Scale and landscape heterogeneity influence the predictive performance of habitat suitability models

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Abstract

Resource selection functions (RSF) are used to predict habitat selection in a wide range of taxa for various conservation and management purposes. Although such predictions often cover large geographic areas, the limitations of extrapolating beyond the original study region are rarely addressed. Our first research objective was to demonstrate the implications of extrapolating RSF predictions across different habitats and at different spatial scales, with regard to varying landscape characteristics. For our second objective, we investigated the impact of individual variation in resource selection. We used a long-term dataset of GPS-collared lynx from two separate regions in Sweden. We built individual-level RSF models at two spatial scales for two different study regions to quantify individual and regional variation in habitat selection, and extrapolated the results from each region across the opposing study area. Individual lynx selected resources differently within and between study regions, and predictions were more accurate within home ranges than between home ranges. When extrapolating across variable landscapes, encountering resource values outside the fitted range of the models led to incorrect predictions. This case study highlights the importance of quantifying a variable's value range in both the model and extrapolation area, taking into account variation in individual resource selection, and understanding the relationship with the order of selection to improve the reliability of habitat predictions. To increase the transferability of models, extrapolations should ideally be limited to areas with overlapping value ranges, to reduce the risk of misidentifying habitat suitability.

Introduction

Habitat suitability models are common tools that use information on landscape attributes at species presence locations to assess suitable habitat for a wide range of taxa (Cianfrani et al. 2010; Marini et al. 2010; Heinänen et al. 2012; Guisan et al. 2013). These analyses are used for a variety of research and management purposes, including to estimate the impact of changing landscape characteristics on the availability of suitable habitat for a single species (Roscioni et al. 2014; Mikoláš et al. 2017), to compare the range and habitat overlap of different species (Boyce 2006; Vergara et al. 2016), and to assess the historic range of a species (Hendricks et al. 2016). Habitat suitability models can be applied at various scales, from an entire species' range (Viña et al. 2010; Yang et al. 2017), e.g. to predict range shifts under changing climate conditions (Marini et al. 2010; Hof et al. 2012; Lyu and Sun 2014; Garden et al. 2015; Luo et al. 2015), to the individual level when predicting the establishment of expanding populations of e.g. invasive species (Broennimann and Guisan 2008; Gormley et al. 2011) or recolonizing native species (Inman et al. 2013; Bleyhl et al. 2015; D'Elia et al. 2015; Bateman et al. 2016; Eriksson and Dalerum 2018).

Resource Selection Functions (RSFs) are a widely used type of habitat suitability models, which predict suitable habitat by comparing resources at known locations of the study species with the overall availability of certain environmental characteristics in the surrounding landscape (Boyce et al. 2002; Manly et al. 2007). Decisions regarding species conservation and management based on RSF models are prevalent (Cianfrani et al. 2010; Marini et al. 2010; Viña et al. 2010; DeCesare et al. 2012; Heinänen et al. 2012; Guisan et al. 2013; Lyu and Sun 2014; Hodder et al. 2014; Garden et al. 2015; Luo et al. 2015; Yang

et al. 2017). Often, when predicting species' reestablishment and reintroduction as well as prospective shifts in a species' range, these habitat predictions are extrapolated to include areas outside the monitored individuals', or the species' current range (Falcucci et al. 2013; Inman et al. 2013; Bleyhl et al. 2015; Bateman 2016; Eriksson and Dalerum 2018).

Specific landscape characteristics and resource availability may differ between regions where a species occurs, potentially reducing the reliability and transferability of predictions, where results are obtained using data from a subset of a larger population (Boyce 2006; Guisan et al. 2013). Furthermore, differences in selection between regions can occur because species may select resources differently under varying environmental conditions or may be more behaviorally adapted to certain conditions than expected (Cianfrani et al. 2010). Individuals within a species may also select resources differently, and individual variation is increasingly recognized as an important factor affecting resource selection and could further evoke differences in predictions (Gillingham and Parker 2008; Tinker et al. 2012; Leclerc et al. 2016; Ladle et al. 2019). Moreover, RSFs are scale-dependent, meaning that the ability of a certain variable in explaining habitat selection and use may vary depending on the spatial scale of the analysis (Johnson 1980; Rettie and Messier 2000; Boyce 2006; Northrup et al. 2013).

