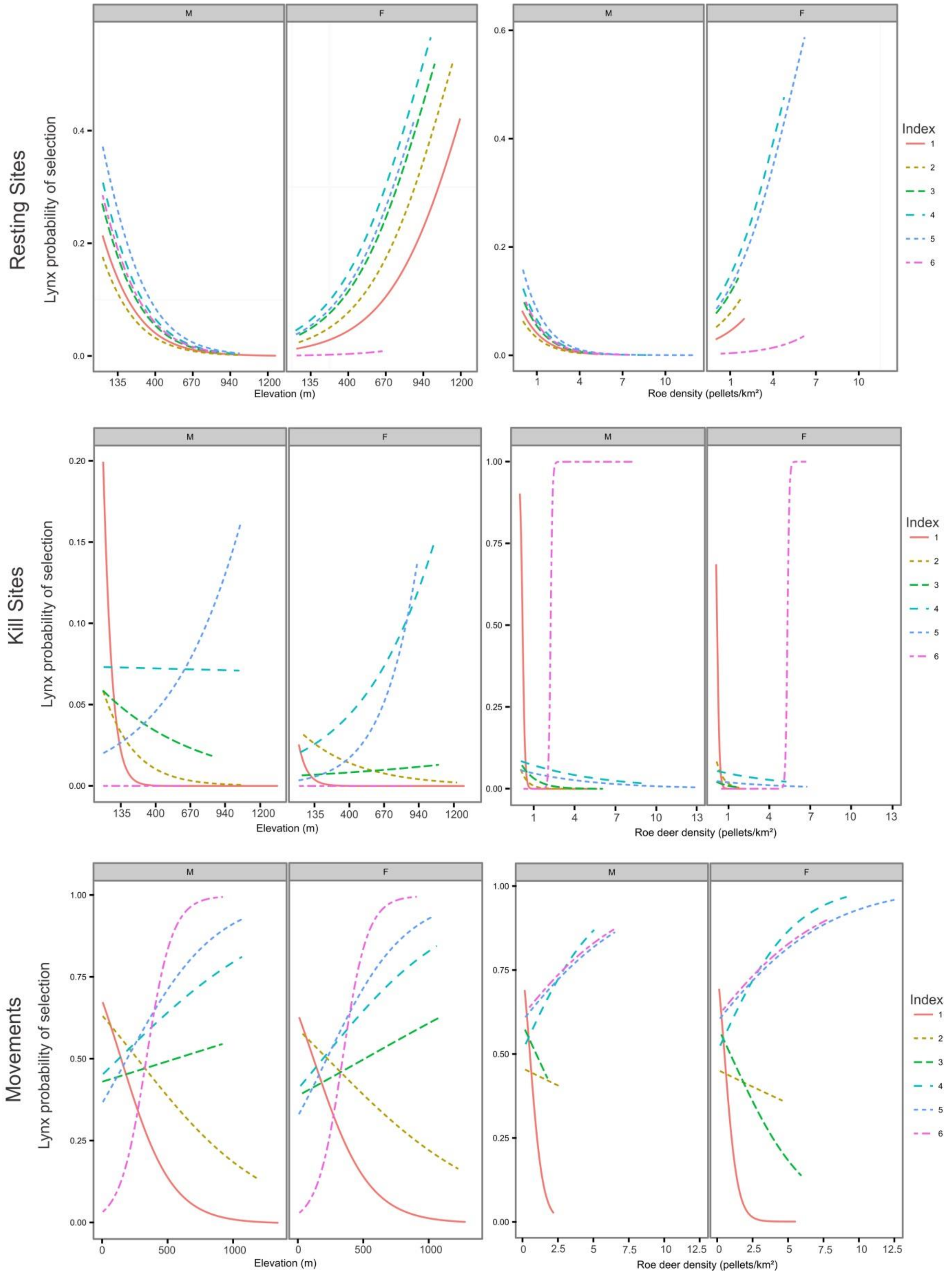

Figure 2. Estimated relationship between the probability of lynx selection and elevation and roe deer density (with the other covariates maintained constant).

Lynx respond to elevation in different ways between behaviors and sex. Males and females show different responses for daybeds but similar responses for kill-sites and movement. For daybeds, females select high elevation for all classes except for the rural-urban interface. Inversely, males select for low elevation for all classes. Lynx kill at low elevation when in forested and rural landscape with low human modification, while they kill at much higher elevation in rural landscape with medium to high human modification. Kills do not happen in the rural-urban interface. Lynx move at low elevation in forested areas and in rural landscape with low human modification, but they move at higher elevation when they are in rural landscape with medium to high human modification as well as in the rural-urban interface.

Daybeds, kill-sites and movements all happen at high forest density. The probability to observe daybeds for females is higher in rural landscapes of low to high human modification but lower in forested areas and in the rural-urban interface. The probability to observe daybeds for males is higher in medium to high human modification rural landscapes and the rural-urban interface. The probability to observe a kill both for males and females in forested areas is low for all the classes of human habitat modification. But males can kill in the high forest density areas in rural-urban interface.

The differential behavioural response of both males and females to roe deer density is not constant: it is similar for kill-sites and movements, but different for. Daybeds can be observed for females at low roe deer density in forested areas and rural landscape with low human modification. They can be observed at medium roe deer density in rural landscapes of medium to high human modification, and in the rural-urban interface. For all the classes, males avoid high roe deer density and select for low roe deer density. Kills happen at low roe deer density for all the classes of human habitat modification except for the rural-urban interface where kills happen at medium roe deer density. Lynx move at low roe deer density when they are in forested areas and in rural landscapes of low human modification. They move at medium to high roe deer density when they are present in rural landscapes of medium to high human modification and in the rural-urban interface.

Discussion

Our study explored how Eurasian lynx in Norway adjusts their specific behavioral traits (day-beds, kill sites and movement) of habitat selection in response to the additive impact of various anthropogenic changes. Our results reveal that lynx actually select for areas with varying degrees of human modification, preferring to use rural areas with a mix of forest and agriculture which are often associated with the presence of human settlements and transport infrastructure. Forested areas of semi-natural habitat and partly urbanized areas where less preferred. Habitat selection of day-beds differed between males and females, with females selecting for more secure landscapes than males. These results confirmed previous observations on lynx habitat selection in human dominated landscapes in the same study area (Bunnefeld et al. 2006; Basille et al. 2009).

The selection by lynx for rural landscapes where human habitat modification is present is probably a direct consequence of roe deer presence. Roe deer represents the main prey species for lynx in this study area (Odden et al. 2006; Gervasi et al. 2014). Roe deer are occurring at highest densities in fragmented areas where human activities provide improved forage through agricultural crops and supplementary feeding sites during winter (Basille et al. 2009; Torres et al. 2011). The data used in our studies also indicate the same pattern, with a predicted pellet density (Bouyer et al. in 2015) increasing from 0.34 pellets/km^2 for Index 1, to 2.65 pellets/km^2 for Index 6 (Figure 3). However, our study reveals also that lynx avoid the most modified landscapes even if roe deer density is highest in such landscapes. This fine-scale avoidance confirms the trade-off between roe deer density and human disturbance previously described at a coarser scale (Basille et al. 2009). By contrast, lynx avoidance of relatively unmodified forested landscapes is probably due to the associated increased energetic costs of hunting roe deer in areas where they occur at lower density.

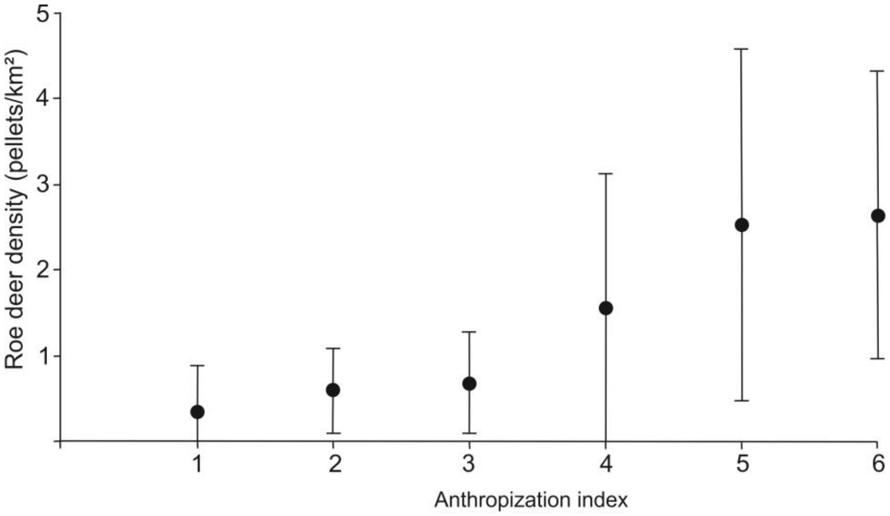

Figure 3. Average roe deer density (pellets/km^2) for each classes of human modification

Even though lynx select for areas with medium to high degree of human modification, our study reveals that they still respond to other environmental characteristics of the landscape. In our analyses, lynx selected for areas with greater degrees of forest cover and with more rugged terrain for all the behaviors considered. These results confirm previous studies conducted on lynx habitat selection (Basille et al. 2009; May et al. 2008; Niedzialkowska et al. 2006; Zimmermann & Breitenmoser 2002; Sunde et al. 1998). Forest represents habitat cover that is known to provide security. Sunde et al. (1998) reported that lynx were tolerant of human proximity when the density of forested areas was high, i.e. when good shelter was available. It is likely that presence of forest, even in relatively small patches, provides sufficient shelter for lynx to avoid being disturbed by humans even at high human densities. Lynx preference for rugged areas can also be associated with shelter and an attempt to avoid disturbance by humans. Lynx are known to select for steep areas in heavily disturbed landscapes as steepness is associated with a low level of human activity (Basille et al. 2008). By contrast, the strength of selection for ruggedness was lower in less modified landscapes (Basille et al. 2009). Terrain ruggedness has not received much focus as a habitat characteristic before, but there is a growing body of literature that indicates how important this landscape characteristic can be at facilitating carnivore use of human dominated landscapes (Nellemann et al. 2007; Petram et al. 2004).

Lynx movements are considered as the most important indicator of lynx activity as it is often unequivocally related to hunting behavior (Jędrzejewski et al. 1993; Schmidt 1999). However, in our study we did not look at the actual path used by lynx, the distance covered or the period of the day when the movements occurred. To better understand the effects of human disturbance on lynx movement, it would be interesting to take into account these information as they seem to have a high impact on other large carnivores. For example, European brown bears and wolves, which are primarily diurnal (Mech 1992), seem to avoid humans by shifting their activity to twilight and night time (Theuerkauf et al. 2003; Ordiz et al. 2012; Ciucci et al. 1997).

Although selection of habitat was mostly similar between the sexes for movements and kill sites, resting males and females did not select for the same habitats. Females selected for rugged areas at high elevation, with medium roe deer density and high forest cover, while males selected for low elevation and low roe deer density. Theory of sexual selection indicates that in polygynous and dimorphic species, males are supposed to take greater risks than females (Trivers, 1985). Bunnefeld et al. (2006) showed than female lynx with newborn kittens displayed a greater avoidance of humans than males, but that this avoidance behavior tended to decrease with kitten age. Even if most of the data on females used in this analysis do not correspond to reproduction period, it seems that females showed a greater avoidance of risks than males. Sleeping is a period of great vulnerability because of a decrease in sensory awareness (Cristescu et al. 2013). Selection of resting sites is therefore important to minimize the risk of detection and maximize the benefits of the sleep period (Lima et al. 2005). Selection of higher areas by females would lead to a reduction of the risk of detection since human activity is more important in the valleys (Zimmerman and Breitenmoser 2002). Females also selected for areas with higher predicted roe deer density which indicates that they select day-beds sites where availability of food is important. All these results suggest that anti-predator behavior is more developed with females than males as shown by their systematic avoidance of areas of very high human modification.

Lynx generally consume their prey where they kill it, feed on the carcass until it is finished, and then leave and search for a new prey (Okarma et al. 1997; Schmidt et al. 1999). For large prey items such as roe deer, lynx usually return to the carcass multiple times over several consecutives days and nights (Jobin et al. 2000). Based on our data, we observed that when a carcass was available and the lynx was not eating, they sometimes slept several hundred meters away from the dead prey, changing the location of resting sites over the days. Belotti et al. (2012) reported that when a kill was close to human trails, lynx tend to move further away from the kill during the day. Even if we did not take into account the distance between kill sites and resting sites in relation to sources of human disturbance, it is clear in our results that lynx select different habitats for resting than for killing. Resting sites are present in areas where disturbance is more likely to be less than at kill sites, which suggests that lynx select resting habitats to lower predation risks while kills occur where the prey is present, independently of the surrounding habitat. The fact that kill-sites and associated day-beds can be spatially disconnected implies that lynx can exploit prey in far riskier habitats than would otherwise be possible.

