Evaluating habitat suitability and connectivity for a recolonizing large carnivore

Heather Hemmingmoore[a,*], Malin Aronsson[a,b], Mikael Åkesson[a], Jens Persson[a], Henrik Andrén[a]

[a] *Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden*
[b] *Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden*

ABSTRACT

The conservation of wide-ranging species presents challenges in a world of intensified human land use, forcing animals to occupy and recolonize human-modified landscapes. Although identifying suitable habitat and ensuring connectivity are important in supporting natural recolonization, these actions are rarely validated due to difficulties in monitoring such events. In Sweden, the Eurasian lynx (Lynx lynx) is now recolonizing its former range, after centuries of persecution. We investigated resource selection based on telemetry data from 108 lynx monitored over 20 years. We assessed the differences between the established population in central Sweden and the recolonizing population in southern Sweden, and between established and dispersing individuals. We found that models based on central Sweden successfully identified core habitat patches for establishment in southern Sweden, validated after recolonization. We also found that lynx selected for higher habitat suitability during the recolonization phase, and that dispersing individuals were less selective than established lynx. Using cost-distance analysis, we assessed connectivity between central and southern Sweden, and found that landscape permeability was higher when based on dispersing lynx compared to established lynx. Altogether, our findings suggest that when landscapes are sufficiently similar between source and recolonization areas, resource selection information from an established population can be useful for managers seeking to facilitate recolonization of wide-ranging species. We recommend more frequent use of validation during and after recolonization events, to improve our common understanding of habitat suitability and connectivity modeling, and therefore to enable more active management of recolonization events.

1. Introduction

Some large carnivores are currently recovering in human-dominated landscapes (Chapron et al., 2014; Gantchoff and Belant, 2017; LaRue and Nielsen, 2016); thus there is a growing need to predict their establishment and to facilitate management actions that help ensure their long-term viability and mitigate potential conflicts (Redpath et al., 2013). Large carnivore movements are increasingly constrained by human land use, forcing them to occupy or cross human-modified landscapes in search of suitable habitat (Fahrig, 2001; Fahrig, 2007; Tucker et al., 2018). Expansion may therefore be determined by animals' potential to successfully move through the landscape, especially in low-density populations exposed to high rates of human-caused mortality (Fahrig, 2007; Tucker et al., 2018). Consequently, identifying suitable habitat patches and ensuring population connectivity are vital for carnivore conservation and management (Beier et al., 2008; Brodie et al., 2015; McClure et al., 2016; Riordan et al., 2015).

Suitable habitat patches are often identified from resource selection functions (RSFs) (Boyce et al., 2002; Manly et al., 2007), and the potential for connectivity is evaluated by assessing the cost of passing through different habitat types based on RSF results (Abrahms et al., 2017; Beier et al., 2008; Chetkiewicz and Boyce, 2009; Sawyer et al., 2011). Dispersal

is the main driver of both population connectivity and recolonization (Jackson et al., 2016; LaRue and Nielsen, 2016; Morrison et al., 2015). As dispersal events often involve long distance movements (Fahrig, 2007; Tucker et al., 2018), and resource requirements may differ between established and dispersing individuals (Abrahms et al., 2017; Chetkiewicz et al., 2006), connectivity should ideally be assessed using actual dispersal events (Beyer et al., 2010). However, studies on habitat connectivity often use data from resident individuals, which could overestimate landscape resistance when dispersers are more inclined than residents to use the low-quality matrix between core habitat patches (Abrahms et al., 2017; Jackson et al., 2016).