Despite the aforementioned issues considering varying environmental characteristics, regional differences in resource selection, and spatial scale, it is common to use data from a limited geographic area to predict habitat selection for a much larger geographic area, due to limitations in data availability (Kuemmerle et al. 2011; Falcucci et al. 2013; Inman et al. 2013; Bleyhl et al. 2015; D'Elia et al. 2015; Bateman et al. 2016; Eriksson and Dalerum 2018). When covering large geographic areas, we are confronted with landscapes consisting of environmental characteristics which may differ significantly from those in the source area of the species occurrence data (Kuemmerle et al. 2011; Inman et al. 2013; D'Elia et al. 2015; Bateman et al. 2016; Eriksson and Dalerum 2018). In extreme cases, environmental predictors used in the original models are even unavailable in the area to predict (e.g. D'Elia et al. 2015), thereby reducing the transferability of the habitat suitability model. Such issues should be acknowledged and addressed (see D'Elia et al. 2015; Wan et al. 2019), since conservation efforts may be less effective if predictions misidentify habitat quality, which can have severe implications when, for example, planning species reintroductions or establishing protected areas aimed to promote species recovery.

As in many European countries, the Eurasian lynx (*Lynx lynx*) population in Scandinavia was nearly eradicated in the early 20th century due to human persecution (Linnell et al. 2010; Chapron et al. 2014). However, lynx were protected in 1928, and in 2018 the lynx population in Sweden was estimated to about 1000–1400 individuals (Tovmo and Zetterberg 2018). Since the beginning of the 21st century, lynx have recolonized almost all of Sweden (Hemmingmoore et al. 2020), thereby inhabiting habitats with vastly different environmental characteristics (Fig. 1a) (Rauset et al. 2013; Hemmingmoore et al. 2020). Due to their occurrence across a wide environmental gradient, the lynx population in Sweden provides an ideal case study in which we can assess the reliability and transferability of habitat predictions using different individuals, between regions and across spatial scales of selection.

We used long-term monitoring GPS-data from adult lynx in two regions, one in southern and one in northern Sweden, to investigate individual differences in resource selection and the efficacy of extrapolating RSF estimates across different landscapes at varying scales of selection. We quantified resource selection at two scales; home range distribution (second order) and within home-range (third order) selection (Johnson 1980). Our aims were to (1) estimate individual variation in habitat selection and its effect on the models' predictive performance within the same geographic region, by quantifying variation in predicted RSF surfaces estimated using different combinations of individuals; (2) quantify the ability to predict habitat suitability using individuals from contrasting landscapes, by using the individual-based models from one study region to predict suitable habitat in an alternative region; and (3) assess whether order of selection influences our ability to accurately predict within and between regions.

Methods

Study regions

Two study regions were used for this study, one in southern and one in northern Sweden (Fig. 1a). Both regions vary greatly from one another in terms of variables deemed relevant to lynx habitat selection (Table 1).

The landscape in the northern study region (Fig. 1b) is mountainous, with valleys at around 300 meters above sea level (m a.s.l.) and high mountains reaching up to 2000 m a.s.l. (Rauset et al. 2013). At lower elevations, bogs and lakes traverse the landscape, which is dominated by mixed coniferous forest consisting of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). At higher elevations, valleys and hillsides birch forests (*Betula pubescens*) grow up to 600–700 m.a.s.l., followed by a low alpine tundra with thickets of willow shrubs (*Salix spp.*) and dwarf birch (*Betula nana*) (Rauset et al. 2013). At higher elevations, lower heaths and meadows grow while the mountain peaks and higher plateaus are characterized by bare rock and glacier (Rauset et al. 2013). Infrastructure and human activity are very low in the northern study region compared to southern Sweden, including a few settlements and roads, and virtually no agriculture. The main prey for lynx in this area are migrating semi-domestic reindeer (*Rangifer tarandus*) managed by the indigenous Sámi people (Mattisson et al. 2011).