Because humans are the major cause of large carnivore's mortality in most landscapes (Woodroffe 2000; Woodroffe & Ginsberg 1998; Treves & Karanth 2003), understanding their behavioral response to human presence is important in a context where large carnivores have to share landscapes with humans. Thus, behavioral responses to human-induced environmental changes can help determine the capacity of a species to adapt to environmental changes and human presence (Tuomainen & Candolin 2011; Sih et al. 2011, 2012). Use of specific behavioral data instead of unclassified location data in our study has proved to be beneficial in the understanding of lynx habitat selection within human modified landscapes in Norway, as their relative selection for, and avoidance of human modification was dependent on the specifics of the behaviour. In general, lynx showed an ability to move through areas that were much more modified than areas where they would consume a kill or rest.

Overall, our results indicate that as long as prey is present, lynx are able to use and select different degree of human modified habitats. Furthermore, we showed that lynx actively select for medium to highly disturbed areas. These results are highly promising in the context of lynx recovery in continental Europe. Today, most of Europe is a mosaic of small forest patches and agricultural habitats crisscrossed by roads and with high human densities. Our results demonstrate that the presence of people, roads and fields are not an obstacle to lynx presence as long as there is some cover (forest and terrain) and prey.

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GENERAL DISCUSSION, CONCLUSION & PERSPECTIVES

The increasing pace and scale of human-induced changes to all the landscapes of the world are often considered as one of the main threats to carnivore populations (Logan & Sweanor 2001; Ripple et al. 2014) as large carnivore persistence has historically been associated with remote wildlands and wilderness areas (Woodroffe 2000). Eurasian lynx, wolves and brown bears are usually considered to be forest-dwellers (Niedziałkowska et al. 2006; Güthlin et al. 2011; Posillico et al., 2004; Jedrzejewski et al. 2005; Theuerkauf et al. 2003a and b) and relatively intolerant of fragmentation and disturbance. The work realized through this study does not agree with this general statement concerning lynx. Rather we highlight the capacity of Eurasian lynx in Scandinavia to adapt to diverse landscapes, including anthropogenic and alpine-tundra landscapes.

I. TOLERANCE AND SELECTION OF HABITATS IN HUMAN-MODIFIED LANDSCAPES

Norway is the least populated country in Europe, and contains large areas of semi-natural habitat, even though true wilderness is lacking. In this context, lynx have the possibility to avoid anthropogenic landscapes and to use relatively remote areas if they chose. This should be particularly true as lynx populations in Norway have clearly not yet reached their maximum carrying capacity due to heavy hunting pressure Linnell et al. 2010). The results presented in our study, however, show that only relatively few individuals use wild areas only, while most of them clearly select for areas with medium levels of human-disturbance and avoid both areas of low or high levels of human-disturbance, on both a broad scale (Chapter 3) and at a fine scale (Chapter 4). This is concordant with recent studies on large carnivore habitat selection in human-dominated landscapes that showed that some species are able to inhabit human-dominated landscapes [e.g. red wolf (Dellinger et al. 2012), cougars (Knopff et al. 2014), wolf (Fechter & Storch 2014; Theuerkauf et al. 2003b]). Tolerance and selection of medium human-disturbed areas by lynx is clearly linked to the presence of roe deer, one of its main prey in Norway (Appendix 1). Roe deer density is associated with human presence (Chapter 4) since roe deer can find attractive sources of food close to human settlements (Bunnefeld et al. 2006) and especially in the forest-farmland ecotones. The presence and density of carnivores in an area is in principle related to the availability of prey (Carbone & Gittleman 2002; Khorozyan et al. 2008; Carbone et al. 2011). For this reason, it is becoming more and more frequent to find higher densities of carnivores close to and in anthropogenic landscapes where they can prey on elevated densities of wild prey, in addition to anthropogenic food sources like livestock, pets and garbage (Athreya et al. 2014; Bino et al. 2010; Beckmann & Berger 2003; Gehrt et al. 2010).

Carnivore response to human activity is often seen as analogous with prey response to predation risk (Frid & Dill 2002). Even if lynx tolerate human presence, they adapt their behaviour to reduce perceived risks by avoiding human presence when in position of greatest vulnerability, i.e. for daybeds (Chapter 4) and reproduction sites (Appendix 2). To do so, lynx mainly select for terrain (ruggedness and altitude) and forest; habitats that provide cover and shelter against predators and people (Chapters 2, 3, 4 & Appendix 2). Sleep decreases the ability of animals to use long-distance perception of danger through scent, sight, hearing, or flight response to cope with risky situations (Cristescu et al. 2013). For these reasons, selection of resting sites is an essential determinant of predation risk during the sleep period as it could minimize the associated costs of fleeing and maximizing survival probability (Ordiz et al. 2011). For example, bears in Scandinavia adjust their resting sites in order to increased cover and avoid human encounters, especially during the hunting periods (Ordiz et al. 2011). For many carnivores, secure den sites may be essential for reproduction (Laurenson 1994). This is especially the case with Eurasian lynx which have a 50% survival rate for kittens of less than a year (Breitenmoser-Würsten et al., 2007) and for which secure and well camouflaged den sites are needed for kitten survival (Appendix 2). If forest was a well-known habitat use for cover, terrain structure, especially ruggedness has not been so commonly considered in habitat selection studies for large carnivores. This landscape characteristic seems however to greatly facilitate lynx use of human dominated landscapes, as it has been shown for other carnivores (Linnell et al. 2000; Nellemann et al. 2007; Petram et al. 2004).

Thanks to the huge amount of data on lynx distribution collected during the last twenty years in Scandinavia, we were able to look at lynx habitat selection at very large scales. While our results showed that lynx can adapt to human-modified landscapes, they also showed inter-individual variability in habitat selection. This variability was first observed on a large scale where individual lynx differ in predatory behaviour as well as in habitat requirement (Chapter 2). For example, in southern Norway, lynx must cope with an average human density of 122 inhabitants per km^2 while in the North individual lynx face 6 inhabitants per km^2 in average. But this variability was also observed at a finer scale (Chapters 3 & 4). Lynx seem able to adapt to a broad range of conditions depending on their surroundings (from wilderness to rural habitat) to the extent that they seem capable of adjusting their behaviour to accommodate anthropogenic infrastructures and development (Chapter 4). For example, in 2013, a female gave birth to kittens a few hundred meters away from a farm near Oslo (Matisson J., personal communication). Even if Eurasian lynx are generally considered a specialist species (Mattson 2004), their adaptability to live in a broad range of environmental conditions, as observed in this study, leads us to consider the Eurasian lynx a habitat generalist species able to tolerate different conditions of habitats and human disturbances. To confirm this flexible behaviour in the species *Lynx lynx*, it would be helpful to look at diurnal activity adjustments of the lynx to human disturbance as well as to extend our study to other populations in Europe. On the other extreme, our studies (chapter 2) have shown that lynx can also occupy alpine tundra habitats at 71 degrees north. Again it appears to be the distribution of prey that drives their habitat selection. In these northern areas semi-domestic reindeer constitute their main prey, and reindeer make frequent use of areas above the climatic treeline – thus forcing lynx to follow.

II. TRANSFERABILITY OF RESULTS

In the context of the return of large carnivores to Europe, it is interesting to ask if the results on lynx tolerance to anthropogenic disturbances observed in Scandinavia, the least populated region of Europe, are transferable to continental Western Europe, the most populated and fragmented region of Europe. To do so, it was necessary to explore the transferability of results obtained from the Norwegian distribution models.

"Everything is related to everything else, but near things are more related than distant things" is a well acknowledge rule in spatial analysis (Tobler's Law of Geography, 1970). When working with large carnivores with home ranges of hundreds of km^2 (Herfindal et al. 2005), the use of interpolative and extrapolative models is often the only practical option. The time and money spent to monitor such animals often force researchers to concentrate only on a subset of a population or on a few individuals. This is particularly true in Norway where lynx home ranges are the largest in Europe (average size = 1000 km^2, Herfindal et al. 2005). Extrapolation of results from one area to another has not given totally accurate results, either at small scales (Chapter 1) or large scales (Chapter 2). This is due to two main factors. The first is related to Tobler's Law. The differences in habitats observed between areas in Scandinavia (Chapter 2) were surely responsible for the low power of extrapolation encountered in our models since we have worked on a very large scale. The second factor probably responsible for the extrapolation difficulty is the generalist capacity of lynx (chapter 2) and their main prey, the roe deer (chapter 1). Indeed, it is more difficult to characterize habitat preferences for generalists than for specialists, as generalists can have different habitat preferences in different parts of their distribution (Fechter & Storch 2014).

Based on the results obtained throughout this research project on extrapolation capacity of statistical models (Chapters 1 & 2), it is clear that we cannot apply our models directly to Western Europe. These results are nonetheless very informative and bring new information on the ability of Eurasian lynx to adapt to human disturbance. The inclusion of the Oslo and Stockholm regions (Chapters 2, 3 & 4), the most populated areas of Scandinavia, give us an insight into the potential ability of lynx to tolerate human presence and fragmentation in Western Europe. The presence of reproductive female lynx established on the edge of Oslo and Stockholm indicate that the threshold at which lynx still tolerate the presence of roads, humans and fields is quite high even if we have only began to define this threshold (Chapter 3). Eurasian lynx in Scandinavia seem to have similar adaptability towards human presence as an increasing number oflarge carnivores around the world [e.g.: leopards in India (Athreya et al. 2013, 2014; Odden et al. 2014; red foxes (Dellinger et al. 2012); cougars (Knopff et al. 2014)].

III. CONCLUSION: IS LAND-SHARING POSSIBLE?

A robust biological and ecological understanding of a species is essential for its conservation. To help preserve a species, carnivore or others, we need to have information on its feeding habits, the range of its niche, its different behavioural traits etc. With large carnivores, it is important to improve our understanding of how they interact with people, in order to minimise the conflicts that will follow their sympatry with humans. In this thesis, we have shown that a European large carnivore, the Eurasian lynx, is able to cope with substantial human impact on the landscape. Other examples of large carnivores dealing with anthropogenic landscapes suggest that many of these species are more adaptable than they were originally thought to be (Athreya 2013, 2014; Gehrt et al. 2010; Knopff et al. 2014; Boitani et al. 2010). Cohabitation between humans and large carnivores is becoming a reality in many regions. But in order to reduce conflicts between humans and carnivores, we need to go from the cohabitation stage to the coexistence stage (i.e.: live in close proximity with presence of conflicts vs. live in close proximity in harmony despite different interests). Many examples proved that such coexistence may be possible. The most emblematic one is surely the case of the lions and Maasai people in Kenya. In Africa, lion populations have declined drastically largely due to ritual and retaliatory killing by local communities who perceive more hindrance than benefits from lion presence. In East Africa, lions are speared to reinforce the role of warriors in society (Hazzah et al. 2014), who are traditionally the protectors of their communities cattle, with a reputation for fearlessly killing lions. To decrease lion killing in Maasailand, two complementary programs run simultaneously: (1) the Predator Compensation Fund (PCF) is based on the model of paying local people for depredated livestock in an attempt to deter retaliatory killing (Verdade & Campos 2004; Agarwala et al. 2010; Boitani et al. 2010, Hazzah et al. 2014), and (2) the Lion Guardians (LG) program employs traditional conflict mitigation techniques to reduce livestock depredation and attempts to incorporate community cultural values and belief systems to improve local tolerance of large carnivores (Infield 2001; Stringer et al. 2006). Concretely, LG employs Maasai Warriors to monitor lion numbers and movements, inform herders of close presence of lions and help construct protective nighttime enclosures called bomas. A study on efficiency of each program revealed that they results in an 87% drop in the number of lions killed for the PCF and in a 99% drop for LG (Hazzah et al. 2014). This example shows that incentive-based schemes, whether they are compensation or participatory programs,can have important consequences on human tolerance for wildlife. People's tolerance for wildlife is an important side of the two dilemmas that are linked to coexistence: (1) the threat that predators represent to humans and livestock and (2) the threat that humans represent to predators (Fascione et al. 2004).

Many solutions have been proposed to resolve the first dilemma and decrease the negative effects of large carnivores on livestock. There are a range of methods that can be used, directed at either the livestock (fences, livestock, dogs etc; Smith et al. 2000; Gipson & Paul 1994) or the carnivores (hunting, translocations: Kaltenborn et al. 2013; Linnell et al. 1997). But the key to coexistence is in the resolution of the second dilemma. By nature, carnivores are predators and damage will always occur with carnivores around, even with all the mitigation procedures in place. It is then important that people be willing to accept the costs induced by the presence of large carnivores and make compromises. The importance of people’s acceptance for the presence of wildlife has generally been well recognised and nowadays it has an important place in national biodiversity conservation plans and in the framework of conservation plans (see Maasai example Hazzah et al. 2014; MacDonald et al. 2010). The mitigation of human-carnivore conflicts is more and more considered to be of conservation, social and economic concern (Thorn et al. 2013). Mitigation methods to help increase people's tolerance toward predators include compensation and protection of livestock, and integration of local-communities into conservation activities and redistribution of the carnivore-generating-income from ecotourism (Ciucci & Boitani 1998; MacDonald et al. 2010; Rust et al. 2014). However, in view of the spatial and temporal variation as well as the effect of social, economic, ecological and environmental factors on people's response to carnivore presence (Graham et al. 2005; Inskip & Zimmermann 2009; Rigg et al. 2011; Kaltenborn et al. 1999), effective mitigation strategies will depend on accurate knowledge of local contexts. Such knowledge and the application of mitigation measures may one day lead to a coexistence that will be ecologically, economically and socially sustainable over time.