Like many carnivores, Eurasian lynx (*Lynx lynx*) declined across Europe in the 19th and early 20th centuries due to human persecution (Chapron et al., 2014). Lynx have recovered in much of Europe, through both natural recolonization and a few successful reintroductions (Chapron et al., 2014; Linnell et al., 2009). The Scandinavian lynx is a distinct subpopulation of Eurasian lynx, which has recovered after near extirpation in the early 20th century (Chapron et al., 2014; Liberg, 1997; Linnell et al., 2010; Linnell et al., 2007). Lynx recolonized central Sweden from northern Scandinavia during the 1990s, and the first documented lynx reproduction in southern Sweden occurred in 2003 (Viltskadecenter, 2005). Today, lynx occupy most of Sweden (Fig. 1a)
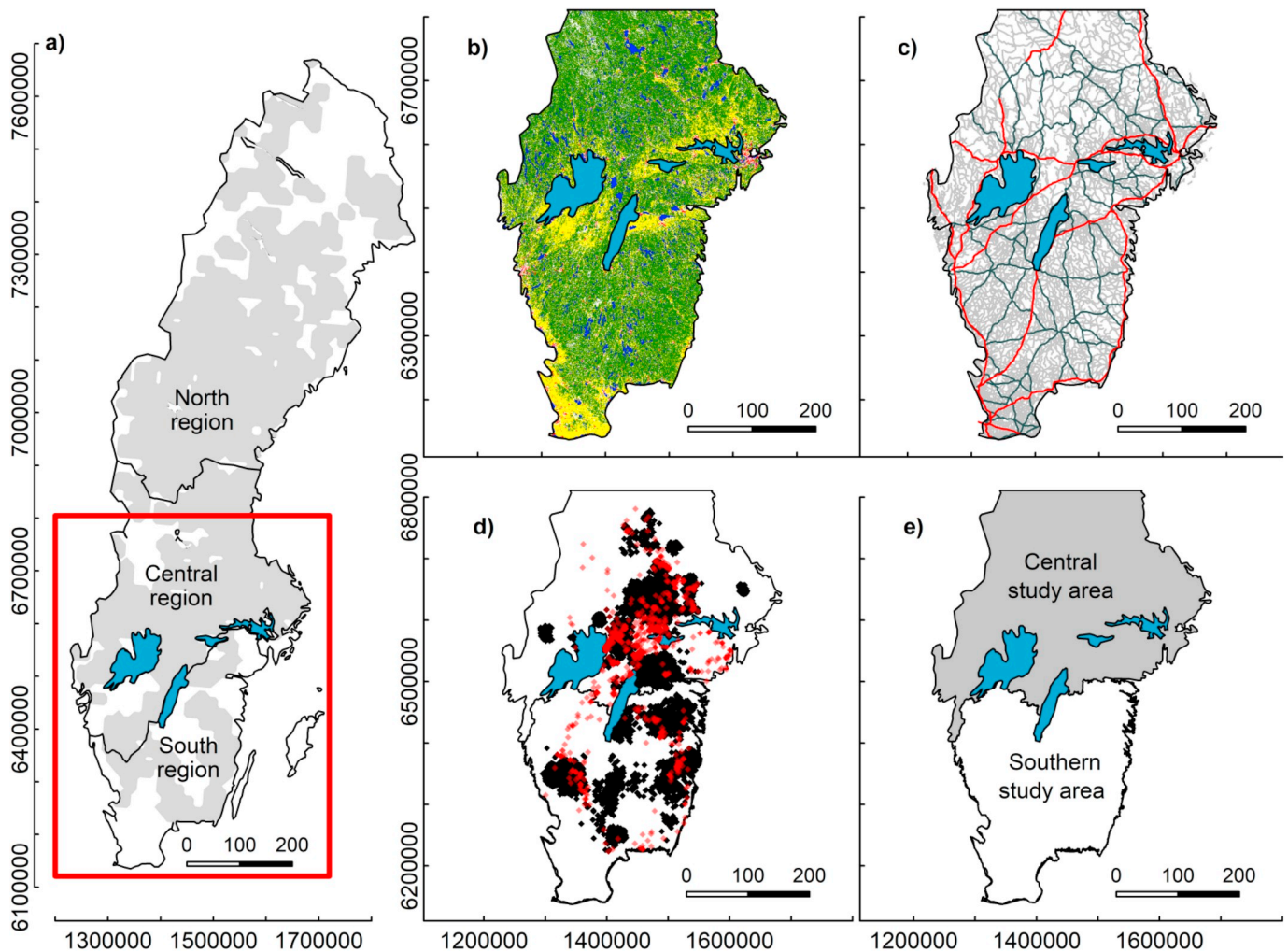
Fig. 1. a) Swedish lynx management regions, our study area outlined in red, and lynx distribution in gray. b) Land cover type (green = forest, yellow = agricultural or grassland, red = urban areas blue = water, white = other). c) Roads, with small roads in light gray, primary roads in black, and national highways in red. d) Telemetry locations from established lynx in black (*n* = 101 individual) and dispersers in red (*n* = 35 individuals). e) Study areas used in this analysis. Scale bar distances are in kilometers and the X- and Y-axes are coordinates in the Swedish grid RT90. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and are estimated at approximately 1200 individuals (Zetterberg and Tovmo, 2017) based on annual monitoring (Supplementary material). Swedish lynx management is decentralized to three regions (Fig. 1a), each with a specified target for minimum yearly count of family groups (females with kittens) (Fig. A1). Population estimates based on monitoring results directly inform management, and lynx hunting is permitted if the population exceeds the regional target on an annual basis (Andrén et al. in press) (see also Supplementary material).

One goal of the Swedish national lynx management plan is to redistribute the population between the central and southern management regions (SEPA, 2016). Connectivity and habitat suitability were not assessed in the management plan. This goal was based on assumed habitat and prey availability in the south as well as sufficient connectivity (SEPA, 2016), although the area between the central and southern management regions consists of a potentially unsuitable matrix landscape for lynx, i.e. densely populated agricultural land interspersed with highways and large lakes (Fig. 1b, c) (Basille et al., 2013; Kramer-Schadt et al., 2004; Zimmermann et al., 2007).

In this study, we took advantage of long-term data from 108 lynx, including both resident and dispersing individuals, fitted with VHF/GPS collars throughout the recolonization of southern Sweden (1996–2015; Fig. 1d). Thus, we had a unique opportunity for an inferentially strong observational study of the recolonization patterns of a

historically persecuted carnivore, more specifically to identify and validate suitable habitat and assess connectivity between source and reestablishment areas. Our first aim was to predict suitable habitat in southern Sweden based on lynx in central Sweden, and to validate these predictions after recolonization of the south. Based on the similarity in habitat composition between the two areas (Table 1, Table A1) we expected that models based on the source area would successfully predict establishment (Guisan et al., 2017). Our second aim was to identify potential areas of connectivity between central and southern Sweden, and to test whether corridors predicted from established lynx differed from those predicted by dispersers. We expected dispersers to be less selective than established lynx and therefore to predict higher landscape permeability, because previous studies suggest that dispersers are more inclined to move through suboptimal habitat than adults (Abrahms et al., 2017; Gastón et al., 2016; Palomares et al., 2000; Vanbianchi et al., 2018).