Most of the southern study region (Fig. 1c) is relatively flat, with elevation levels increasing from the southern to the most northern part of the southern study region, ranging from 0 to around 370 m.a.s.l. The landscape is interspersed with lakes and largely covered with intensively managed forest (Norway spruce and Scots pine interspersed with birch (*Betula sp.*)) (Andrén et al. 2002). In addition, fields traverse the landscape, with agriculture and grassland covering 19% of the land (Hemmingmoore et al. 2020). Human population density is high and increasing towards the south, and consequently there is a much denser network of cities and towns, roads and highways in the southern compared to the northern study region. The main prey for lynx in this area are roe deer (*Capreolus capreolus*) (Andrén and Liberg 2015).

Lynx GPS-location data

The southern dataset is based on GPS-locations from 36 resident adult lynx (21 males and 15 females) collected between 2008 and 2015 (Fig. 1c). The northern dataset is based on GPS-locations from 17 resident adult lynx (eight males and nine females) collected between 2001 and 2010 (Fig. 1b). Where more than one location per day was available for an individual, we randomly selected one location per day to reduce both temporal autocorrelation and bias, which occurs when one individual is sampled more frequently than others (Nielsen et al. 2002; Frair et al. 2004), resulting in 8,194 and 10,701 locations in the northern and southern study region, respectively. All lynx were captured, immobilized, and fitted with GPS-transmitters (GPS plus mini, Vectronics Aerospace, Germany; Televilt Posrec 300 and Tellus 1C, Followit, Sweden) according to Swedish Animal Welfare Agency's ethical-approved protocols (Andrén et al. 2006; Arnemo and Fahlman 2009; Rauset et al. 2013).

Individual-based resource selection

We *a priori* selected four environmental predictors shown to influence lynx habitat selection in a variety of landscapes; 1) distance to forest edge (Niedziałkowska et al. 2006; Rauset et al. 2013; Samelius et al. 2013; Zimmermann and Breitenmoser 2007), 2) distance to human infrastructure (which includes settlement, roads, railways, and industrial sites) (Bunnefeld et al. 2006; Bouyer et al. 2015a; Gehr et al. 2017), 3) elevation (Bouyer et al. 2015b) and 4) terrain ruggedness (Rauset et al. 2013; Bouyer et al. 2015b) (Table 1). Distance variables were logtransformed ($\log(x + 1)$), and all variables were scaled across both study regions prior to analysis, to maintain comparability of results (Tables A4 and A5). For all variables, a resolution of 25 x 25 meters was used.

We used logistic regression in R (R Core Team 2018) to model RSFs for each of the two study regions using a series of individual-based RSFs. The RSFs were based on a use-availability design, in which presence points of the animal (hereafter "used points") are compared to potential locations of an individual within the landscape (hereafter "availability points") (Boyce and McDonald 1999; Johnson et al. 2006; Manly et al. 2007). For each order of selection separately, available points were generated at random for each used point at a ratio of 5:1 (Hemmingmoore et al. 2020). The same presence data was used for both orders of selection. To quantify how animals select home-range placement within a larger landscape (second order selection) we defined the second order available area by creating 95% minimum convex polygons around all individual locations within each study region, scaling them up to 200%, merging them, and clipping the resulting polygon by the Swedish border. Available locations were randomly generated from within this area (Fig. 1; dark grey). To assess habitat selection within the established home-range (third order selection), available locations were randomly sampled for each individual from within their specific home-range, calculated as 95% minimum convex polygons around an individual's locations (Fig. 1; very dark grey). To quantify the region-level distributions in beta coefficient estimates, we first ran individual-level RSF models. Secondly, we bootstrapped coefficients by subsampling beta coefficients from the individual-level RSF models x times, where x is $2 * \text{number of individuals}$, and calculated the median value within the subgroup. This was repeated 10,000 times to obtain mean, standard deviation, median and confidence intervals for the beta coefficients (Ladle et al. 2019).