IV. PERSPECTIVES

This research project was born in 2009, after several sightings (unconfirmed) of Eurasian lynx occurred in Belgium and Luxembourg. The idea of the presence of the Eurasian lynx in the Benelux countries was a very exiting one, but the potential return of this species also implied important consequences in terms of conflicts with farmers and hunters and in terms of lynx population viability in the very anthropogenic landscape of Western Europe. Based on the results obtained throughout this research project on extrapolation capacity of statistical models (Chapter 1 & 2), it is clear that we cannot apply our Scandinavian models directly to the Benelux. This is even truer when considering that the level of habitat fragmentation is much higher in the Benelux countries than in Scandinavia, a factor than may have an important impact on lynx use of habitat and their vulnerability to humans. In order to apply the knowledge obtained during this project on lynx response to human disturbance in the Benelux landscapes, a possible solution would be to use rule-based habitat modelling. Such models have been applied for assessment of suitable habitats for lynx and wolves in Germany and have proven to be effective (Schadt et al. 2002; Fechter & Storch 2014). In rule-based models, a priori assumptions are made about the species and its habitat relationships to predict suitable habitats. These assumptions can be based either on expert opinion or data from other populations. Using information on the tolerance of lynx to human presence as well as information on lynx habitat use from countries like Germany and France, a logical next step would be to construct a rule-based habitat model for lynx in the Benelux and to try to obtain estimates of the size of a lynx population that could potentially find its home in the Benelux landscapes. However, the most abundant data on lynx distribution in continental Europe are from Switzerland and the Czech Republic, two areas that do not have the same level of fragmentation as the Benelux. To really obtain accurate information on lynx ability to dwell in human-modified and fragmented landscapes, we will probably need data from areas that have not been sampled yet.

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APPENDIX

APPENDIX I - THE SPATIO-TEMPORAL DISTRIBUTION OF WILD AND DOMESTIC UNGULATES MODULATES LYNX KILL RATES IN A MULTI-USE LANDSCAPE

The spatio-temporal distribution of wild and domestic ungulates modulates lynx kill rates in a multi-use landscape.

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Abstract

Depredation on livestock and competition with hunters for game species are prominent among the conflicts that the return of large carnivores generates in multi-use landscapes. The relative magnitude of the conflict strongly depends on what prey selection patterns predators will adopt once established in a new area. We explored prey selection and kill rates from 24 Eurasian lynx *Lynx lynx* in Southern Norway, between 2006 and 2011, using Global Positioning System collars. We recorded 603 lynx predation events on a wide range of prey species, ranging from passerines to large ungulates. During summer, domestic sheep were the most frequent prey, representing 64% of the ungulates killed, for an average kill rate of 8.2/100 days, whereas roe deer *Capreolus capreolus* were killed in about 33% of cases (kill rate = 4.2/100 days). In winter, when sheep were unavailable, roe deer were the most frequent prey, accounting for about 73% of the kills, for an average kill rate of 9.4/100 days, whereas red deer were found at 17% of the kill sites, corresponding to a kill rate of 2.2/100 days. Lynx-killed prey provided an average of 400 kg of meat per 100 days, irrespective of prey density. In both seasons, the proportion of each species killed by lynx was determined by the combined effect of all prey densities, so that the density of wild ungulates had the potential to affect the rate of depredation on sheep, to the same extent as the abundance of sheep could influence the kill rate on wild ungulates. Our results underline the complexity of carnivore–ungulate trophic interactions in multi-use landscapes where livestock and wildlife co-occur, and suggest that changes in densities of prey, predators or both may produce undesired outcomes, if such complexity is not taken into account during the decision-making process for management and conservation.

Introduction

Large carnivores have returned or are returning to several densely populated areas of Europe and North America, as a consequence of the profound ecological and social changes of recent decades (Kellert *et al.*, 1995; Linnell, Salvatori & Boitani, 2008). Along such a recovery process, they have proved to be more tolerant and adaptable to human presence than many could have foreseen (Linnell, Swenson & Andersen, 2001; Treves & Karanth, 2003). As a result, large carnivores are now inhabitants of many multi-use landscapes, in which predation, reproduction and dispersal occur simultaneously and in sympatry with a diversity of human activities.

Among the conflicts that such co-occurrence generates, depredation on livestock and competition with hunters for game are prominent, and the relative extent to which recolonizing carnivores will affect the first or the latter conflict depends on what type of predation patterns (especially concerning prey choice) they will adopt once established in a new area (Graham, Beckerman & Thirgood, 2005). In some instances, in fact, recolonizing carnivores rely almost exclusively on livestock, such as sheep or cattle, especially when they are abundant, lack anti-predatory behaviour and are not protected by appropriate herding practices (Odden *et al.*, 2002; Sangay & Vernes, 2008; Linnell, Odden & Mertens, 2012). This usually generates high social conflicts and economic costs, related to the implementation of compensation and mitigation actions (Treves & Karanth, 2003).

In other instances, carnivores rely mostly on the wild component of their prey spectrum, thus entering in direct competition with hunters for the harvest of game species (Breitenmoser *et al.*, 2010). In this case, while the combined effects of predation and human harvest have the potential to generate a decline in wild ungulate populations (Vucetich, Smith & Stahler, 2005; Gervasi *et al.*, 2012), a few individual carnivores may, in some circumstances, show an inclination to kill livestock (Stahl *et al.*, 2002). These individuals often have the tendency to kill a surplus of domestic prey (Odden *et al.*, 2002), and to consume only a minor portion of them, so that a specific behavioural pattern by a few animals can generate high economic costs and a dramatic increase in the social and psychological perception of the conflict (Linnell *et al.*, 1999). For this reason, the effect of wild prey density on livestock predation has been widely studied and is a key debate in wildlife conservation and management (Meriggi *et al.*, 1996; Stahl *et al.*, 2001; Odden *et al.*, 2008).

In all instances, recolonizing carnivores, their wild and domestic prey, and humans (either as hunters or herders) are all part of an interconnected trophic system. Inside such a system, prey selection patterns by carnivores, and their functional response to prey density or accessibility, are the key underlying mechanisms, determining which specific part of the system will carry most of the costs related to allowing carnivore presence in a given landscape. Considering that large carnivores are still expected to expand and increase in numbers in the coming decades (Ray *et al.*, 2005), understanding which factors affect their prey selection patterns in a multi-use landscape is central to both biodiversity conservation and human well-being.

To this aim, the recovery and expansion of the Eurasian lynx *Lynx lynx* population in Southern Norway offers a good opportunity to explore the issue of predator–prey dynamics in a multi-use landscape (Linnell *et al.*, 2010). The interspersed forest ecosystem of Southern Norway hosts a diverse assemblage of wild and domestic ungulate species, in a context of intensive human use of the services provided by the ecosystem (grazing, hunting, logging, etc.). Moreover, a strong spatial gradient and seasonal variation in both domestic and wild prey distribution exist in the area, which exposes lynx to different conditions of prey availability and accessibility in space and time. Given these premises, we explored lynx prey selection patterns and kill rates in the area during a 6-year study period, focusing on the two most common wild ungulate prey, red deer *Cervus elaphus* and roe deer *Capreolus capreolus*, and on domestic sheep *Ovis aries*. We examine how the spatio-temporal variation in the availability of all prey species has the potential to affect lynx predation patterns and to shape the dynamics of the multi-prey system. We also discuss the consequences of such an interconnected trophic system on the management and conservation of carnivores in multi-use landscapes.

Materials and methods

Study area

The 25 000 km^2 Østafjells study area encompasses an environmental gradient (north-west–south-east) in Buskerud, Telemark and Oppland counties in Southern Norway (Fig. 1). The north-western part of the area is dominated by steep elevation gradients from valleys and up to mountains >1000 m above sea level, and it is marginally suitable for roe deer. The area is forested with a domination of Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. The south-eastern portion of the study area includes patches of deciduous forest, and the landscape is more human modified. Here, the forest is fragmented by cultivated land, and roe deer occur at higher densities. Red deer have recolonized the area within the last few decades and remain at low population densities partly due to harvesting. Furthermore, red deer perform an altitudinal movement from a low-elevation winter range to a high-elevation summer range (Mysterud *et al.*, 2001), and they are therefore more available for lynx predation during winter. Roe deer also migrate, but to a lesser degree than red deer (Mysterud *et al.*, 2012). All parts of the study area have free-ranging sheep grazing in forest and alpine habitats from June to September, with very limited supervision, no guarding and few constraints on their movements. However, the density and distribution of sheep vary considerably inside the area. The north and western parts have the widest distribution of grazing areas and the highest densities of sheep. Further south and east, the density of sheep can still be high locally, but sheep grazing areas are more patchily distributed. Wild mountain reindeer *Rangifer tarandus* are seasonally available at higher altitudes in the northern parts. Throughout the study

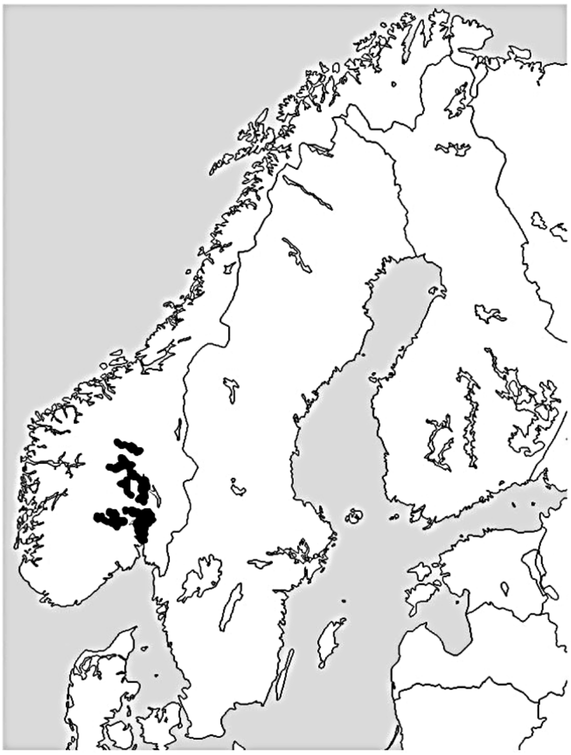

Figure 1 The study area in Buskerud, Telemark and Oppland counties, Southern Norway. The black dots represent all the 24 000 lynx Global Positioning System locations collected during the study in the period 2006–2011.

area, roe deer co-occur with moose *Alces alces*, mountain hares *Lepus timidus*, beavers *Castor fiber* and forest birds such as black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus*. Eurasian lynx are widespread throughout the area, having recolonized it in the 1980s. The population is controlled through hunter harvest, such that its size has fluctuated around 60–70 individuals since 2003 (Linnell *et al.*, 2010).

Animal capture

Between 2006 and 2011, we captured 14 female and 16 male lynx and monitored them using Global Positioning System (GPS) collars, summing up to almost 4000 tracking days and to a total of 76 kill rate sequences with intensive positioning. Adult lynx and juveniles (>5 months) were captured in wooden box traps and spring-loaded foot snares placed around lynx kills. All procedures were approved by the Norwegian Experimental Animal Ethics Committee, and permits for wild animal capture were obtained from the Norwegian Directorate for Nature Management. Based on snow tracking in winter and the marking of kittens in natal lairs, we were able to assess the reproductive status of each radio-collared female lynx in each year and season, and to determine if it was accompanied by dependent kittens.

Lynx kill rates

We collected data on kill rates between November and April in winter, and between May and September in summer. During the period 2006–2008, we monitored four lynx using 'store-on-board' GPS collars with a schedule of two locations per day. Thus, we identified potential kill sites using GIS software (ArcGIS 9.2, ESRI, Redlands, CA, USA) and visited them after the collars had dropped off. After 2008, we fitted lynx with GPS-GSM (Global System Communication) collars, which allowed us to visit potential kill sites right after the animal had left the area. Furthermore, the monitoring schedule was increased up to 19 locations per day during predation sequences. We defined clusters as a set of at least two locations within 100 m, and visited them to confirm a predation event. When a carcass was found, we identified the species, and whenever possible its sex and age class (calf/fawn, yearling, older individual). We defined seasonal species-specific kill rates for each individual lynx as the number of individuals of a given species killed in 100 days. To convert kill rates into an overall prey biomass, we used values of 26, 150 and 70 kg for adult roe deer, red deer and sheep, respectively (Silva & Downing, 1995; Andersen, Duncan & Linnell, 1998). We also used a monotonic growth model to estimate the body mass of juvenile and yearling prey in each month of the year (Tjorve & Tjorve, 2010).