We first modeled lynx resource selection by sex, region, and status (established vs. dispersing), to assess what resources lynx are selecting for in the landscape. We used these models to spatially predict habitat suitability across both study areas, and used these habitat suitability values to identify large core habitat patches supporting lynx establishment. We then used these predictions to create cost-distance surfaces across the landscape, to assess connectivity between identified habitat patches.

Table 1
Resource variables used in resource selection function (RSF) models, which informed core habitat patch identification and cost-weighted distance analysis.

Category	Variable	Measure	Scale	Source	Biological meaning/hypothesis	Values
Prey	Roe deer hunting bag	Number of roe deer shot per 1000 ha, for the year in which the lynx location was taken	Swedish hunting district, 54 to 6704 km²	Swedish Association for Hunting and Wildlife Management	Possible selection for higher roe deer availability because they are the main prey in this area. (Herfindal et al., 2005, Odden, Linnell and Andersen 2006, Gervasi et al. 2014).	Central study area: Min/Max/Mean 0.01/210/57 South study area: Min/Max/Mean 22/337/93
Human disturbance	Distance to large roads	Distance from primary and secondary roads (Swedish Transport Agency Road numbers up to 499)	Euclidean distance in meters	National Land Survey of Sweden, raster calculated in QGIS 2.18.2	Possible avoidance of human activity (Basille et al., 2009, Basille et al., 2013, Kramer-Schadt et al., 2004)	Central study area: Min/Max/Mean 0/33 139/5000 South study area: Min/Max/Mean 0/23 975/3958
	Distance to small roads	Distance from tertiary roads (Swedish Transport Agency road numbers 500+)	Euclidean distance in meters	Swedish Land Survey Authority (*Lantmäteriet*), raster calculated in QGIS 2.18.2	Possible avoidance of human activity (Basille et al., 2013, Basille et al., 2009, Kramer-Schadt et al., 2004)	Central study area: Min/Max/Mean 0/13 077/1833 South study area: Min/Max/Mean 0/10 310/1181
	Human population density	Human population per km²	25 × 25 meter grid cells	Center for International Earth Science Information Network (CIESIN), Columbia University	Possible avoidance of human activity (Bouyer et al., 2015a, Andrén et al., 2006, Bunnefeld et al. 2006, Gehr et al., 2017)	Central study area: Min/Max/Mean 0/4076/42 South study area: Min/Max/Mean 0/1662/48
Land cover	Land cover class	Land cover category,	25 × 25 meter grid cells	National Land Survey of Sweden	Possible selection for certain land cover types (e.g. forest) and avoidance of others (e.g. agricultural land and urban areas) (Rauset et al., 2013, Samelius et al. 2013)	See Table A1
	Distance forest to edge	Distance from edge between forest and agriculture or grass land	25 × 25 meter grid cells	Calculated in QGIS 2.18.2 based on SMD land cover classes, National Land Survey of Sweden	Possible selection for forested areas and areas immediately outside the forest (Zimmermann, Breitenmoser-Würsten and Breitenmoser 2007)	Central study area: Min/Max/Mean 0/8342/235 South study area: Min/Max/Mean 0/6319/259
Terrain	Elevation	Meters above sea level	50 × 50 meter grid cells	Digital Elevation Model	Possible preference for areas of high elevation in flatter study areas, as this one is (Bouyer et al., 2015b)	Central study area: Min/Max/Mean −5/948/163 South study area: Min/Max/Mean −5/374/128
	Ruggedness	Terrain ruggedness index (TRI)	50 × 50 meter grid cells	(Riley 1999) calculated in QGIS 2.18.2	Possible preference for rugged terrain due to concealment (Bouyer et al., 2015b, Rauset et al., 2013)	Central study area: Min/Max/Mean 0/173/5 South study area: Min/Max/Mean 0/127/5

2. Methods

2.1. Study system and data

The central and southern study areas (Fig. 1e) are divided where an agricultural belt (78% wheat and barley) and the two largest lakes in Sweden interrupt otherwise continuous forest (Fig. 1b). This biogeographic border does not follow county borders, as do the lynx management regions. Consequently, our southern study area overlaps most of the southern management region and the southwest area of the central management region (Fig. 1a, e). The central and southern study areas are characterized by 70% and 63% forest, respectively (Table A1), most of which is intensively managed Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Andrén et al., 2002). Agricultural land (cropland and grazing areas) and natural grassland together constitute a larger proportion of the south (24%) compared to the central study area (14%) (Table A1). Most land in southern Sweden is privately owned (63%), followed by corporate and state ownership. Only approximately 3% of the land in southern Sweden is protected, and the largest protected area is 78.5 km^2. In both study areas, the main prey is roe deer (*Capreolus capreolus*) (Andrén et al., 2006; Aronsson et al., 2016).

