A potential habitat network for the Eurasian lynx *Lynx lynx* in Scotland

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ABSTRACT

1. The severe and early destruction and fragmentation of woodland habitats due to human activities is thought to have been a leading factor in the extirpation from Britain of several large, forest-dependent mammal species, such as the Eurasian lynx *Lynx lynx*. However, during the 20th century, Scotland in particular has experienced rapid, large-scale reafforestation. In order to assess if this reafforestation has been sufficient to permit the potential restoration of extirpated forest mammal species with large spatial requirements, a Geographical Information System (GIS) analysis of potential habitat of one species, the Eurasian lynx, was performed for the Scottish mainland.
2. A rule-based analysis, incorporating data and expert opinion from Switzerland, an environmentally similar area where lynx now occur, was used to identify patches of suitable lynx habitat in Scotland. A connectivity analysis was used to investigate whether and how these patches are connected to form larger interconnected networks of potential lynx habitat that would allow lynx to sufficiently interact with one another to form a single interbreeding population.
3. Scotland has over 20 000 km^2 of suitable lynx habitat split into two main networks of interconnected patches: the Highlands (*c*. 15 000 km^2) and the Southern Uplands (*c*. 5000 km^2). A further 800 km^2 of potential habitat, contiguous with the Southern Uplands lynx habitat network, lies across the border in England. Although connectivity between the Highlands and Southern Uplands networks is currently weak, the implementation of measures to mitigate the barrier effects of busy roads in central Scotland could facilitate the movement of lynx between the two areas.
4. Based on the availability of prey resources, Scotland could support around 400 adult and subadult lynx in the Highlands and around 50 in the Southern Uplands. A Scottish population of this size would be the fourth largest lynx population in Europe considering current population estimates.

Keywords: habitat connectivity, habitat networks, reafforestation, reintroduction, species restoration

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INTRODUCTION

The overall woodland cover of Scotland is thought to have declined, mainly through human activities, from a maximum of around 75% of total land cover 5000 years ago to 4% by the latter half of the 18th century (Warren, 2002; Stewart, 2003). This loss of woodland habitats, experienced throughout the British Isles, is likely to have been one of the principal causes of decline and extirpation of a number of large, forest-dependent species across Britain, including wild boar *Sus scrofa*, elk *Alces alces* and brown bear *Ursus arctos* (Kitchener, 1998). Deforestation and the consequent decline of woodland deer populations are thought to have been the main causes of the extirpation, during the late Middle Ages, of the Eurasian lynx *Lynx lynx*, a species that typically requires large, well-forested areas to survive (Hetherington, Lord & Jacobi, 2006). However, over the course of the 20th century, large-scale reafforestation has taken place (Mather, 1993) and has led to a marked growth and spread of woodland deer populations (Ward, 2005). However, none of the larger, extirpated mammals has yet been reintroduced to Scotland, and it is not clear if the extent of reafforestation has been sufficient to permit the successful reintroduction of woodland species with large space requirements.

Since the 1970s, the lynx has been successfully reintroduced to several European countries, and its return to Britain, in particular Scotland, has been discussed in recent years (Dennis, 1995; Kitchener, 1998; Yalden, 1999; Macdonald & Tattersall, 2001; Wilson, 2004; Hetherington *et al*., 2006). International treaties, such as the Bern Convention (1979) and the Rio Convention (1992), encourage signatory states, such as the UK, to reintroduce native species, while the European Union's Habitats and Species Directive 92/43 obliges the UK to study the desirability of reintroducing the Eurasian lynx among other species. However, the IUCN Guidelines on Reintroductions (IUCN, 1998) state that the factors responsible for a species' extinction should no longer be operating, if it is to be considered for reintroduction. It is imperative therefore to assess the availability in the modern landscape of suitable habitat for a reintroduced lynx population.

Habitat suitability and connectivity models are valuable tools in feasibility studies relating to the reintroduction of species (e.g. South, Rushton & Macdonald, 2000; Carroll *et al*., 2001; McClafferty & Parkhurst, 2001; Paquet *et al*., 2001; Schadt *et al*., 2002a,b; Kramer-Schadt *et al*., 2004). Two different modelling methods of identifying suitable habitat for Eurasian lynx in Europe have been used to date: a statistical model (Schadt *et al*., 2002a; Zimmermann & Breitenmoser, 2002) and a rule-based model (Schadt *et al*., 2002b; Doswald, Zimmermann & Breitenmoser, 2007). Both approaches use spatial data within the modelling process. A rule-based model can allow for greater interpretation by the habitat modeller of data from across the scientific literature and from communication with species experts, which can be better tailored to the environment in question.