Prey density

To model the spatial and temporal variation in sheep density during our study, we used data from the Norwegian Forest and Landscape Institute (http://www.skogoglandskap.no/) for the years 2006–2011, which reports the number of sheep released in spring in each grazing area. The average size of grazing areas was about 50 km^2, about one-tenth of an average lynx home range (Herfindal *et al.*, 2005); therefore, we assumed homogeneous sheep density inside grazing areas. For roe and red deer, we did not have direct estimates of the spatial variation in their density. We used predictive density maps with a 1 km resolution (Bouyer *et al.*, unpublished data) for each of the two prey species, derived from a set of pellet count surveys, performed along 430 transects during the study period. The maps were inferred from hurdle models (Zuur *et al.*, 2009) applied on environmental and anthropogenic variables, such as altitude, road density, human density, habitat composition, average snow depth, etc. The models were validated using cross-validation and two independent datasets related to prey densities. The models allowed us to predict the spatial variation of prey density inside each lynx home range, and thus provided an index of roe and red deer density to be associated with each lynx kill. We estimated roe deer and red deer density at increasing buffer distances around each kill, ranging from 1 to 10 km, and found that the closest relationship between prey density and kill probability was observed when using a 4 km buffer, which we used for all subsequent analyses.

Statistical analyses

Given the seasonal variation in the spatial distribution of both wild and domestic prey in our study area, we performed separate analyses of prey selection patterns on winter and summer kills. In summer, we focussed on roe deer and sheep, which comprised the vast majority of lynx kills, whereas in winter, we analysed the roe deer/red deer prey selection patterns because sheep were largely unavailable. Before performing successive analyses, we used binomial generalized linear model (Zuur *et al.*, 2009) to test for any variation in the proportion of other species among lynx kills, and found that their proportion was constant across the gradient of all prey densities, across sexes and seasons, and independent of the reproductive status of female lynx. This assured that no bias was introduced in the prey selection analysis by the exclusion of this group of prey species. Then, we used binomial generalized linear mixed-effects models in R (R Development Core Team, 2008), using the package *lme4* (Bates, Maechler & Bolker, 2011), to test what factors affected the proportion of the two main prey among lynx kills in each season. As some individuals were followed for more than 1 year and had multiple kill rate estimates, we fitted mixed-effects logistic regression models with individual lynx as a random effect, to account for pseudoreplication (Hurlbert, 1984). We used the density of each of the two focal prey species as explanatory variables, and for each of them fitted a linear, logarithmic, quadratic and second-order polynomial function. We also tested for a difference in prey selection patterns among males, solitary females and females with dependent kittens. In each season, we performed a preliminary variance inflation analysis (Zuur *et al.*, 2009) to assess the degree of collinearity among explanatory variables, which highlighted a negative correlation between roe deer and red deer density (Pearson's $\rho = -0.5$). Thus,

Table 1 Seasonal composition of the prey species killed by solitary females, females with kittens and male lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

	Solitary females (%)		Females with kittens (%)		Males (%)	
Prey type	Summer (16)	Winter (64)	Summer (73)	Winter (87)	Summer (188)	Winter (64)
Beaver *Castor fiber*	0	0	0	0	0	0.5
Domestic goat *Capra aegragus*	0	0	0	0	0.5	0
Hare *Lepus timidus*	10.5	12.5	13.7	16.5	12.9	4.3
Moose *Alces alces*	0	0	0	0	0	1.2
Red deer *Cervus elaphus*	5.4	7.8	2.7	6.2	1.1	22.6
Red fox *Vulpes vulpes*	0	1.5	0	0	0	1.8
Wild reindeer *Rangifer tarandus*	0	0	0	0	0.5	0.6
Roe deer *Capreolus capreolus*	52.6	67.2	24.7	67.0	23.1	56.7
Domestic sheep *Ovis aries*	10.5	0	45.2	3.1	55.4	12.3
Squirrel *Sciurus vulgaris*	0	0	0	1.0	0	0
Tetraonids	10.5	9.4	12.3	6.2	3.8	0
Other birds	10.5	1.6	1.4	0	2.7	0

Numbers in parentheses indicate the total number of kills for a given lynx category and season.

to avoid overfitting the models and underestimating the variance, we fitted a linear regression model between roe deer and red deer density, and used the residuals from this model as an independent estimate of red deer density in the study area (Jakob, Marshall & Uetz, 1996). Thus, the resulting contribution of this variable represents the effect of red deer on lynx prey selection, after accounting for the proportion of variance already explained by roe deer density.

After generating reduced models, we selected the most parsimonious one using the Akaike information criterion (AIC_c) of model fit (Burnham & Anderson, 2002).

Results

Seasonal predation patterns

During the study period, we recorded 603 lynx predation events on a wide range of prey sizes, spanning from small birds up to ungulates as large as moose (Table 1). In both seasons, ungulate prey constituted about 80% of lynx diet, whereas most of the remaining proportion of kills involved hares, black grouse and capercaillie. Among ungulates, a clear difference in predation patterns emerged between the two seasons. During summer, sheep were on average the most frequent prey, representing 64% of the ungulates killed, but large differences between individuals were evident. Some lynx, especially males and females with dependent offspring, relied almost totally on sheep predation, whereas others, including several solitary females, showed the opposite tendency to almost exclusively kill roe deer (Table 1). Only five red deer and one wild reindeer were killed in summer during the whole study period. In winter, roe deer were the most frequent prey species, accounting for about 73% of the kills, whereas red deer were found at 17% of the kill sites. Also in this case, we observed a large individual variation around the average values, with a general tendency for males to kill a larger proportion of red deer than females (Table 1).

Table 2 Age distribution of the ungulates killed by lynx in summer and winter in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

	Winter				Summer			
Age class	Red deer		Roe deer		Sheep		Roe deer	
	N	%	*N*	%	*N*	%	*N*	%
Juvenile	18	52	47	47	75	93	20	41
Yearling	11	31	16	16	1	1	9	18
Adult	6	17	38	37	5	6	20	41
Unknown	11	23	100	50	57	41	32	39

The proportion of ungulates killed in each age class was calculated on the total number of individuals for which we were able to determine age, whereas the proportion of 'unknown' was calculated on the total number of prey items for a given species and season.

We were able to attribute an age class to about 65% of the ungulate prey found. Among them, 93% of the sheep killed by lynx were lambs (Table 2). Predation on juvenile red and roe deer accounted for 52 and 45% of all the kills, respectively, but lynx killed a larger proportion of adult roe deer (~40%) than adult red deer (17%; Table 2).

Kill rates and the effect of prey density

Lynx kill rate on roe deer was on average 4.2/100 days in summer and 9.4/100 days in winter (Table 3), but a large variation was evident around these mean values, with some individuals killing up to 23 roe deer every 100 days, whereas others did not kill any roe deer (Table 3). As expected from the seasonal variation in their availability, sheep were killed by lynx to a larger extent in summer than in winter, as the summer kill rate was on average 8.2/100 days, but only 1.0/100 days in winter. Also in this case, some individual lynx showed extremely high kill rates on sheep, with up to 54 kills in a 100-day period, whereas several other individuals killed no

Table 3 Average kill rate estimates (number of prey killed/100 days) on wild and domestic ungulates for solitary females, females with kittens, and male lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

	Roe deer		Red deer		Sheep	
Lynx type	Summer	Winter	Summer	Winter	Summer	Winter
Solitary females	5.5 (0–9.3)	8.9 (1.8–13.8)	0.2 (0–0.9)	1.0 (0–3.4)	9.4 (0–14.3)	0.0 (0–0)
Females with kittens	3.5 (0–14.3)	10.8 (3.1–21.2)	0.6 (0–4.8)	0.4 (0–2.7)	6.4 (0–13.3)	0.2 (0–2.6)
Males	7.2 (0–22.7)	9.0 (0–20)	0.4 (0–3.4)	3.1 (0–12.5)	14.6 (0–54.5)	1.6 (0–20.7)
Mean	4.2	9.4	0.2	2.2	8.2	1.0

Numbers in parentheses indicate the range of observed kill rates for each season, lynx category and prey species.

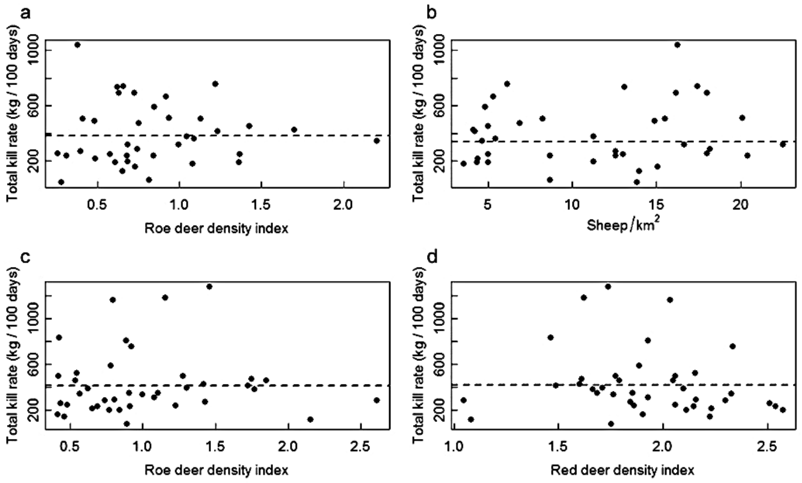

Figure 2 Seasonal relationship between prey density and the individual lynx total kill rate expressed as kilograms of meat. The graphs show the functional relationship between roe deer density and roe deer kill rate in summer (a) and winter (c), between sheep density and sheep kill rate in summer (b), and between red deer density and red deer kill rate in winter (d). Dotted lines are regression curves between prey density and total kill rate, whose slopes are all not significantly different from zero.

sheep (Table 3). Lynx predation on red deer emerged especially as a winter habit for males. The average winter kill rate was 2.2 red deer killed/100 days, but reached 3.1/100 days for males and only about 0.5–1.0/100 days for females (Table 3).

When kill rates were expressed in terms of total biomass killed, we found that variation in prey density did not contribute to explain differences among individuals. Both in winter and in summer, lynx-killed ungulates summed to an average of about 400 kg per 100 days irrespective of prey density, with significant inter-individual variation (Fig. 2). This is notable if we consider that the study area included an almost threefold spatial variation in red and roe deer density and up to a fivefold variation in sheep density. Therefore, differences among kill rates of lynx individuals were predominantly the result of different prey selection patterns, rather than of a limitation in predation efficiency due to the effect of prey density.

Seasonal models of prey selection

The logistic regression analysis of summer prey selection patterns showed that the proportion of roe deer and sheep killed by lynx was determined by the combined effect of both prey densities. The best supported model (model 1 in Table 4) included a linear effect of the two variables, whereas a quadratic effect was slightly less supported. Furthermore, an effect of lynx sex and reproductive status was included in all the best models, showing an increased probability for males and females with kittens to kill sheep. Figure 3 shows a positive response by lynx to roe deer density, but also that sheep abundance had the potential to modulate such responses, especially at low and intermediate roe deer densities. In areas with low sheep density (continuous line in Fig. 3a), the prey selection function rapidly reached an asymptotic level, at which lynx were predicted to kill almost exclusively roe deer. In contrast, in areas where sheep were abundant (dashed line in Fig. 3a), lynx exhibited a reduced response to roe deer density, so that sheep were the main prey along a substantial portion of the roe deer density gradient. The other side of the coin is that roe deer density also strongly modulated the response of lynx to sheep density (see Fig. 3b). Lynx showed almost no response to variation in sheep density, when roe deer were abundant in their home range (continuous line in Fig. 3b), but exhibited a typical positive asymptotic response when roe deer density was low (dashed line in Fig. 3b). The functional relationship between prey density and lynx prey selection patterns in summer was best described by a surface, whose determinants were local densities of both roe deer and sheep (Fig. 3c).

Table 4 Model selection results for the binomial GLM analysis of summer prey selection patterns of lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

N	Model	AICc	ΔAICc	Weight
1	Roe deer + Sheep + Sex*Reproductive status	423.06	0	0.43
2	Roe deer + Sheep + (Sheep)^2 + Sex*Reproductive status	425.04	1.98	0.16
3	Roe deer + (Roe deer)^2 + Sheep + Sex*Reproductive status	425.05	1.99	0.16
4	Roe deer + (Sheep)^2 + Sex*Reproductive status	425.55	2.49	0.12
5	(Roe deer)^2 + Sheep + Sex*Reproductive status	426.51	3.45	0.08
6	Roe deer + $\mathrm{Log}_{(\mathrm{Sheep})}$ + Sex*Reproductive status	427.98	4.92	0.04
7	$\mathrm{Log}_{(\mathrm{roe\ deer})}$ + Sheep + Sex*Reproductive status	429.94	6.88	0.01
8	Roe deer + Sheep	441.78	18.72	0.00
9	Roe deer + Sex*Reproductive status	446.52	23.46	0.00
10	Sheep + Sex*Reproductive status	457.74	34.68	0.00
11	Roe deer	461.15	38.09	0.00

GLM, generalized linear model.