Within region prediction of habitat suitability

To assess to what extent regional RSFs are influenced by individual variation, for each study region and on both orders of selection we randomly partitioned the individual lynx RSF predictions into two subsamples, each consisting of 50% of the individual lynx. For each subset, we calculated a mean RSF value for each 25 x 25 m map pixel using the environmental predictors in Table 1, to create a spatial predictive surface for each subset. We then obtained the Pearson correlation coefficient between the two surfaces. This process was repeated 10,000 times for both the second and third orders of selection in both regions to obtain a distribution of correlation coefficients based on multiple subsamples. To test the differences in the distribution of the correlation coefficients between the second and third orders of selection for each study area, we subtracted the third order distribution from the second order distribution to attain the probability density of their difference.

Between region prediction of habitat suitability

To test the ability of RSFs at predicting suitable habitat when extrapolating to a different location within the species range, we 1) generated spatial predictive surfaces for both the northern and southern study region based on the mean estimated RSF coefficients derived from all individuals within each study region, using the available area in each study region (Fig. 1, the area within dashed lines), 2) calculated spatial predictive surfaces for each study region using lynx from the alternate region and 3) estimated the overlap between the areas of the highest 20% predicted values based on the model from each region itself and the model based on the alternate region. This was repeated at both orders of selection.

Results

Individual-based resource selection

At the second order of selection, lynx in the north selected for ruggedness and against elevation and distance to forest, whereas distance to human presence overlapped zero and was therefore neither selected for nor against (Fig. 2a, Table A2). Lynx in the south also selected for ruggedness and against distance to forest. Unlike in the north, southern lynx selected for increased distance from human infrastructure (Fig. 2a). A high variation among southern individuals regarding elevation resulted in no selection for or against at the regional level (Fig. 2a, Tables A2).

At the third order of selection, the direction of selection in the north was retained for elevation, ruggedness and distance to forest (Fig. 2b, Table A3). Northern lynx were again indifferent in terms of selection of distance to human infrastructure (Fig. 2b). Southern lynx selected for ruggedness and distance to human infrastructure. Coefficient estimates for both elevation and distance to forest overlapped zero suggesting no preference, and there was high individual variation in their selection for elevation at the third order, as at the second order (Fig. 2a).

Within-region prediction of habitat

The ability of models to predict suitable habitat within the same region was slightly lower at the second order compared to the third order of selection in both study regions (Fig. 3). Within the northern study area, 66% of the 10,000 bootstrapped correlation coefficients for the third order of selection have a higher value than those for the second order of selection. Within the southern study area, 91% of the correlation coefficients for the third order selection are higher than those for the second order of selection.

Between region prediction of habitat

In the northern study region, when comparing the area including the highest 20% RSF values of predictions based on either northern or southern models, we found an overlap of 59.5% and 29.5% at the second and third orders of selection, respectively (Fig. 4c, 4i). The expected overlap at random was 20%. Models for northern individuals predicted lower elevation valleys as high RSF values, while southern lynx models predicted the western higher elevation, rugged regions to have high RSF values for lynx. This pattern was consistent, irrespective of the scale of selection used (Fig. 4a, 4b, 4g, 4h, Figs. A1, A2).

In the southern study region, the highest 20% RSF values based on northern or southern models overlapped by 49.9% and 59.5% at the second and third orders of selection, respectively (Fig. 4f, 4l). The expected overlap at random was 20%. Northern models failed to identify high RSF value patches in the center of the southern study region, and estimated larger areas with very low elevation levels in the eastern part of the southern study region as higher RSF values than southern models at both orders of selection (Fig. 4d, 4e, 4j, 4k, Figs. A1, A2).

Discussion

We used a long-term dataset of GPS-collared lynx collected from two study regions in Sweden with distinctly different environmental characteristics, within the Scandinavian lynx population, to assess individual variation in habitat selection as well as the ability to reliably predict suitable habitat when extrapolating RSF estimates across contrasting landscapes at the second order (home range selection within the landscape) and third order (within home range) of selection. Our findings showed that extrapolating data to other regions with different ranges of environmental predictor values led to poor predictions of habitat suitability at both orders of selection.

