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Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states

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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 induced impacts (forest fragmentation, human density, different types of transport infrastructure) influence distinct lynx behaviors. Furthermore, they have not examined the extent to which lynx modify their fine scaled avoidance behavior of anthropogenic landscape features according to the specific behaviors (resting sites, kill sites, movement) in which they are engaged and how these relationships are modified by prey density or the sex of the lynx. We used Resource Selection Functions to examine how 19 GPS-marked lynx in southeastern Norway responded 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 resting sites. Terrain (ruggedness and elevation) appears to be important in permitting lynx to exploit heavily modified areas. Our study demonstrates that lynx show a nuanced response to human habitat modification, which offers hope for their conservation in Europe.

1. 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. Transport infrastructure, forest-related activities and forest conversion to agriculture continually fragment and disturb habitats, and can affect species behavior, abundance and survival (Vos and Chardon, 1998; Kramer-Schadt et al., 2004; Northrup et al., 2012; Fahrig and Rytwinski, 2009; Trombulak and Frissell, 2000; Baldwin et al., 2004). Human density and related infrastructure, above some thresholds, are often linked to avoidance behavior (Basille et al., 2009). Of all the species negatively affected by human developments and activities, large carnivores are generally considered as particularly sensitive because of their large spatial requirements and low densities (Fahrig and Rytwinski, 2009; Cohen and Newman, 1991; Crooks, 2002). These spatial requirements imply that large carnivore conservation, especially in crowded areas like some parts of Western Europe, require their integration into human-dominated landscapes because protected areas are too small (Chapron et al., 2014). In addition to their indirect effects (habitat fragmentation, development of road networks, loss of prey availability, Huck et al., 2010; Putman and Staines, 2004; Milner et al., 2007), humans are considered as the most dangerous intra-guild predators for large carnivores (Woodroffe and Ginsberg, 1998; Treves and Karanth, 2003) directly causing mortality through hunting, poaching and 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 species' response to predation risk (Frid and Lawrence, 2002). For example, large carnivores will 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

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large carnivores often occur at higher densities close to artificial 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, individual predators should balance their choices between access to resources and mortality risks induced by human proximity (Valeix et al., 2012). 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; Niedziałkowska et al., 2006; Ordiz et al., 2013). However, these studies have not been able to explore the way the species adapt to human-modified landscapes at fine scales.

Quantification of species–habitat relationships can be done through habitat selection modeling. Habitat selection can vary depending on behavioral state 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 (Wilmers et al., 2013). Spatial segregation of the resources for different behaviors can theoretically induce specific behavioral differences in habitat selection (Owen-Smith et al., 2010; Roever et al., 2014). Quantifying habitat selection from pooled data (including different behavioral states) can have important implications for conservation and management (Roever et al., 2014). Indeed, one major effect of pooling data is the risk of reducing 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) Opposing patterns of habitat selection between behaviors may lead to an overall 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 forms 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, 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 habitat selection in a human-dominated landscape. We differentiate between the sexes and between three broad behaviors (resting sites, kill sites, movement) in our attempt to understand how lynx respond to different degrees of human impacts (Riffell et al., 1996). In addition, we examine how prey density and topography modulate these patterns.

Contrary to previous studies on lynx habitat selection in Norway, we were interested in the cumulative effects of different types of human modifications to the landscape. We considered that effects were cumulative 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 (Harriman and Noble, 2008; Semeniuk et al., 2014). For example, an agricultural field surrounded by forest 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. In contrast, an agricultural 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 lynx would select for areas with medium human modification, and avoid areas of both very low and very high cumulative land-uses. Taking into consideration the evolutionary significance of the different behaviors (Krebs and Davies, 1981), we predicted that resting sites would show a stronger selection for less disturbed areas, and kill sites would 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 a complex topography (based on ruggedness and slope) would increase lynx tolerance of human land uses because of the variability in cover and security provided.

2. Material and methods

2.1. 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 contains 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).

2.2. Animal capture

Between 2008 and 2013, 19 individual lynx (8 females and 11 males) were captured, as part of a Scandinavian project on lynx, following pre-established protocols. We used GPS-collars that transferred data via the GSM network (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). Lynx were trapped in wooden walk-through box-traps and foot snares. Box traps were equipped with two SMS-alarms that permitted access to the box by fieldworkers within an average of 5 h. Foot snares were continually monitored using radio-alarms which permitted a reaction time always less than 15 min. Animals 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), 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 detected as a result of collaring among these animals.

2.3. Behavior identification

We selected data collected during periods of intensive location collection (up to 19 locations per day; 570 lynx days: 431 for females and 239 for males) in order to identify the behavior related to each GPS point. Only resident individuals with stable home range were selected for this analysis. For reproductive females, we removed GPS locations obtained between the beginning of June and the end of August, which correspond to the three first months of offspring when their movement was constrained while the kittens remained within a natal lair. Differentiation between behaviors 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