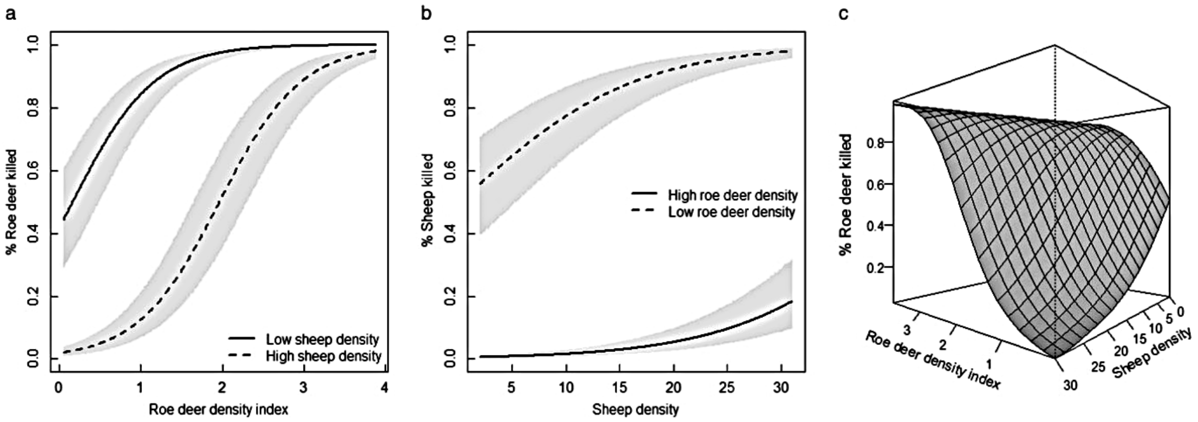

Figure 3 Functional relationship of roe deer (a) and sheep density (b) with the proportion of roe deer *Capreolus capreolus* killed by lynx in summer in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011. (c) shows the surface describing the overall functional response of lynx to both roe deer and sheep density in summer. Sheep density in expressed as number of sheep /km^{-2}.

A similar pattern was revealed by the analysis of winter prey selection patterns. The most supported model (model 1 in Table 5) included a linear effect of both roe deer and of the residuals of red deer density. A slightly less supported model (model 2 in Table 5; $\Delta AIC_c = 1.19$) also included the effect of lynx sex and reproductive status, corresponding to a higher probability for male lynx to kill red deer, with respect to both solitary and accompanied females. Given the negative correlation between roe and red deer densities, separating the effects of the two prey species in winter was not as straightforward as in summer. Still, model predictions show that an increase in roe deer density (and coincident decrease in red deer density) corresponded to a higher proportion of roe deer killed (Fig. 4), whereas the residual effect of red deer density, after accounting for the portion of variance already explained by the correlated part, was relatively weak, although significant. Figure 4c shows the shape of the surface, describing lynx functional response to prey density in winter.

Discussion

Managing carnivore-ungulate communities (especially with a mix of wild and domestic ungulates) in multi-use landscapes is a challenging task. Different cultural approaches, resulting in competing goals, usually drive the actions directed at the different members of the community: (1) wild ungulates are usually managed to ensure that their harvest is sustainable, balancing population persistence and yield, while minimizing the potential damage that high ungulate densities can cause to forestry interests or with vehicle collisions; (2) livestock herding mainly responds to the goals of animal production, in which any loss of capital (a depredation event) reduces the

Table 5 Model selection results for the binomial GLM analysis of winter prey selection patterns of lynx in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011

N	Model	AICc	ΔAICc	Weight
1	Roe deer + Red deer	271.91	0	0.36
2	Roe deer + Red deer + Sex*Reproductive status	273.1	1.19	0.20
3	Roe deer + (Roe deer)^2 + Red deer + Sex*Reproductive status	274.07	2.16	0.12
4	(Roe deer)^2 + Red deer + Sex*Reproductive status	274.14	2.23	0.12
5	$\text{Log}_{(\text{Roe deer})}$ + Red deer + Sex*Reproductive status	274.56	2.65	0.09
6	Roe deer + $\text{Log}_{(\text{Red deer})}$ + Sex*Reproductive status	275.69	3.78	0.05
7	Red deer	277.45	5.54	0.02
8	Roe deer + (Red deer)^2 + Sex*Reproductive status	278.12	6.21	0.02
9	Roe deer	278.56	6.65	0.01
10	Roe deer + Red deer + (Red deer)^2 + Sex*Reproductive status	279.25	7.34	0.01

AICc, Akaike information criterion; GLM, generalized linear model.

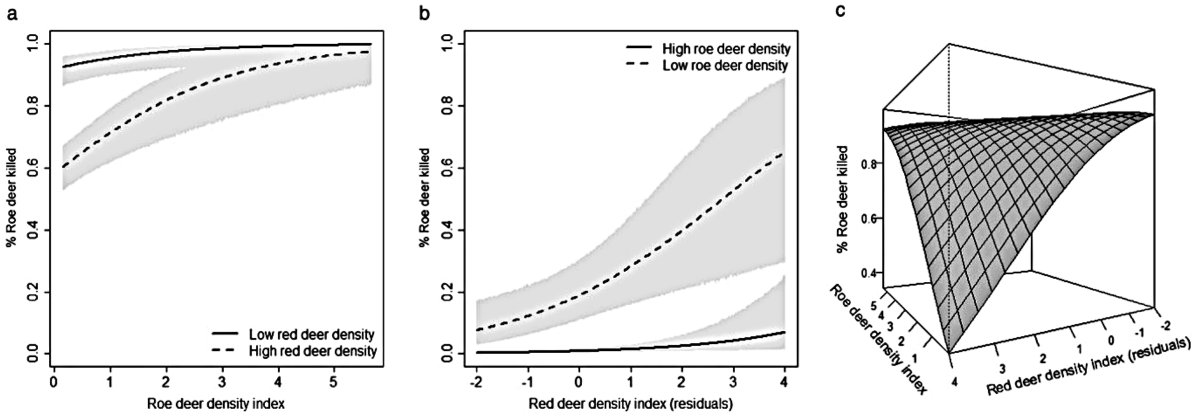

Figure 4 Functional relationship of roe deer (a) and red deer density (b) with the proportion of roe deer *Capreolus capreolus* killed by lynx in winter in Buskerud, Telemark and Oppland counties, Southern Norway, 2006–2011. (c) shows the surface describing the overall functional response of lynx to both roe deer and red deer density in winter.

potential profit of the economic activity, and is therefore to be minimized via protection measures or compensation using alternative financial mechanisms (Schwerdtner & Gruber, 2007); (3) under the protection of international legislation, carnivores have progressively gained a right to exist in multi-use landscapes (Linnell *et al.*, 2010; Trouwborst, 2010), but often only within the boundaries of certain population targets, aimed at limiting the economic and social impact of their presence (Linnell *et al.*, 2010).

In this context, our increasing understanding of the complexity of trophic interactions in terrestrial communities suggests that changes in densities of prey, predators or both may produce undesired management outcomes (Sinclair & Byrom, 2006) if such complexity is not taken into account during the decision-making process. The results of our study provide empirical evidence of such complexity in a trophic system in which wild ungulates, livestock and an efficient opportunistic predator occupy an ecosystem at a high economic and social cost. The multivariate nature of lynx prey selection patterns (Figs 3 and 4) shows that the density of wild ungulates in Southern Norway has the potential to affect the rate of depredation on livestock, to the same extent as the abundance of sheep in the study area can influence the level of potential competition between lynx and wild ungulate hunters. If we consider that roe deer density in many parts of Southern Norway has been generally decreasing over the last decade (Melis *et al.*, 2010), that red deer are in turn expanding in range and numbers (Milner *et al.*, 2006), while about 30 000 sheep are annually compensated in Norway as being predated by large carnivores (Linnell *et al.*, 2010), the potential economic and social consequences of failing to account for the complexity of lynx–prey interactions during such a modification of the community structure are evident.

Our study site provided a diverse prey base for lynx. At least 16 prey species occurred in the diet of 24 individuals over a 6-year period, and we did not detect any effect of variation in prey density on the amount of biomass that lynx were able to obtain when hunting. In all respects, lynx seemed to kill what they needed, likely based on their energetic requirements, whereas the relative abundance of each prey species in their home range determined to a large extent the proportions of species killed.

The structure and the dynamics of the lynx–ungulate system in Southern Norway are similar to several other multi-use landscapes, in which large carnivores are returning or have recently returned across Europe and North America. As the expansion of carnivore populations is accompanied by a similar trend in several species of large herbivores (Putman, Apollonio & Andersen, 2011), prey availability is likely to be not a limitation for most of the carnivore populations settling in new areas, whereas the prey selection patterns they will adopt will determine to a large extent the cost and the potential conflicts associated with their presence in the landscape. This is the case for the recolonizing wolf population of the Western Alps in Italy and France, which occupies an area with four wild and two domestic ungulate species (Marucco, Pletscher & Boitani, 2008; Marucco & McIntire, 2010), and for the expansion of pumas *Puma concolor* in the Patagonia region, which hosts a complex assemblage of domestic and wild prey, some of them seriously threatened with extinction (Wittmer, Elbroch & Marshall, 2012). This further underlines the need to explore the main factors driving predation patterns of recolonizing carnivores and their potential demographic impact on wild and domestic prey species in a multi-prey context. If prey availability is unlikely to be a limiting factor in most of these socioecological contexts, traditional functional response approaches (Holling, 1959; Vucetich, Peterson & Schæfer, 2002), based on the limitations imposed by searching and handling time on predation efficiency, are likely to fail in properly addressing the issue. While the results of our study highlight the importance of further exploring the main ecological drivers of prey selection in large carnivores, they also suggest that the underlying energetic requirements of carnivores might be a unifying approach to the study of predator–prey interactions in a multi-prey context (Carbone, Teacher & Rowcliffe, 2007; Jeschke, 2007). Understanding the mechanisms linking individual energy budgets to prey selection, to kill rates and, ultimately, to predation impact, can potentially provide a theoretical framework to inform the decision-making process for the management and conservation of human–wildlife communities in multi-use landscapes.

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APPENDIX II - SELECTION OF NATAL DENS AND EARLY MATERNAL HOME RANGES IN FEMALE EURASIAN LYNX IN NORWAY

Selection of natal dens and early maternal home ranges in female Eurasian lynx in Norway.

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Abstract

Large carnivores with income breeding strategies that give birth to altricial young should be expected to face complex trade-offs when selecting natal dens and early maternal home ranges. This study investigated Eurasian lynx (*Lynx lynx*) natal den site selection across multiple-use landscapes in Norway and whether the selection of early maternal home ranges involved a trade off of security for access to their preferred prey species, roe deer (*Capreolus capreolus*). The characteristics of natal dens and home ranges from 33 denning female lynx were quantified across southeastern and northern Norway. Natal dens were located in terrain further from the most accessible and disturbed areas (public roads) and in terrain more rugged than generally available. Early maternal home ranges were characterised by low human and low road density, higher terrain ruggedness and across southeastern Norway, slightly lower indexes of roe deer. Humans are the dominant cause of lynx mortality across Norway and subsequently our findings suggest that lynx primarily chose areas which limited their interaction with people during the denning period when their kittens were most vulnerable.

Introduction

For many carnivore species with altricial offspring, securing suitable dens sites with associated early maternal home ranges may be essential for reproduction (Gittleman and Thompson, 1988; Laurenson, 1994), especially for those that do not excavate their own shelters (Fernandez and Palomares, 2000; Ross et al., 2010). The use of natal dens for the birth and early rearing of young provides vulnerable newborn offspring with refuge against infanticide, intra-guild predation, and inclement weather (Laurenson, 1994; Magoun and Copeland, 1998; Fernandez et al., 2002). Understanding natal den site selection is thus essential to ensure that these habitats are conserved. Obtaining such knowledge is especially pertinent for the denning period, as successful reproduction in carnivores may be negatively affected by human activities (Linnell et al., 2000; Olson et al., 2011) and female carnivores face significant energetic demands during this period. At present there is a dearth of information concerning the denning behaviours of wild felids, such as the pattern of breeding den use after parturition and during the early rearing of kittens.

The Eurasian lynx (*Lynx lynx*) is a solitary polytocous felid that breeds seasonally, producing litters of two to four kittens (Gaillard et al., 2013). Kittens have a 50% survival rate over their first year (Breitenmoser-Würsten et al., 2007) with mortality highest during the first three to four month (Jedrzejewski et al., 1996), when kittens are most vulnerable (Schmidt, 1998). During this early denning phase however, no reliable data exists accounting for kitten mortality, but natural mortality is thought to be a primary factor (Andrén et al., 2006; Boutros et al., 2007). Consequently the quality of den sites may be a critical factor affecting population productivity for this species. Only two detailed studies, undertaken in Poland (Schmidt, 1998) and Switzerland (Boutros et al., 2007), have described Eurasian lynx denning behaviours, with both studies reporting that secure and well camouflaged den sites are a prerequisite for kitten survival. No published data exist from northern Europe, where climatic conditions are especially challenging and where there are important differences in lynx management practices that may influence patterns of habitat selection. For instance, northern lynx populations are harvested annually (Linnell et al., 2010) in an attempt to mitigate conflicts with various livestock husbandry practises (Odden et al., 2002; Nybakk et al., 2002). As a consequence, anthropogenic actions are responsible for almost 90% of mortality events reported in Scandinavian lynx, due to legal hunting in addition to poaching and road traffic incidents (Andrén et al., 2006). Additionally, poaching is considered an important threat across all European lynx populations (von Arx et al., 2004).