Within-region prediction of habitat selection

We found low individual variation at both the second and third order of selection within both study regions for the majority of coefficients (Fig. 2). The standard deviation increased at the second compared to the third order for distance to forest and distance to human infrastructure, while for elevation and ruggedness in the north, they remained similar between the two orders of selection (Table A2, A3). This indicates a higher individual variation at the second order, which has indeed been observed in both study regions for all variables, however to different extents (Fig. 2). From the third to the second order, individual variation in the south increased most for distance to human infrastructure followed by elevation, in the north the highest increase in individual variation was observed for distance to forest.

However, the bootstrapped correlation coefficients at the third order of selection were higher than at the second order of selection in both study areas, indicating a potentially higher variation in habitat selected by individual lynx at the second order (Fig. 3). Therefore, the scale of selection can influence the quality of predictive RSF models. High individual variation within a few explanatory variables, e.g. distance to human infrastructure and elevation for southern individuals at the second order (Fig. 2), were potentially enough to drive slightly lower correlation in the predicted RSF values at the second order compared to the third order of selection. These results emphasize the importance of visualizing and quantifying individual variation in habitat selection, rather than relying solely on the mean values to represent the regional-level estimates and associated predictive surfaces.

A number of factors influence an individual's selection, including intraspecific competition, reproductive status, sex, and hierarchical social structures within the population (Svanbäck and Bolnick 2007; Araújo et al. 2011; Tinker et al. 2012; Ladle et al. 2019). The effect of individual variation is however often ignored in RSF modelling efforts, even when predicting within the study regions where individuals were sampled (McLoughlin et al. 2010 but see Leclerc et al. 2016). Our results highlight that individual variation could in fact influence the predictive performance of RSF models and that it should be considered when predicting suitable habitat. One way of assessing individual variation and understanding its effect on predictions is the approach taken here: estimating models at the individual level, constructing population-level coefficient estimates and quantifying variance within estimates using a bootstrapping approach. This approach offers potential to both predict regional-level RSF maps and individual variation around regional-level RSF maps.

Between region prediction of habitat

Models performed poorly when used to predict RSF values in the contrasting study region (i.e. south predicting north and north predicting south). Extrapolation from one area to another can lead to invalid inference because the range of available resource values may not fully overlap between regions, thus forcing the model to extrapolate its predictions to available values beyond those used to train it (Figs. A1 and A2). Considering the second order of selection in our case study, lynx showed a positive selection for distance to human infrastructure in the south, but the population mean used for predictions was negative in the north. There is a high density of human infrastructure in the south and a very low density in the north (Table 1). As a consequence, when southern models were used to generate predictions for the northern study region, they overestimated RSF values, and northern models overestimate RSF values due to predicting selection against greater distance to human infrastructure in the southern region. This example illustrates that one should avoid including a variable with extremely low or non-existent values in one part of the studied region when modelling suitable habitat, since it will confront the model with unknown values, thereby reducing the model's predictive performance and reliability. Regarding elevation, the southern study region is relatively flat, with value ranges falling largely below the northern values. Since northern lynx selected on average against elevation, avoiding the very high mountain peaks in the northern study region, northern models overestimated RSF values when extrapolated to the southern region. In contrast to northern lynx, the population mean for southern individuals was positive for

elevation at the third order of selection. This suggests a quadratic relationship, meaning that lynx likely select for intermediate values of elevation at the third order of selection. Because non-linear relationships have the potential to strongly impact the outcome of habitat suitability predictions when extrapolating to regions which differ strongly in availability, this comparison emphasizes the importance of understanding the effect of the availability distributions when extrapolating. But even when individuals in both study regions select a resource in the same direction, the availability distribution can affect the results. We found that northern and southern individuals both selected for ruggedness at both orders of selection. However, because ruggedness availability values in the north vastly exceeded those in the south, this further contributed to an overestimation of RSF values by southern models when extrapolated in the north, despite the agreement in direction of selection.