We used 26,569 locations from 108 individuals (59 males and 49 females) monitored in the central (1996–2015) and southern (2007–2015) study areas (Fig. 1d). All lynx were captured, immobilized, and equipped with collars following Swedish Animal Welfare Agency's ethical-approved protocols (Andrén et al., 2006; Arnemo and Evans, 2017). Animals were fitted with VHF collars (1996–2008: MOD335 and MOD400NH Telonics, Mesa, AZ, USA) or GPS collars (2003–2015: GPS plus mini, Vectronics Aerospace, Germany; Televilt Posrec 300 and Tellus 1C, Followit, Sweden). Two individuals were fitted with both GPS and VHF collars, at different times, resulting in 75 VHF-collared individuals (216 ± 364 SD locations/individual) and 36 GPS-collared individuals (295 ± 200 SD locations/individual). One location per day per individual was randomly selected to reduce temporal autocorrelation and reduce potential biases due to differences in sampling frequency between animals (Aronsson et al., 2016; Frair et al., 2004; Nielsen et al., 2002).

Lynx natal dispersal events typically start at 10–11 months of age, and most individuals establish their own home range by 18 months of age (Samelius et al., 2012). We used net squared displacement (NSD) (Bunnefeld et al., 2011) to separate dispersing individuals (hereafter "dispersers," $n = 35$) from those with established home ranges (hereafter "established," $n = 101$) based on movement pattern. Locations that were classified as unknown or in a pre-dispersal phase were omitted. NSD is a method used for identifying movement behavioral states of animals based on the squared distance they have travelled from their first location, with distinctly different patterns for various movement states (Bunnefeld et al., 2011).

Lynx monitoring locations of family groups collected between December 2002 and March 2018 (www.rovbase.se, accessed 2 April 2018, see Supplementary materials) were used as validation data ($n = 645$ in the central and $n = 441$ in southern study area).

2.2. Resource selection

Predictor variables were chosen based on previous studies of lynx resource selection (Table 1). Land cover classes were consolidated using prior categorizations of the 2000 Swedish Land Cover National Land Survey of Sweden maps (i.e. the latest available update of Swedish land cover) (Rauset et al., 2013) and modified to provide further granularity regarding forest type (Table A1) because lynx may use deciduous and coniferous forest differently. Prey availability was assessed from regional roe deer hunting bag sizes, which is a proxy for roe deer abundance (Aronsson et al., 2016; Melis et al., 2013).

We used conditional logistic regression to estimate resource

selection functions (RSFs) by sex, study area, and dispersal status (Chetkiewicz and Boyce, 2009). RSFs rely on a use-availability design, wherein locations used by the animal (hereafter "used points") are compared to the available surrounding landscape (Boyce and McDonald, 1999; Johnson et al., 2006; Manly et al., 2007). For availability data, we generated circular buffers around each VHF or GPS location using a radius of 16 km for established lynx (approximate home range size based on our data and published studies) (Aronsson et al., 2016; Herfindal et al., 2005) and 5 km for dispersers (approximate daily step length for dispersers; our data). Five random points were generated within each buffer to represent available locations (hereafter "available points") (Boyce et al., 2003). We also tested three other buffer radii (one, five, and 22 km for established lynx and one, 16, and 22 for dispersers) to validate our buffer size choice. The one kilometer buffers were uninformative and completely overlapped zero, and the direction of selection was the same for all variables using five, 16, and 22 kilometer buffers. We used binomial generalized linear mixed effects models with logit links in the lme4 package (Bates et al., 2014) for R Studio 1.0.40 (R Core Team, 2018) to model RSFs. Individual identity was included as a random effect to account for correlation between used points. Initially we included the point cluster identity of used and corresponding available points as a nested random effect within individual (Fieberg et al., 2010; Gillies et al., 2006), but removed point cluster identity after finding that the variance explained was not significant. All predictor variables were checked for collinearity using Pearson's correlation coefficient (Crawley, 2014) and variables with $r > 0.3$ were not included in the same model. Therefore, "distance to agricultural land" was removed in favor of "distance to forest." All continuous variables were standardized to a mean of zero and a standard deviation of one. Determinants of resource selection were grouped into the categories of prey, human disturbance, land cover, and terrain (Table 1). A set of candidate models were identified based on these groups, which include all variables, each category separately, one model with all variables except prey, and one with land cover and terrain variables. Models were selected based on Akaike information criterion (AIC) values (Burnham and Anderson, 2003) (Table A2).

2.3. Model validation and prediction

To test the predictive ability of our RSF models, we generated predictive surfaces (raster maps) wherein every pixel is assigned a resource value according to the coefficients for the model with the best fit (Chetkiewicz and Boyce, 2009; Hebblewhite et al., 2011; Inman et al., 2013). Because we oversampled availability points at a ratio of 5:1, an approximate value for neutral selection in this case is 1/6, or 0.167. We removed random effects from the models that were used to inform predictive surfaces due to limitations in generating predictive maps using mixed effects models, which did not change the direction of selection in any model.