In order to reduce the probability of mortality risk, lynx are expected to avoid areas with high human activity (Bunnefeld et al., 2006). Paradoxically however, research investigating lynx spatiotemporal distributions across central and southern Norway (Bunnefeld et al., 2006; Basille et al., 2009) has revealed a preference for habitat in rural lowland areas associated with higher human activity than average, as these areas support high densities of roe deer (Torres et al., 2011), the preferred prey species of lynx in this area. Human dominated areas may therefore constitute population sinks for lynx (Bunnefeld et al., 2006), as an abundance of roe deer attracts lynx and concurrently, mortality risk increases due to a closer proximity to human activity (Basille et al., 2009; 2013).

This study investigated the landscape characteristics associated with the location of lynx natal dens and early maternal home ranges in relation to the annual home ranges of individual female lynx throughout Norway. Based on the above, we were interested in investigating to what extent lynx select for remote and rugged terrain during this period to minimise disturbance and provide maximum security, and if this selection came at a cost in terms of reducing their access to prey.

Materials and Methods

Study Sites

This study investigated den site selection for lynx populations situated in southern and northern Norway (Fig. 1). Data were obtained from individual VHF and GPS-collared females between 1996 and 2011. In Southern Norway data from female lynx (n=22), were collected over a large study area encompassing the six counties of Hedmark, Buskerud, Akershus/Østfold, Vestfold and Telemark between ca 58°N and 63°N (Fig. 1) and in Northern Norway (n=11) from the counties of Troms and Finnmark between ca 68°N and 70°N (Fig. 1). For a description of both study sites refer to Herfindal et al. (2005) and Mattisson et al. (2011). In short, both study sites are subject to intensive management of wildlife populations and habitat, becoming increasingly human modified further south. Roe deer are the main prey species in the southern study site (Herfindal et al., 2005) but are absent from the northern sites where semi-domestic reindeer form the main prey (Mattisson et al., 2011).

Lynx movement data

From 1995 to 2012, female lynx were captured as part of the large scale research project Scandlynx (http://scandlynx.nina.no/). Female lynx were equipped with either VHF or GPS collars following standard handling protocols approved by The Norwegian Experimental Animal Ethics Committee. Details on lynx capture can be found elsewhere (Herfindal et al., 2005; Arnemo et al. 2006). For female lynx that experienced reproductive events, 11 individuals were equipped with VHF collars (Telonics MOD-335, Telonics Inc., Mesa, AZ, USA), with two individuals fitted with store-on-board GPS collars, (Lotek 3300SL, Lotek Wireless Inc., Ontario, Canada, Televilt Posrec 300, Followit AB., Lindesberg, Sweden) and 13 individuals fitted with GPS-GSM collars (Tellus 1C, Followit AB and Vectronic GPS PLUS, Vectronic Aerospace GmbH, Berlin, Germany). A minimum of two locations per month were recorded for each VHF collared lynx, usually more often, and was primarily achieved through the use of aircraft. On the ground search effort was also implemented, which varied in intensity, but increased dramatically during the denning period, including many periods with continual tracking. The accuracy of locations for VHF collar lynx was considered to be within 500m of the estimated location, based on observer experience, while GPS locations were more accurate. GPS-collar positioning schedules varied from a basis of 3-4 per day to every hour.

We used 95% minimum convex polygons (MCPs) to determine the maximum probable home range from each breeding female (Ranges 8; Kenward et al., 2008). Consistent with other home range studies (Linnell et al., 2001; Herfindal et al., 2005; Reynolds et al., 2007; Basille et al., 2013), a prerequisite of at least 20 locations over a minimum of six months were required to calculate the annual home range for individual lynx, reducing potential autocorrelation.

However, in our analysis,, only three home ranges were generated with less than 150 locations, and all lynx had annual home ranges constructed with >40 locations, with a northern mean of 1092 points (± 335.84 SD) and a southern mean of 363.54 (± 293.26 SD). A minimum of 14 locations calculated from locations up to 8 weeks after parturition were used to define the maternal home range. (Linnell et al., 2001; Dawson et al., 2010; Basille et al., 2013). Only three lynx in this study were close to this low threshold. The remaining maternal home ranges were constructed using >30 locations with an northern maternal range mean of 329.45 points (± 283.89 SD) and a southern maternal home range mean of 106.45 (± 86.69 SD). 95% MCPs were also used for estimating the maternal home range, peeled around the harmonic mean centre (Spencer & Barrett, 1984). The above approaches to home range calculation are concurrent with existing carnivore denning studies (Kaartinen et al., 2010; May et al., 2012) that compare use to availability.

Den-site monitoring

Female lynx adopt a central place foraging behaviour centred around the natal den for the first 6-8 weeks after parturition in May and June (Schmidt, 1998). Repeated re-visits to any one location by a female lynx during this timeframe indicated a possible den site and suspected natal lairs were generally visited when kittens were between 2 and 6 weeks of age to confirm parturition, accurately locate natal dens, and record kitten demographic parameters.

Environmental covariates

A total of 33 reproductive events from 26 individual lynx were used in the analysis. Explanatory covariates considered likely to be important in influencing the denning behaviour of female lynx (Table 1) were extracted from GIS-based digital maps using ArcGIS 9.3.1 (ESRI, 2009). For den sites, the value extracted was that closest to the locality, depending on the resolution of the data (Table 1). For annual and maternal ranges, mean values were calculated based on all values falling within the respective ranges.

Within ranges, potential human impact was measured as both road density and human (resident) density. Road density (public and private roads) was calculated as the total length of roads within each home range type divided by the area of the relevant home range. Public roads are high traffic roads, ranging from municipal roads to national highways, while private roads are those which are characterised by little traffic in connection to farming, logging or recreational areas. We divided roads into these two categories (public and private) to account for the different levels of potential disturbance (May et al., 2012). Although private roads penetrate further into semi-natural habitats than public roads, many private roads are closed seasonally (winter and early spring) due to snow fall, while public roads remain open throughout the year. Human density was calculated as the mean density within the home range type, based on available data of residential addresses (Table 1). Human accessibility to lynx habitat was calculated by estimating the distances between den sites and the nearest private and public roads as well as human settlement. Mean values of elevation, Terrain Ruggedness Index (TRI, Riley et a., 1999) and Slope-Aspect Index (SAI, a common topo-climatic index that assigns highest values to steep, east-facing slopes) were calculated based on those raster cells that fell within the respective home range areas.

An index of roe deer density, based on extrapolation from pellet-group count techniques within lynx home ranges, was inferred from a separate study investigating density patterns of large carnivore prey species in southern Norway (Bouyer et al., 2015). Thirty circular 10m^2 plots were distributed regularly along a triangular transect (1km on each side) and were surveyed for roe deer pellet-groups within lynx home ranges. Data were collected in spring (mainly May and early June) to reflected the habitat use for a period extending from autumn, through winter, to spring. Due to slow decomposition in northern environments, some summer pellets may have been counted as well. The results should be viewed as reflecting roe deer year round distribution. Using the pellet counts, hurdle models were used to create an index representative of the broad scale variation in relative abundance and distribution of roe deer in southeastern Norway (Bouyer et al. 2015).

Statistical analysis

Comparison of environmental covariates between ranges

Paired t-tests were performed to compare mean environmental covariates between maternal and annual home ranges. When required, data were log transformed to achieve normality. For this initial statistical analysis both northern and southern study sites were investigated separately. Statistical analysis was performed using R 3.1.1 (R Development Core Team, 2014).

Habitat selection at den sites and across ranges

Based on existing knowledge from other studies of this species and related felids, biologically meaningful models *a priori* determined as likely to influence den site selection were constructed to compare den sites against environmental conditions across the maternal and annual home ranges. Models were evaluated using conditional logistic regression to identify possible relationships between den site selection and environmental covariates (Manly et al., 2002). Values recorded at each den site were compared with those recorded at 40 random points within each corresponding home range (maternal or annual) thus employing a used (den locations) and available (random locations) design to create resource selection functions (Manly et al., 2002). For analyses, all covariates were separated between northern and southern lynx. Model selection using the roe deer index covariable was performed with a reduced sample size (n=22) encompassing lynx home ranges in southern Norway only. Mean values of environmental covariates were also compared between maternal and annual home ranges using standard logistic regression. All non-normally distributed covariates were log transformed prior to analysis.

Model selection was performed based on the corrected Akaike information criteria (AIC_c) score and Akaike weights (Burnham & Anderson 2002). In cases where a single model did not have strong support (model weight >0.7), model averaging was employed to obtain final parameter estimates. Models with a ΔAiC_c value of <3 were used to synthesise the parameters of the final model. Due to repeated reproductive events for some individuals (n=8), alternative models were constructed, firstly with and without a random term to account for potential effects of repeated measurements from individual lynx and secondly using a single randomly chosen reproductive event for each individual. In all cases parameter estimates for models did not differ significantly, therefore results reported are for models with all reproductive events included.

Validation of site selection functions

The models derived from the above analyses represent den-site resource selection functions at different spatial scales. In order to evaluate the predictive strength of these models, the K-fold cross-validation procedure of Boyce et al. (2002) was employed, based on Spearman rank correlation between ranked resource selection values (divided into ten bins) and area-adjusted den site frequencies. The dataset was divided into four 'folds' for evaluation.

Results

Home range sizes

Mean annual home range sizes (95%MCP) were 730 km^2 for females in the northern study sites and 381 km^2 in the southern study sites (SD=383 km^2 and 152 km^2 respectively), while maternal home ranges had an average of 63 km^2 in the north and an average of 25km^2 in the south (SD=114 km^2 and 23 km^2 respectively).

Maternal home range covariate comparisons

Comparison of habitat features associated with the location of early maternal home ranges against those of annual home ranges revealed that maternal home ranges were situated in areas with higher terrain ruggedness values in both northern ($P<0.05$) and southern study sites (<0.01) using paired t-tests (Table 2). Mean elevation values for early maternal home ranges were also greater than annual home range sites ($P<0.01$) for southern ranges only. Human density in the northern regions of Norway displayed no significant difference between home ranges types with on average 1.4 people per km^2 (± 1.5 SD) within the annual home range sites and 0.8 people per km^2 (±2.1 SD) in early maternal home range sites (Table 2). In southern Norway, human density within annual home ranges (12.7 people per km^2 ± 17 SD) was significantly higher ($P<0.001$) than human densities recorded within early maternal home ranges (2.4 people per km^2 ± 4.6 SD). Roe deer densities (southern areas only) showed a slight, but significant, difference after log transformation of data ($P<0.05$) between annual and maternal home ranges, with annual areas (1.10 roe deer per km^2 ± 0.8 SD) having higher densities of roe deer than maternal areas (0.8 roe deer per km^2 ± 0.9 SD).

Maternal home range selection

At a home range scale, in northern Norway, (8 models fitted), no single model had strong support, but three models had a $\Delta AIC_c<3$ (Table 3) and were used to derive an averaged model. The models suggested that northern maternal home ranges were in areas of lower elevation, lower human density and higher terrain ruggedness relative to annual home ranges, consistent with the t-test results (Table 2). The averaged model also included Slope-Aspect Index, and suggested selection for more west-facing and lower sloped areas. For southern lynx populations the maternal home ranges were also associated with more rugged terrain than annual ranges, and in areas with lower public and private road density than available. The averaged model also included selection for areas with lower human density and lower elevation. These effects were broadly consistent with the t-test analyses, although there was some evidence of different preferences between northern and southern populations in the t-tests, which may be linked to overall differences in topography and landscape between the different regions. When the roe deer covariate was introduced to model selection for the southern population (15 models fitted), again no strong support for any single model was observed and the roe deer index did not feature in the top models. The models included in averaging did not incorporate the roe deer index variable suggesting that this is not a strong determinant of maternal range selection. Other variables included were largely consistent with the combined analysis, although SAI was not included.