Effect of order of selection on predictions

RSF estimates should start with a clear understanding of the species' ecology and the landscape from which available values are being sampled; however the scale at which the analysis is taking place also informs the results (Boyce et al. 2003; Boyce 2006; Fuller and Harrison 2010; DeCesare et al. 2012; Leclerc et al. 2016; Holbrook et al. 2017; Reed et al. 2017). In our study, the predictive performance of the models were potentially less accurate at the second order compared to the third order of selection within the same study regions as judged by the probability densities of the correlation coefficients (Fig. 3, Table A2, A3). Larger available areas at the second order could cover more diverse landscapes and hence a broader range of available values relative to those found at the third order of selection. Therefore, higher landscape heterogeneity at the second order has the potential to impact the reliability of habitat predictions on different scales because individuals can select their habitat from a larger variety of resources at the second order compared to the third order of selection. (Boyce et al. 2003, Herfindal et al. 2009; Bjørneraas et al. 2012).

When extrapolating predictions between the two study regions, we found an inverse effect based on study region, with northern models being better in predicting habitat in the southern study region at the third order of selection while southern models were more reliable in predicting habitat in the northern study region at the second order of selection. Therefore, when extrapolating, the direction and also strength of selection has potentially a higher impact on the predictions' outcome than the order of selection when extrapolating. This further underlines the need to pay attention to a variable's available range and its implications for resource selection between study regions with distinct environmental characteristics.

Conclusions and recommendations

We used an extreme example of predictive RSF models presented in this case study to illustrate and discuss potential drawbacks related to the extrapolation of RSF models and to highlight the need for caution, especially when extrapolating RSF results to regions with different availability distributions from the source region. This could be particularly useful to those considering the development of management

strategies using habitat predictions, e.g. to assess suitable habitat for species reintroduction, for the designation of protected areas, or to predict range expansions or shifts.

First, it is important to be aware of any lack of overlap between available values used to fit the models and the regions for which extrapolation is done, as values that fall outside of the range the models were informed with will decrease the reliability of predictions. Consequently, there is a need to sample across a gradient of available values for all the variables that will be used in the model, capturing as much landscape heterogeneity as possible. When such a sampling scheme is not possible, for instance when predicting range shifts based on climate scenarios (e.g. Li et al 2016) or predicting the establishment of an expanding population (e.g. Inman et al 2013), it is important to discuss the limitations inherent in extrapolating beyond the range of available values. Additionally, differences in management practices between regions can have a large effect on habitat availability, e.g. if a species is excluded from areas that would otherwise provide suitable habitat (e.g. Recio et al. 2018). This should be taken into consideration when projecting, for example, areas for possible reestablishment since the exclusion of a species from regions within the study region can bias a species' used locations relative to the assumed available landscape (Eriksson and Dalerum 2018), adding further error to estimated habitat suitability. In our example, all models tended to misidentify habitat suitability when extrapolating to other areas. Hence, there would have been the risk that an area would be designated for protection although it does not provide adequate habitat for the species of conservation concern, or that individuals would be released in areas that had been misidentified as suitable. Therefore, extrapolations should ideally be limited to areas where the range of available values for the variables used are overlapping those of the study region upon which the original RSF is based, to increase transferability and reliability of the models' predictions.

Second, because resource selection is scale-dependent, it is important to apply a multiscale approach within resource selection studies to ensure that patterns of habitat use are accurately described and that the appropriate scale to answer the research or management question at hand is chosen (Boyce 2006, Manly et al. 2007, DeCesare et al. 2012; Northrup et al. 2013). Moreover, to allow an adequate reflection of resource selection across a heterogeneous landscape, an effort should be made to minimize any spatial bias in sampling individuals, to obtain a distribution as uniform across the relevant landscape as possible, which we acknowledge can be difficult.

Third, while literature regarding habitat predictions often include maps indicating the area of data origin as well as the area of extrapolation, it is not common practice to report the values ranges of variables used to fit the model as well as the range of variables in the extrapolation area (Schadt et al. 2002; Kuemmerle et al. 2011; Falcucci et al. 2013; Inman et al. 2013; Bleyhl et al. 2015; Eriksson and Dalerum 2018). The inclusion of such information (Tables A1, A4 and A5) would however be useful to understand the reliability of the predictions.

Increasing the transparency of research regarding the data and methods used to generate habitat predictions will contribute to the credibleness of the analysis conducted. By doing so, users are more

likely to identify the order of selection which is more relevant to the research or management question as well as to avoid the false identification of unsuitable habitat as suitable when extrapolating data.