We validated the predictive power of these surfaces by calculating the mean predicted habitat quality score of the lynx monitoring data that was not used in training each model, and comparing it to the predicted values from the training data using Welch two-sample *t*-tests. To verify whether lynx actually used areas of higher habitat suitability compared to the available landscape, we ran two-way repeated ANOVAs by individual, comparing the mean habitat suitability scores of each lynx's used and available points. We also used Tukey HSD tests to make pairwise comparisons between groups, based on study area and dispersal stage.

2.4. Core habitat patches and connectivity

To test whether core habitat patches supporting lynx establishment in southern Sweden were identifiable based on data from central Sweden, we used the results of the central area RSF to identify patches of contiguous habitat large enough to encompass one, two, and three

female home ranges or more (i.e. 315, 630, and 945 km^2; (Aronsson et al., 2016; Herfindal et al., 2005), with habitat quality scores >0.15 (0.167 being an approximate value for neutral selection). This value was chosen because lynx can tolerate some non-optimal habitat in their home ranges, as mean habitat values for 95% kernels and 95% minimum convex polygons for established individuals are 0.170 ($\pm$ 0.018 SD) and 0.174 ($\pm$ 0.019 SD), respectively. The results for the threshold of two female home ranges were identical to using a threshold value of three female home ranges (Fig. A2). The single home range size resulted in the identification of five additional smaller patches, two of which were in the matrix habitat between the large lakes (Fig. A2).

To evaluate connectivity between the core habitat patches, we used cost distance analysis to assess the resistance of the landscape (Sawyer et al., 2011). We calculated cost-weighted distances based on the habitat values assigned to each map pixel, based on the RSF model results using Linkage Mapper 1.1.1. (McRae and Kavanagh, 2011). This was done separately for dispersing and established lynx RSF models, resulting in two raster maps, wherein pixel values provided the cost-weighted distance to the nearest core habitat patch (McRae and Kavanagh, 2011). We calculated the ratio between these rasters to test whether predictions made based on established or dispersing animals are sufficient to identify landscape that can facilitate dispersal. We focused on the permeability of the overall landscape between core habitat patches and did not use least cost paths (LCPs) or corridors because these methods are restrictive in that they identify single pixel-wide paths (LCPs) and rely on arbitrary cut-off thresholds in their cost-weighted distances (corridors), which can lead to loss of information and conclusions that are not biologically meaningful (Moilanen, 2011).

3. Results

3.1. Resource selection

The full models, including all variables, were the top RSF models for both male and female established lynx in both study areas. In contrast, dispersers were less selective, as both anthropogenic effects and prey were absent in the top RSF models based on dispersers (Table A3, A4). For variables that were in both top models, dispersers tended to select in accordance with established lynx (Table A3, A4). All groups selected for forest and against semi-natural areas, marshland, human infrastructure, and waterways (Table A3, A4). Where selection differed, the two sexes tended to be in alignment within each area for all variables except prey (Table A3, A4). Southern established lynx of both sexes and central males selected against areas of higher roe deer availability, whereas central females selected for roe deer availability. Both groups of established lynx selected for longer distance to large roads. Central established lynx of both sexes selected for proximity to small roads, whereas southern males selected against road proximity (Table A3). Established lynx of both sexes selected for grassland and agricultural land in the south and against these land cover types in the central area.

3.2. Model validation and prediction

We identified areas of high quality habitat based on models informed by central established lynx (Fig. 2a), southern established lynx (Fig. 2b), and dispersers (Fig. 2c). According to all three models, all groups of lynx selected for higher habitat quality scores than the surrounding available landscape (Fig. 2d–f). Southern established lynx selected higher quality habitat compared to central established lynx and dispersers, irrespective of the predictive surface used ($p < 0.001$ in all cases) (Fig. 2d–f). Dispersers and central established lynx did not differ as much in the quality of habitat they selected. The mean used habitat quality score for dispersers, although slightly lower than scores for central established lynx in all three cases, did not differ significantly from central established lynx ($p = 0.284, 0.057, 0.281$ for the northern, southern, and disperser models respectively) (Fig. 2d–f). According to

the model based on central established lynx which informed our subsequent analysis, mean habitat quality score did not differ between animals that were used to train the model and government monitoring locations in the same area ($p = 0.97$).

3.3. Core habitat patches and connectivity

Eight large core patches of potential lynx establishment ranging between 1388 and 26,720 km^2 were identified across both study areas, covering 49% of the landscape (46% in central and 52% in the south; Fig. 3a). Two of these patches were fully within the southern study area and two were primarily in the central study area, with small portions extending into the south (Fig. 3a). Lynx monitoring locations were found more often within these patches in both areas (73%, $n = 645$, G = 99, df = 1, $p < 0.001$ in central and 77%, $n = 441$, G = 62, df = 1, $p < 0.001$ in southern). The two large core habitat patches identified in southern Sweden were 10,220 and 26,720 km^2, and therefore could contain 31 and 82 non-overlapping female home ranges, respectively (Fig. 3a). Additionally, five core habitat patches the size of a single female home range or smaller were identified, four in the central study area and one spanning the border between the two.