Den site selection

Den sites were on average, further from public roads in both the southern (2.2 km ± 1.5 SD) and northern study sites (3.6 km ± 4.0 SD) than private roads (0.4 km ± 0.2 SD and 2.2 km ± 2.5 SD respectively). Den sites on average were located at >6 km from settlements in the southern study site and >13 km from settlements in the north. Across northern Norway, at the den site scale (22 models fitted), the most parsimonious model for the location of den sites in both home range types, identified den site locations in areas characterised by complex and rugged terrain and at lower elevation than available (AIC_c = 64.83, w= 0.35 for best supported maternal model and AIC_c = 58.36, w= 0.26 for best supported annual model) (Table 4 & 5). All models included in the averaging contained the elevation and TRI covariates at both scales. Models including the Slope-Aspect Index were also important for the location of den sites at both home range scales with a summed AIC_cw of 0.28 for maternal site models and 0.38 for annual site models (Table 4). Den sites were located in areas of lower elevation than available in both home range types, possibly indicating a trade-off between elevation and ruggedness). Selecting den sites in areas further from public and private roads and settlements was less important in the northern study area at both scales. In southern Norway (29 models fitted), selection for den sites in more rugged terrain than available was also consistently selected for, and dens were also found to be further away from private roads at both scales, (AIC_c = 137.12, w=0.39 for best supported maternal model and AIC_c = 131.37, w=0.15 for best supported annual model). Selecting den sites in areas further from public roads was also important across the southern annual home ranges (summed AIC_cw of 0.56) but appeared less important in maternal home ranges. Plots of the predicted den site selection relative to different environmental covariables at the two scales considered are shown in Figures 2 - 5.

Validation of resource-selection functions

For both den-site analyses (comparison with maternal and annual ranges), the resource selection functions derived from the averaged models effectively predicted locations chosen

(Northern maternal range, mean r_s = 0.795, p<0.01; annual range, mean r_s = 0.757, p<0.05, Southern maternal range, mean r_s = 0.801, p<0.01; annual range, mean r_s = 0.813, p<0.01).

Discussion

This study compared habitat features associated with lynx natal den sites to available sites within maternal and annual home ranges. As predicted, lynx den sites were located in areas which offer greater protection to newborn kittens than averagely available. This is similar to results from other carnivore den-site studies (Laurenson, 1994; May et al., 2012). Across Norway female lynx were found to utilise natal dens in areas associated with greater security by selecting for rugged and isolated terrain in areas which minimised interaction with humans, their primary predator and source of disturbance (Andrén et al., 2006). In southern Norway, maternal home ranges were also characterised with lower human and public road densities than available and were situated in areas with slightly lower densities of roe deer. Our findings support the suggestions of Bunnefeld et al. (2006) that female lynx in Norway avoid risky habitats in the early phase of rearing vulnerable kittens and emphasises the importance of quantifying the impacts of human disturbance on denning carnivores, especially in human dominated landscapes (Ciuti et al., 2012; Ahmadi et al., 2014).

Den site placement

For the environmental variables considered, the most consistent features that lynx preferentially selected across Norway for were den sites associated with more rugged terrain than available, similar to denning lynx elsewhere in Europe (Boutros et al., 2007; Krofel et al., 2012). In southern Norway, den sites were also located further from frequently used public roads, as also noted for other denning carnivores such as brown bears *Ursus arctos* (Swenson et al., 1997; Linnell et al., 2000), wolves *Canis lupus* (Kaartinen et al., 2010; Ahmadi et al., 2014) and wolverines *Gulo gulo* (May et al., 2012) where the level of human activity was determined to be the primary factor for avoidance. The Norwegian landscape is highly accessible, with many public and private roads penetrating even the remotest areas (Basille et al., 2009, c.f. Figure 1). Even in such landscapes, lynx chose natal dens far from the more intensively used public roads in both northern (>3.5km) and southern study sites (>2.0km). Lynx harvested in Norway are predominately killed within 3km of a road (Basille et al., 2013), therefore female lynx that display a denning preference for areas further from frequently used roads may reduce mortality risk, although the kitten raising period does not overlap with the hunting season. Moreover, utilising natal dens in rugged terrain potentially reduces disturbance and predation risk (Magoun & Copeland, 1998; Boutros et al., 2007) and likely offers physical protection for newborn kittens. This pattern of avoiding areas that are easily accessible for humans has been found in other felid species (Ross et al., 2010).

Despite other carnivore denning studies reporting a selection for higher elevations than available (Magoun & Copeland, 1998; May et al., 2012), lynx in the northern study site preferentially selected den sites at lower elevations. This may reflect the distribution of prey species in Norway (Basille et al., 2009). Other authors (Petram et al., 2004) have suggested a den site selection at higher elevations reduces encounters with humans, but as lynx den sites in this study were generally not located in areas easily accessible to humans, denning females may be less inclined to occupy higher elevations as an avoidance strategy as long as they can access rugged terrain at lower elevation. The structure of the Norwegian landscape is such that most steep slopes occur at low to intermediate elevation (this is also where forest cover is densest) with most higher elevations being less steep (plateaus) and less forested.

Denning at the Home Range Scale

At the home-range scale, early maternal home ranges were located in rugged terrain and in areas with lower densities of humans than available. When the roe deer index covariate was added to the analysis (southern populations only) selection for lower public road density was also important. Contrary to what might be expected, lynx maternal home ranges in southern Norway were not located in areas with higher densities of roe deer than available, potentially reflecting a trade off between food and security during the early critical phase of denning. As lynx are central place foragers in the early kitten raising period (Orians and Pearson, 1979; Krofel et al., 2012) we speculated that the selection of natal dens would be influenced by feeding optimisation (Stephens & Krebs, 1986; Laurenson, 1995) to meet the higher energetic demands imposed upon lactating females (Gittleman and Thompson, 1988). Previous research investigating lynx space use in southern Norway (Bunnefeld et al., 2006; Basille et al., 2009; 2013) has revealed that lynx generally trade safety for food, identified through an attraction to human dominated areas which support higher densities of roe deer (Torres et al., 2011). However a clear trade off in lynx habitat selection has been shown to exist with intermediate roe deer and human disturbance selected for, with lynx avoiding the most human disturbed areas with highest road densities (Basille et al., 2009, 2013).

Disrupting reproductive behaviours likely represents a greater evolutionary cost than disrupting feeding behaviour (Wilmers et al., 2013) and reducing mortality risk may be the most important factor during the early phase of denning (Laurenson, 1995). Despite poor support in our analysis for the selection of denning habitat associated with high or low prey densities, other carnivore species (Van der Meer et al., 2013), including denning felids (Laurenson, 1995; Durant, 2000; Fernandez and Palomares, 2000; Wilmers et al., 2013), have been shown to select secure denning habitat over access to food. Female lynx in Norway may also be selecting for secure denning habitat over access to food, at least during the early weeks of the kittens life, although further investigation into the densities of other, smaller, prey is needed. The energetic effect of the use of areas with less prey may not be costly, as Eurasian lynx are extremely effective hunters and are adept at catching roe deer even at very low densities (Nilsen et al., 2009).

Conclusions and recommendations

Across Norway, the selection of natal den sites and early maternal home ranges by Eurasian lynx appears to be influenced by a combination of landscape features and the impacts of human activity. The sympatric occurrence of humans and large carnivores can induce behavioural changes in a species, as humans are the primary cause of mortality for carnivores, including lynx, in the modern world (Andrén et al., 2006). Human disturbance has already been shown to stimulate den relocation for lynx species (Arnemo et al., 1999; Fernández et al., 2002;

Boutros et al., 2007; Olson et al., 2011), yet what cost disturbance incurs remains unclear. Despite a high mortality risk associated with selecting habitat within human dominated landscapes (Ciuti et al., 2012; Bunnefeld et al., 2006; Basille et al., 2009) lynx can persist in these areas by making behavioural changes which favour their survival during different life stages (Basille et al., 2013). Our findings indicate that during the denning period, these behavioural changes involve predator avoidance strategies, with lynx utilising terrain further from the most accessible and disturbed areas thus reducing interactions with humans. Although selection for rugged terrain to reduce interactions with humans has been shown with denning and non-denning brown bears (Nellemann et al., 2007; Sahlén et al., 2011), relatively few carnivore studies to date have focused on the selection of secure terrain to reduce mortality risk (Linnell et al., 2000) and it may well be productive to explore how landscape and terrain structure promote the ability of these species to cope with the presence of human infrastructure and disturbance.

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487 **Tables**

488 **Table 1** Environmental variables used in analysis and source of data.

Environmental variable	Data Source and Scale/Resolution
Elevation	Obtained from the Norwegian State Mapping Authority. Derived from a raster digital elevation model (DEM) with a spatial resolution of 100m^2.
Terrain Ruggedness Index (TRI)	Measured by taking the square root of the sum of squared differences in elevation of each pixel in a 100m DEM to its eight neighbours (May et al., 2012).
Slope-Aspect Index (SAI)	SAI (May et al., 2012) assigns highest values to east-facing areas with steep slopes. Slope & aspect derived from a 100m^2 resolution DEM.
Public/ Private Road and Settlement distances	Calculated from digital 1:50000 topographic maps obtained from the Norwegian Mapping Authority.
Human Density	The number of individuals per square km^2. Spatial resolution of 1km^2. Obtained from Statistics Norway (Takle, 2002).
Index of Roe deer Density	Obtained through pellet group counts from Bouyer et al., (2015). Spatial resolution of roe deer raster dataset was 1km^2.

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Table 2 Comparison of mean values of environmental covariables between lynx maternal and annual home ranges in different parts of Norway.

Variable	Maternal home range (Mean ± SD)	Annual home range (Mean ± SD)	t-value	*df*	*P*
Northern Norway					
Human density (people /km^2)	0.88 ± 2.12	1.4 ± 1.5	1.495	10	0.166
Public road density (km/km^2)	0.061 ± 0.098	0.075 ± 0.053	0.509	10	0.622
Private road density (m/km^2)	0.072 ± 0.154	0.092 ± 0.057	0.857	10	0.411
TRI	632.42 ± 559.72	443.56 ± 401.78	3.709	10	0.004
Elevation (m.a.s.l.)	374.76 ± 255.93	423.71 ± 204.55	.835	10	0.4
SAI	5.20 ± 7.70	10.17 ± 8.43	2.731	10	0.021
Southern Norway					
Human density* (people /km^2)	2.38 ± 4.59	12.70 ± 16.90	6.038	21	<0.0001
Public road density (km/km^2)	0.114 ± 0.156	0.375 ± 0.228	8.273	21	<0.0001
Private road density	0.970 ± 0.530	1.009 ± 0.214	0.951	21	0.353

(m/km2)					
TRI[*]	218.96 ± 210.83	145.51 ±132.25	2.487	21	0.021
Elevation (m.a.s.l.)	461.17 ± 194.03	425.08 ± 175.06	2.506	21	0.021
SAI	10.75 ± 10.31	13.26 ± 6.70	1.378	21	0.182
Roe deer Index[*]	0.88 ± 0.98	1.09 ± 0.86	2.734	21	0.012

[*] Data were log transformed to achieve normality for analysis

Table 3 Summary of variables included in averaged models assessing selection of maternal home ranges relative to environmental conditions in annual home ranges using logistic regression. Models shown here had ΔAIC_c values of <3 and were therefore included in averaged models.

Model	Elevation	Human density	TRI	Public road density	Private road density	SAI	AIC_c	ΔAIC_c	AIC_c w
Maternal versus annual (Northern populations)									
1	x	x	x				30.27	0.00	0.366
2	x					x	33.01	2.73	0.193
3		x					33.15	2.88	0.117
Averaged coefficient	-0.012	-2.692	3.135			-0.081			
St. Error	0.005	1.663	1.442			0.059			
Maternal versus annual (Southern populations)									
1				x			43.51	0.00	0.339
2			x	x	x		44.53	1.01	0.204
3		x		x			45.78	2.27	0.109
4	x			x	x		46.21	2.70	0.088
Averaged coefficient	-0.004	-0.151	0.541	-14.601	-3.198				
St. Error	0.003	0.075	0.289	5.754	2.241				

Table 4: Summary of variables included in averaged models assessing lynx den-site selection at the maternal range scale across Norway. Models shown here had ΔAIC$_c$ values of <3 and were therefore included in averaged models.

Model	Elevation	TRI	Distance to public road	Distance to private road	SAI	AIC$_c$	ΔAIC$_c$	AIC$_c$ w
Northern populations								
1	x	x				64.83	0.00	0.358
2	x	x			x	66.49	1.66	0.156
3	x	x	x			66.58	1.75	0.149
4		x		x	x	66.82	1.99	0.132
Averaged coefficient	-0.005	1.113	0.217	0.095	-0.002			
St. Error	0.002	0.376	0.144	0.051	0.003			
Southern populations								
1		x		x	x	137.12	0.00	0.394
2		x		x		138.89	2.77	0.098
3	x	x			x	138.99	2.88	0.029
Averaged coefficient	-0.004	0.801		0.463	-0.005			
St. Error	0.002	0.228		0.218	0.002			

Table 5: Summary of variables included in averaged models assessing lynx - den selection at the annual range across Norway. Models shown here had ΔAIC_c values of <3 and were therefore included in averaged mode

Model	Elevation	Distance to urban	TRI	Distance to public road	Distance to private road	SAI	AIC_c	ΔAIC_c	AIC_c w
Northern populations									
1	x		x				58.36	0.00	0.26
2	x	x	x			x	58.82	0.46	0.21
3	x		x	x			59.59	1.24	0.14
4	x		x		X		59.63	1.27	0.13
5	x		x		X	x	60.36	2.01	0.09
6		x	x	x		x	60.86	2.50	0.08
Averaged coefficient	-0.006	0.962	1.152	0.202	0.339	-0.004			
St. Error	0.002	0.601	0.317	0.178	0.178	0.003			
Southern populations									
1			x	x	X		131.37	0.00	0.15
2			x	x			131.54	0.17	0.14
3			x	x		x	131.79	0.41	0.13
4			x		X		132.07	0.70	0.11
5	x		x	x	X	x	132.54	1.16	0.09
6	x		x	x			133.51	2.13	0.05
7			x				133.51	2.14	0.05
8	x		x			x	133.65	2.28	0.05
Averaged coefficient	-0.002		0.822	0.483	0.388	-0.004			
St. Error	0.002		0.196	0.103	0.265	0.002			

Figure legends:

Figure 1 Location of both study sites in Norway and the distribution of Eurasian lynx annual home ranges (n=33) (Purple polygons). All green dots represent natal den sites, as determined by observers or interpreted from telemetry data. Red lines represent public roads.