Declarations

Highlighted Student Paper

This study demonstrates why RSF model results should not be extrapolated to areas whose landscape variable values extend beyond those of the original study area, for which few case studies exist.

Declaration of authorship

This study was conducted within long-term research projects led by HA and JP. The original concept for this study was proposed by HH, and all authors contributed to the design. Material preparation and data collection were performed by MA, JP and HA. The analysis was performed by AL, AP, HH, and MA, with support from HA. The first draft of the manuscript was written by AP with support from HH, MA and AL. All authors contributed to subsequent versions of the manuscript, and all authors read and approved the final version of the manuscript.

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Conflicts of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval

All lynx were captured, immobilized, and fitted with transmitters according to Swedish Animal Welfare Agency's ethical-approved protocols (Arnemo and Evans 2017).

Consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

The datasets generated during and/or analyzed during the current study are available in the figshare repository at DOI 10.6084/m9.figshare.14823690.

Code availability

The code used during the current study is available in the figshare repository at DOI 10.6084/m9.figshare.14823690.

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Table 1

Table 1. Mean (range) of the environmental predictors elevation, terrain ruggedness index, distance to human infrastructure and distance to forest for used and available points of the 2nd and 3rd order selection separated by study region.

Environmental predictor	Used	2 nd - order available	3 rd - order available
North			
Elevation (m)	711 (301 – 1784)	726 (189 – 1983)	853 (295 – 1975)
Terrain ruggedness index	6.60 (0.0 – 45.4)	2.84 (0.0 – 27.3)	4.2 (0.0 – 52.2)
Distance to human infrastructure (km)	16.0 (0 – 55.7)	18.8 (0 – 70.5)	17.9 (0 – 55.3)
Distance to forest (m)	559 (0 – 13946)	1685 (0 – 20945)	1871 (0 – 14648)
South			
Elevation (m)	131 (1 – 319)	129 (0 – 358)	131 (0 – 325)
Terrain ruggedness index	1.38 (0.0 – 14.8)	1.02 (0.0 – 14.8)	1.1 (0.0 – 16.5)
Distance to human infrastructure (km)	2.6 (0 – 8.20)	2.2 (0 – 9.8)	2.55 (0 – 8.78)
Distance to forest (m)	19.2 (0 – 520)	49 (0 – 2261)	29.6 (0 – 1965)

Figures

Figure 1

a) Sweden with permanent lynx distribution (very light gray), sporadic lynx distribution (light gray), overlapping 95% MCP lynx home ranges (very dark gray) representing the available area for 3rd order selection in the northern and southern study areas respectively, and with available areas for 2nd order selection (dark gray). Maps b) and c) show the northern and southern study areas, respectively, with used points (black), available area for 3rd order selection (very dark grey), and available area for 2nd order selection (dark grey). Dashed lines indicate the available area used to predict suitable habitat

Figure 2

Boxplots of the bootstrapped beta coefficients of the environmental predictors elevation, ruggedness, distance to forest (Forest) and distance to human infrastructure (Human) for 2nd order of selection and 3rd order of selection. Grey (left boxes) represents the northern lynx and white (right boxes) the southern lynx

Figure 3

Correlation coefficients between sets of individual lynx for 2nd order selection and 3rd order selection. Dashed lines represent the mean correlation coefficient. Grey represents northern lynx and black represents southern lynx

Figure 4

Maps indicating the top 20% of RSF-values for both study regions on both orders of selection (black; left and middle column) as well as the overlap between patches of high RSF-values by both original and external models (dark grey; right column). **Maps a – f represent 2nd order selection**; a) north based on northern models, b) north based on southern models, c) overlap of high RSF-values in the north based on either northern or southern models, d) south based on southern models, e) south based on northern

models, f) overlap of high RSF-values in the south based on either northern or southern models. **Maps g – I represent 3rd order selection**; g) north based on northern models, h) north based on southern models, i) overlap of high RSF-values in the north based on either northern or southern models. j) south based on southern models, k) south based on northern models, l) overlap of high RSF-values in the south based on either northern or southern models

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