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Integrated spatially-explicit models predict pervasive risks to recolonizing wolves in Scandinavia from human-driven mortality

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ABSTRACT

Human-driven wildlife mortality is caused by both indirect causes and direct persecution due to conflicts of interests. The wolf, a predator frequently at risk from human-wildlife conflict, is returning to areas where it was historically extirpated in Scandinavia (Sweden and Norway). The wolf is expanding via a management strategy that allows wolves to reproduce exclusively in a wolf breeding range (WBR) in the south-central region. We modelled wolf territory occurrence in the WBR and all of Scandinavia, accounting for biotic and anthropogenic variables, and we also modelled the occurrence of human-driven mortality (traffic collisions, culling and illegal killing). We integrated territory distribution and mortality models in a two-dimensional model estimating habitat suitability and mortality risk for wolves. Forest was the main variable driving territory occurrence, and mortality was a consequence of variables associated with traffic infrastructure, human population, prey densities, and wolf management levels. Only < 0.1% of the WBR was not characterized by these risks. Our results confirm that human-related conflicts resulting in wolf mortality occur wherever the species is present, which leads to actions to control the population expansion. Considering the adaptability of wolves and the presence of potential suitable habitat in Scandinavia, their survival and expansion will be dependent on changes in public attitudes about illegal killing, and a review of policies and management actions. Our framework can be used to assist management of human-wildlife conflicts of recolonizing wolves elsewhere, or of other species at high risk from human-induced mortality.

1. Introduction

Large carnivores are top-predators frequently perceived as a threat to human interests and are associated with multiple and pressing conservation dilemmas due to their predatory habits on game, livestock, pets, and even humans (Chapron and Treves, 2016; but see also Kuijper et al., 2016). Consequently, human-carnivore interactions result in complex, persistent, and often intractable concerns that require proactive conservation strategies (Bekoff, 2001). The wolf (*Canis lupus*) is probably the most striking example of a long-standing conflict that results in complex synergies of people's perceptions, social reactions, and political and management decisions (Miller et al., 2016) that has often resulted in the persecution and extinction of the species in many areas of its historic distribution range (Chapron et al., 2014).

After decades of conservation initiatives in Europe, the wolf is currently returning to areas of its original distribution range where it could potentially occupy a broad range of human-affected habitats (Chapron et al., 2014). A specific case of the wolf return is that in the Scandinavian Peninsula, i.e. Sweden and Norway (hereafter Scandinavia). Although considered as functionally extinct in the early 1960s (Haglund, 1968; Wabakken et al., 2001), the number of established wolf territories of wolf pairs and families in the Scandinavian population was estimated as ~70 in winter 2015–16 (Wabakken et al., 2016). The wolf is currently under different legal statuses and management regimes that vary between and within the two countries. Sweden is an EU member; consequently, the management of the species is ruled by the Habitats Directive (92/43/ECC). Norway, as a non-EU member, is only a signatory of the Bern Convention (Boitani et al., 2015). In Sweden, wolves are only allowed to establish territories south of the reindeer husbandry area that ranges from central to northern regions; therefore, most wolves entering the reindeer husbandry area are promptly killed. In Norway, wolves are limited to the 'Norwegian wolf zone' in the south-eastern part of the country bordered by Sweden to the east and by the area of free-ranging domestic sheep to the west and

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north. The number of wolves in Norway is restricted to a population goal defined by a given number of reproducing packs per year. Therefore, today the wolf breeding range (hereafter WBR) bounds the distribution of the wolf population in Scandinavia to the southern-central region, which is geographically isolated from the closest neighboring Finnish-Russian population to the north-east. The rate of genetic exchange with the Finnish-Russian population to the north-east (Åkesson et al., 2016), and human-related mortality including illegal killing (hereafter poaching, Liberg et al., 2012, Milleret et al., 2017) are important for the dynamics, size, spatial distribution, and genetic viability of the population. Consequently, given the conflicts associated with the species, the population size and viability, there is a need to spatially identify the drivers of wolf territory occurrence in the WBR accounting for the geographic distribution of potential wolf-human related mortality risks, including those that result from management decisions (i.e. culling).

The association between wildlife species and environmental features is often studied using species distribution models (SDM), which are valuable to assist conservation and management strategies (Miller, 2010) and to predict population expansion/reduction (Guisan and Thuiller, 2005). Spatial analyses to model the occurrence of carnivore-related conflicts due to livestock attacks (Treves et al., 2011; Miller, 2015) or game hunting interests (Recio and Virgós, 2010) have been hitherto applied to varied species like canids and felids (Treves et al., 2004; Edge et al., 2011; Behdarband et al., 2014; Miller, 2015; but see also Recio and Virgós, 2010). However, the combination of SDM providing concise information on ecological drivers of species distribution, and of models on conservation threats (e.g. human-related threats), can be of relevance to tailor and refine analytical frameworks for decision-making in systems with manifold human-wildlife conflicts. Studies on brown bears (*Ursus arctos*) in Europe incorporated mortality data into occurrence models to identify sink and source habitats (by accounting for habitat heterogeneity in demographic performance, Naves et al., 2003), or by discarding demographic features but approximating sink-like and source-like areas (through the independent modelling of the occurrence of presences and mortality events, Falcucci et al., 2009). However, because the brown bear is an endangered large carnivore of low reproductive rate, highly impacted by habitat loss, direct persecution, distributed in metapopulations, and often below viable population sizes (Wiegard et al., 1998; Ciucci and Boitani, 2008), the species may not be representative for other large predators. Further applications of SDM accounting for assorted human-driven mortality data are still required for large carnivores of high adaptability, medium-to-high reproductive rate, and high capacity of rapid expansion at geographic scales, such as the wolf.