Figure 2 Plots of the predicted den site selection relative to different environmental covariables at the northern annual home range scale.

Figure 3 Plots of the predicted den site selection relative to different environmental covariables at the northern maternal home range scale.

Figure 4 Plots of the predicted den site selection relative to different environmental covariables at the southern annual home range scale.

Figure 5 Plots of the predicted den site selection relative to different environmental covariables at the southern maternal home range scale.

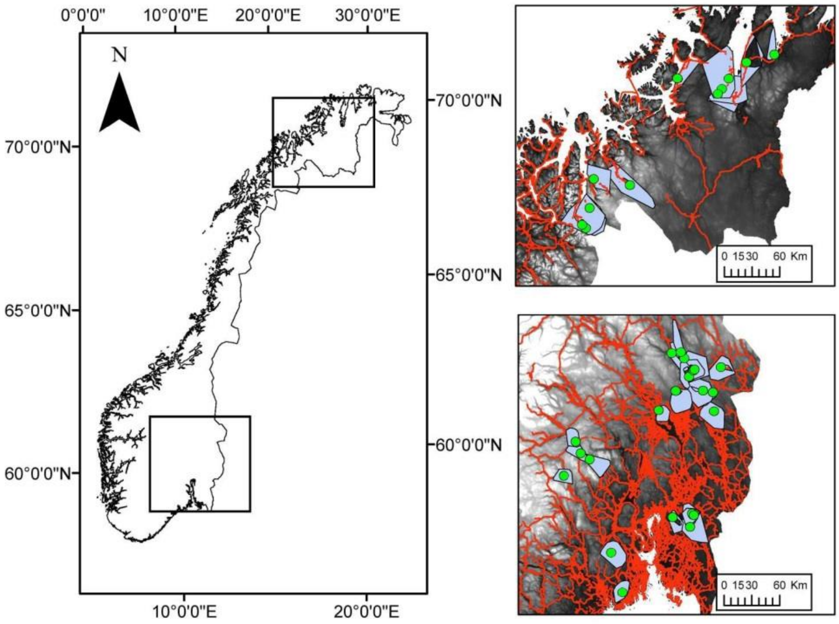

Figure 1 Location of both study sites in Norway and the distribution of Eurasian lynx annual home ranges (n=33) (Purple polygons). All green dots represent natal den sites, as determined by observers or interpreted from telemetry data. Red lines represent public roads.
185x156mm (300 x 300 DPI)

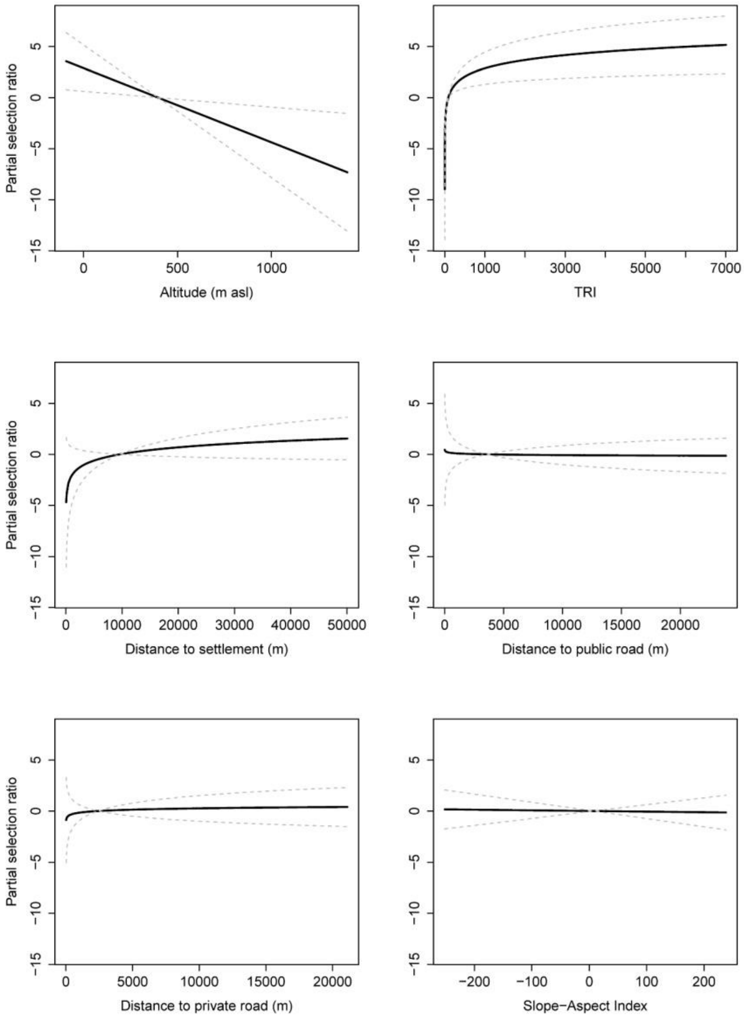

Figure 2 Plots of the predicted den site selection relative to different environmental covariables at the northern annual home range scale.
296x419mm (300 x 300 DPI)

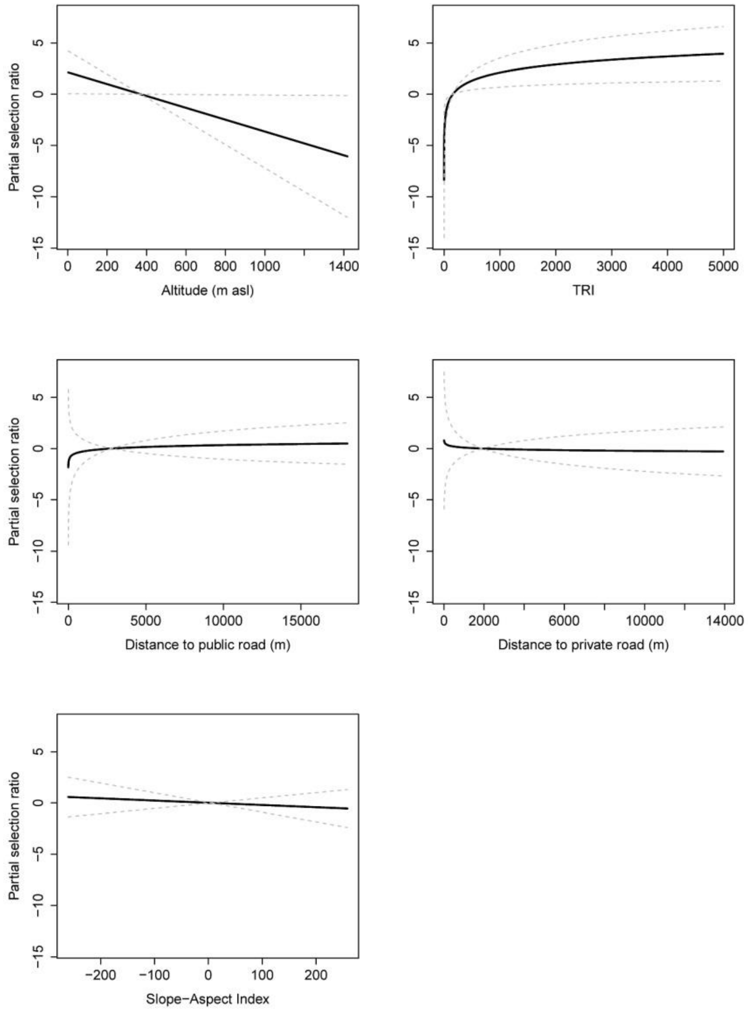

Figure 3 Plots of the predicted den site selection relative to different environmental covariables at the northern maternal home range scale.
296x419mm (300 x 300 DPI)

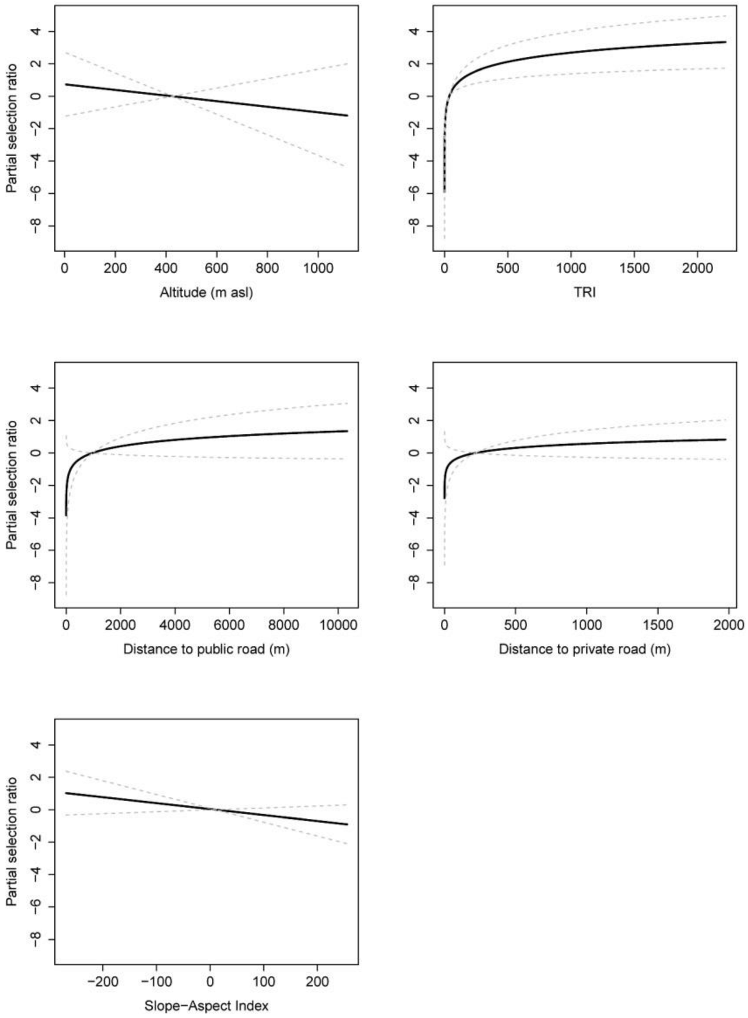

Figure 4 Plots of the predicted den site selection relative to different environmental covariables at the southern annual home range scale.
296x419mm (300 x 300 DPI)

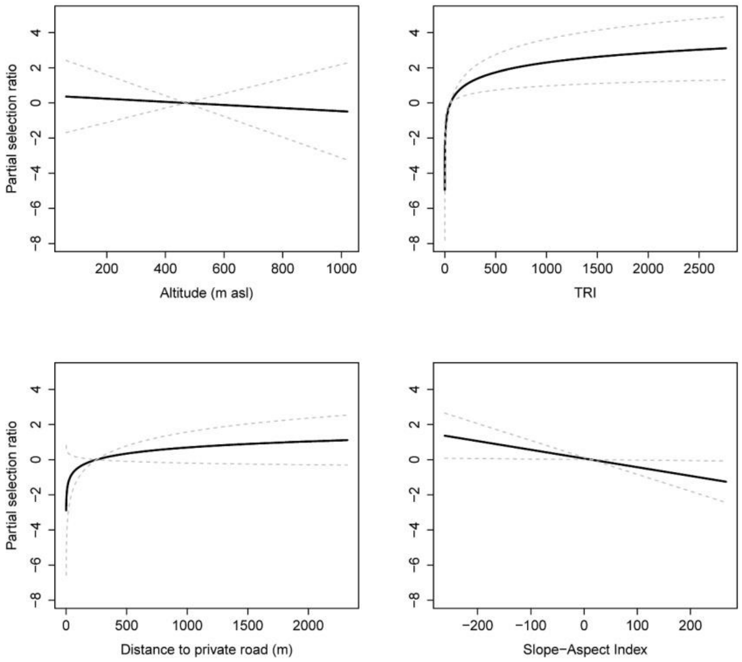

Figure 5 Plots of the predicted den site selection relative to different environmental covariables at the southern maternal home range scale.
296x419mm (300 x 300 DPI)