Cost-weighted distances between the large core habitat patches based on established lynx (Fig. 3b) and dispersers (Fig. 3c) identified very similar areas of permeability, although the resistance of the landscape was estimated to be higher for surfaces based on established lynx models. The median cost distance value based on established lynx was 26% higher than for dispersing lynx, with minimum, first quartile, third quartile, and maximum of 0%, 22%, 31%, and 94% higher values respectively for established lynx.

4. Discussion

The ability of large carnivores to recolonize their former ranges is a central conservation issue in many parts of the world (Chapron et al., 2014; Gantchoff and Belant, 2017; LaRue and Nielsen, 2016; Mattson and Clark, 2010). Therefore, in this study we predicted areas of lynx recolonization based on resource selection functions (RSFs) from the source area, and successfully validated these predictions with data from individuals in the settlement area and with independent monitoring data (Fig. 2). We also found that landscape permeability was predicted to be lower when using data from established individuals compared to dispersers, showing that dispersers were less selective and more likely to move through suboptimal habitat (Fig. 3). Consequently, we provide support for the feasibility of an essential management action, namely predicting core habitat patches and connectivity to facilitate recolonization, even when presence data are limited. Such extrapolation is possible when the source and recolonization areas are similar in terms of habitat composition (Guisan et al., 2017) as in this case, while we still caution that the predictive ability of these models could deteriorate as recolonization areas diverge structurally from those in which the source population originates (Boyce, 2006).

4.1. Resource selection

The resource selection of lynx in this study aligned with previous studies, as both established and dispersing individuals selected for forests (Müller et al., 2014; Niedziałkowska et al., 2006; Schadt et al., 2002b) and rugged terrain (Basille et al., 2009; Bouyer et al., 2015b; Rauset et al., 2013), both of which provide essential cover, while avoiding large roads (Basille et al., 2009). We found that lynx selected for proximity to small roads, which they use for movement and scent-marking (Krofel et al., 2017). The unexpected selection away from high roe deer density by females in the south and by males could be explained by lynx selecting for other factors related to prey catchability, e.g. proximity to forest edges, rather than for high prey density (Balme et al., 2007; Basille et al., 2009; Hebblewhite et al., 2005; Hopcraft
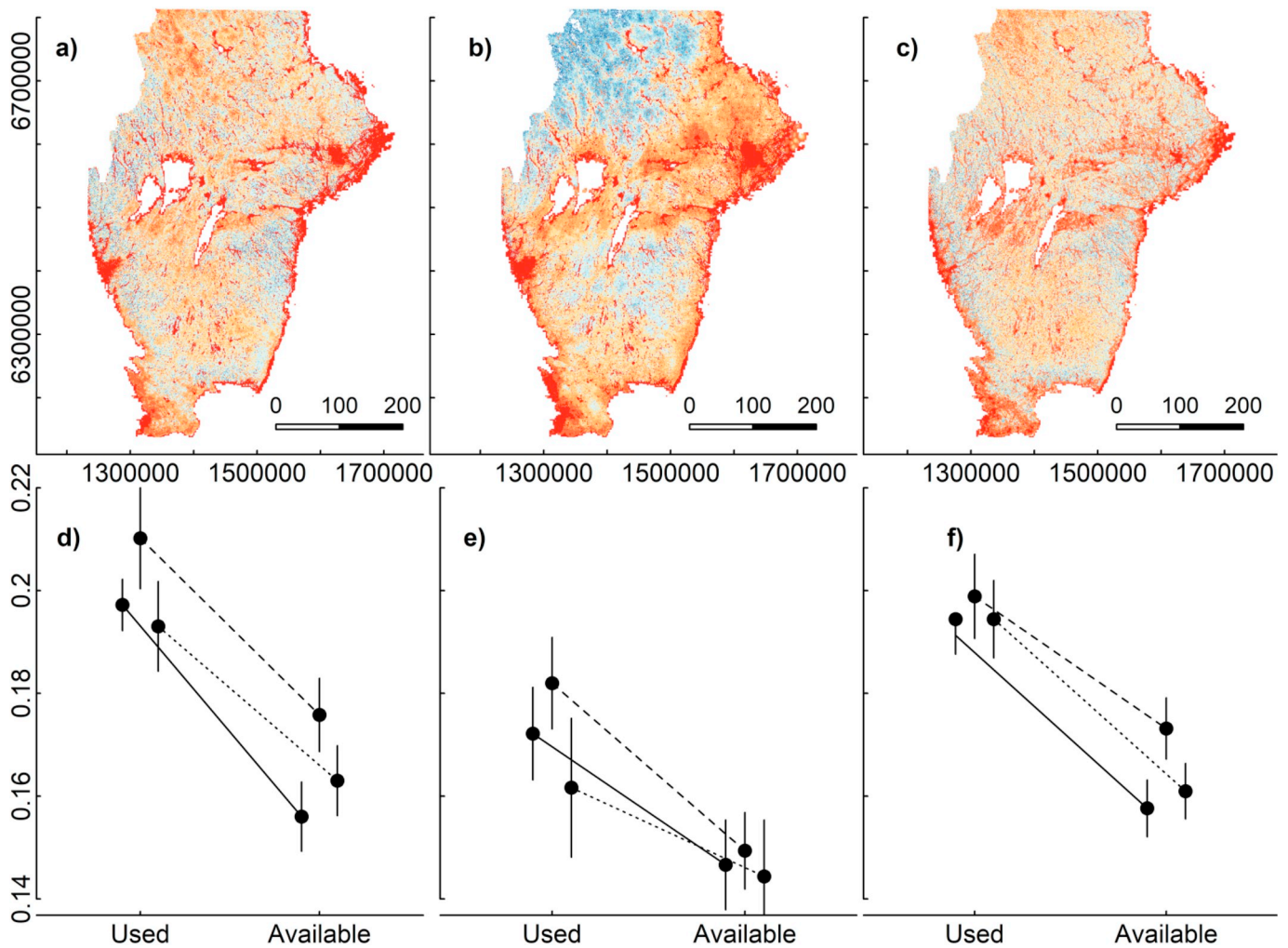
Fig. 2. a–c) Predictive surfaces identifying habitat quality with a theoretical range from 0 (red) indicating total avoidance to 1 (blue) indicating selection, with 0.1667 indicating approximate neutral selection. a) Predictions based on central established lynx models ($n = 66$ individuals), b) Predictions based on southern established lynx ($n = 43$ individuals), c) Predictions based on dispersing lynx ($n = 35$ individuals); d-f) Difference in habitat quality score between used and available points, based on each of the three models; solid line, dashed line, and dotted lines indicates values for central established lynx, southern established lynx, and dispersers respectively. Scale bar distances are in kilometers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2005), especially as roe deer density in our study areas was high enough to minimally affect the lynx kill rate (Andrén and Liberg, 2015; Nilsen et al., 2009).