Considering the wolf in Scandinavia is restricted today by management actions to constrain its demography and distribution to the WBR, we first elaborated a SDM to identify the biotic and anthropogenic variables driving the spatial occurrence of wolf territories and to predict the potential distribution of wolf territories in the WBR. Second, we explored these predictions for all of Scandinavia assuming the hypothetical scenario where the species would be allowed to reproduce elsewhere under the same management strategy applied in the WBR. To devise a framework able to account for mortality risks, we also modelled the occurrence of human-caused mortality on wolves due to traffic, culling or poaching, and identified key habitat variables predicting each of these mortality causes. Although culling is based on management decisions, we aimed to explore possible associations between these mortality events and surrogates of likely conflict such as human, livestock, and ungulate presences. We then produced a final integrated two-dimensional model that combined information on the predicted occurrence of mortality causes and the produced SDM to identify heterogeneity in the potential suitability of habitats accounting for mortality risk levels. Because the wolf is a generalist species that was once broadly distributed in Scandinavia (Lönnberg, 1934), we predicted a potential broad distribution of wolf territories in the

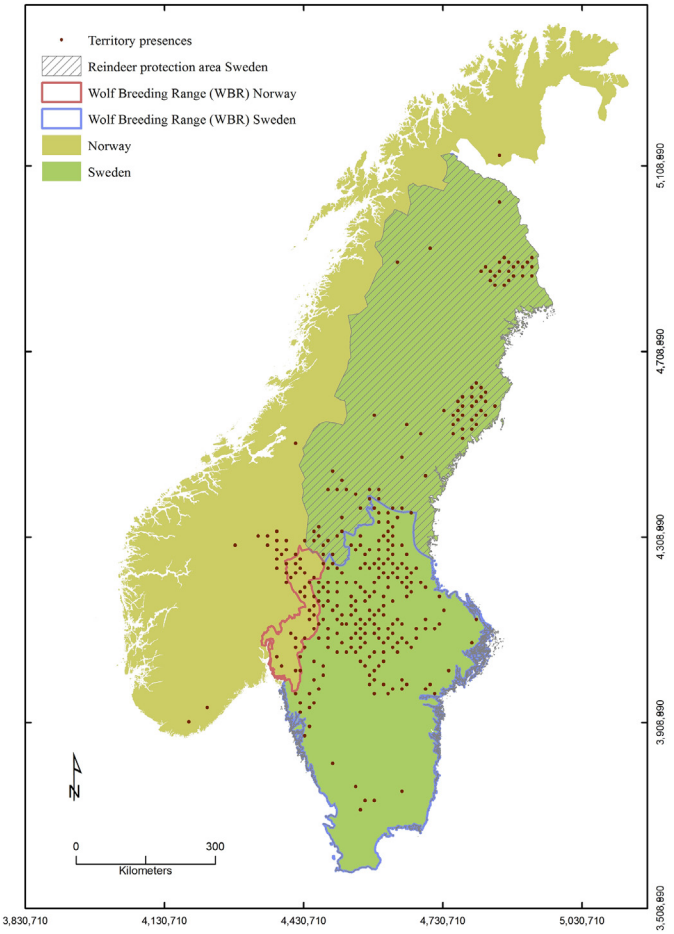

Fig. 1. Study area of the Scandinavian Peninsula including Sweden and Norway with the areas of the wolf breeding range (WBR) and the selected presences of wolf territories. The wolf is subject to different protection laws within the WBR in Sweden and Norway. Outside these areas wolves are generally killed through management actions.

southern parts of the WBR area and all over Scandinavia, a pattern highly shaped by human presence and persecution. Our framework can provide spatially-explicit predictions on wolf expansion and the potential distribution of wolf mortality risks under a conceptual case. This methodological framework can be applied in the management of wolf populations or other species worldwide at risk from human induced mortality.

2. Methods

2.1. Study area

We conducted research in the Scandinavian Peninsula over an area of 773,585 km^2 comprising Sweden and Norway (Fig. 1). The Scandes in the west-central area of Scandinavia is the only mountainous region in Sweden, otherwise mostly occupied by hills of boreal forest ridges and lakes in the north and an increasing proportion of arable land in the south. Norway is dominated by mountains, fjords, boreal forest, wherein valleys are often inhabited by humans with farming of domestic animals. About 75% of the total vegetation coverage is dominated by boreal coniferous forest, mainly Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. An expanding widespread network of forest roads is used by forest exploitation. Extensive agriculture occurs mostly to the south, and semi-domesticated reindeer farming takes place in the northern half of the peninsula. Human population is mostly distributed and concentrated in sparse urban areas in the central and southern parts