While lynx neither selected for nor avoided coniferous forest (Table A3, A4), they selected for all other forest types, and every individual had ≥50% forest cover in their home range (mean 78% ± 9 SD), which aligns with other studies showing that lynx need forest (Niedziałkowska et al., 2006; Schadt et al., 2002a; Schmidt-Posthaus et al., 2002). Although southern lynx selected for agricultural patches, they remained near forest edges, with median distance of 25 m from forest while in agricultural land. This aligns with previous findings that lynx utilize fields to hunt in proximity to forest (Filla et al., 2017; Gehr et al., 2017).

4.2. Core habitat patches and connectivity

We validated that lynx in the southern area surrounded themselves with higher quality habitat than those in central Sweden (Fig. 2d–f). This indicates that when high-quality habitat is available for a re-colonizing population, individuals settle in these areas to a greater extent than in lower quality habitat. This highlights the importance of taking the extent of the recolonized area, as well as the stage of re-colonization, into account in RSF modelling, where the analysis of a

population at an early stage of a recolonization event may suggest selection for higher quality habitat than would ultimately be used at later stages of recolonization and thus underestimate habitat availability.

Models based on established lynx estimated the landscape to be slightly less permeable than those based on dispersers, although the areas of highest permeability were similar (Fig. 3b–c). This suggests that it was easier for dispersers to move through the landscape than models based on established individuals would indicate. This is consistent with other studies of wide-ranging carnivores showing that dispersers select similar habitat but are less selective than established adults, and are therefore more prone to move through less-optimal habitat (Abrahms et al., 2017; Blazquez-Cabrera et al., 2016; Gastón et al., 2016; Jackson et al., 2016; Mateo-Sánchez et al., 2015; Vanbianchi et al., 2018). Therefore, even when data on dispersing individuals is unavailable, dispersal habitat can be identified based on data from resident individuals, although some lower quality dispersal habitat may be missed.

Although there were gaps between core habitat patches, matrix habitat was available, which can facilitate dispersal. Possible dispersal routes for lynx in south-central Sweden are narrowed by four large lakes and crossed by major fenced highways (Fig. 1d), which were avoided by lynx in this study and can act as barriers to lynx dispersal
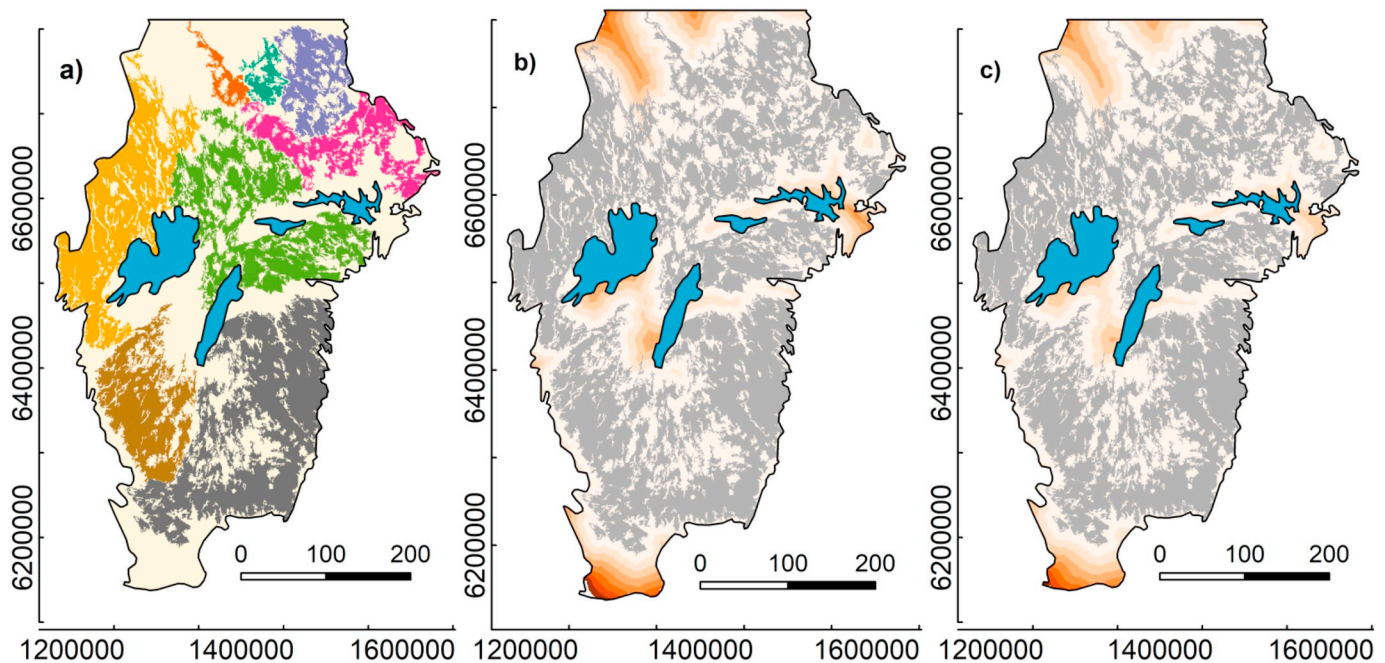
Fig. 3. a) Core habitat patches larger than a single female home range as identified by the model based on established lynx in the central study area; b) cost distance to nearest habitat patch based on established lynx (dark colors indicate higher cost distance); c) cost distance to nearest habitat patch based on dispersers (dark colors indicate higher cost distance). Scale bar distances are in kilometers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Zimmermann et al., 2007). Moreover, the agricultural belt between the two study areas could also discourage dispersal (Magg et al., 2016; Niedziałkowska et al., 2006) (Fig. 1b), as agricultural land was avoided by central established lynx and by dispersers. Although agricultural land was slightly selected by southern established lynx (Table A3, A4), they stayed close to the forest edge and were therefore unlikely to use large patches of agricultural land.

Lynx broad use of dispersal habitat indicates that seeking to identify and protect narrow movement corridors should not be over-emphasized when planning for recolonization by habitat generalists and in areas dominated by permeable habitat (Woodroffe, 2003). In such cases, we would instead recommend using a whole-landscape approach to assess where the population is likely to establish, and to assess their potential use of matrix habitat during dispersal.

4.3. Conclusion

The successful recolonization of lynx in southern Sweden demonstrates that the management goal to increase the population in the southern management region was realistic. Lynx have recolonized southern Sweden, despite passing through areas of high human disturbance without access to protected areas (Linnell et al., 2001). Although lynx in this study generally avoided areas of high human density, they selected for proximity to small roads and agricultural land, in line with previous studies showing that lynx select for areas of moderate levels of human activity (Basille et al., 2009; Bouyer et al., 2015a; Bouyer et al., 2015b). Although recolonization success is clear from monitoring data, we validated the management assumption that enough core habitat is available to support lynx. Additionally, our identification of two large patches of core lynx habitat in the south, together the size of 113 non-overlapping female home ranges, as well as a patch the size of a single home range between them (Fig. A2b) suggests that the current population target for southern Sweden of 40 family groups is conservative.

The ability to predict establishment based on existing populations, as we demonstrate here, is a useful tool in planning for reintroductions

or natural recolonizations (Bleyhl et al., 2015; D'Elia et al., 2015; Gehring and Potter, 2005; Inman et al., 2013), and in promoting connectivity between isolated sub-populations (Marini et al., 2010; Peters et al., 2015). It would also be useful to complement or validate other modelling approaches that require more data or do not rely on source population information like those used to predict suitable reintroduction sites, such as for proposed lynx reintroduction in Scotland (e.g. Ovenden et al., 2019; Philips, 2019).

Although RSFs and similar models are widely used in conservation planning, core habitat patches and connectivity between them are often not validated after management actions are implemented. We show that independent data sources, such as monitoring data, can be used to validate models. Therefore, as recolonizations progress, regular validation and updates associated with new findings could inform management and conservation actions by identifying areas of potential recolonization (Eriksson and Dalerum, 2018; Recio et al., 2018), and to plan for successful reintroductions or expansions by identifying overlaps between areas of high human activity and high quality recolonization habitat, so as to proactively mitigate human conflicts that are often associated with large carnivores (Bleyhl et al., 2015; Eriksson and Dalerum, 2018; Recio et al., 2018). Today, much work seeks to extrapolate the predictive ability of RSFs from small study areas to scales at the national or even continental level (e.g. Bleyhl et al., 2015; D'Elia et al., 2015; Inman et al., 2013; Kuemmerle et al., 2011), and the implications of these broad extrapolations should be further explored. We hope that this study will help to inform the ongoing recolonization of lynx in southern Sweden, and inspire others to validate modelling efforts concerning reintroductions and natural recolonizations around the world.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108352.

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