Connectivity analyses, which measure the ease with which an animal can move across a landscape from one patch of habitat to another, have been conducted for a range of species (e.g. Schippers *et al*., 1996; Rushton *et al*., 1997; Ferreras, 2001; Singleton, Gaines & Lehmkuhl, 2002; Bruinderink *et al*., 2003). Recent studies have attempted to quantify inter-patch connectivity for the Eurasian lynx in Germany (Schadt *et al*., 2002b; Kramer-Schadt *et al*., 2004; Kramer-Schadt, Revilla & Wiegand, 2005) and Switzerland (Zimmermann & Breitenmoser, 2007). Schadt *et al*. (2002b) and Zimmermann & Breitenmoser (2007) employed similar methodologies, using the cost–path and cost–distance functions of ArcView extension Spatial Analyst (ESRI, 2000). Zimmermann & Breitenmoser (2007) evaluated connectivity between the Jura Mountains and adjoining areas of lynx habitat in the Alps, Vosges and Black Forest. They attributed costs to paths, thought to have already been utilized by lynx (e.g. between the Jura and the French Alps), and for the purposes of comparison, also calculated path costs for real routes taken by radio-tracked, dispersing lynx in the Swiss Jura and Swiss Alps.

The aims of this study are first to identify and quantify areas of suitable habitat for lynx in Scotland, based on the habitat requirements of lynx living in similar, human-modified and fragmented landscapes in Mainland Europe; and second, to address the question of whether any patches of suitable lynx habitat are connected in a way that would allow a founder population to expand their range and colonize new territory.

Eurasian lynx are solitary animals, but a typical male home range encompasses those of up to three females (Breitenmoser *et al*., 2000). The species has large spatial requirements, which vary in scale across Europe according to prey density and composition (von Arx *et al*., 2004). Small ungulates are their most important prey item, and when present, roe deer *Capreolus capreolus* are the most significant (Jedrzejewski *et al*., 1993). As roe deer are found in both coniferous and broadleaved woodland, as well as in open areas near to the woodland edge (Fawcett, 1997), wooded habitats provide lynx with an important food resource and also the cover in which to ambush their prey. Despite occurring across a wide spectrum of elevations and topographies, forest cover is a constant component of lynx habitat throughout the species' range in Europe, although in areas where suitable prey is abundant but where woodland does not occur, they can may make use of alternative cover such as scrub and rocks (Breitenmoser *et al*., 2000; Zimmermann & Breitenmoser, 2002).

The amount of forest within typical lynx home ranges varies across Europe. For example, in Białowieża Forest, Poland, where there are large contiguous areas of forest, lynx use wooded habitats almost exclusively (B. Jedrzejewska, personal communication). Elsewhere, lynx exist in a more heterogeneous landscape, where woodland is more fragmented (Breitenmoser-Würsten *et al*., 2001). The lowest proportion of woodland and scrub cover identified within a Swiss Alpine lynx home range was 38%, although forest always tended to be the most intensively used part of the home range, while open areas, such as meadows and pasture, were used much less despite being the dominant habitat by area in most cases (Breitenmoser-Würsten *et al*., 2001). In the more densely wooded Jura Mountains, at least 60% of an average adult lynx home range is wooded (F. Zimmermann, personal communication). Despite stronger habitat preferences than other European large carnivores (Breitenmoser, 1998), lynx have shown adaptability in human-modified landscapes. Radiotelemetry from Switzerland has revealed that lynx will often rest during the day in close proximity to human settlements and other areas of intensive, and often noisy, human activity (Zimmermann & Breitenmoser, 2007).

Juvenile lynx disperse from their mother's home range at around 10 months old, and may have to travel some distance to establish a territory. Radiotelemetry of lynx has revealed mean dispersal distances of several tens of kilometres in both Poland and Switzerland (Schmidt, 1998; Zimmermann, Breitenmoser-Würsten & Breitenmoser, 2005). In general, dispersing lynx prefer to stay within woodland habitats, and in north-east Poland, where open farmland appeared to be a barrier, subadult lynx changed direction whenever they encountered it (Schmidt, 1998). In the more fragmented landscapes of the Swiss Jura, although 75% of radiotelemetry locations from dispersing lynx came from woodland, 25% were in open habitats, such as natural open habitats, pasture and agricultural land (U. Breitenmoser, personal communication). Nevertheless, lynx tend to use woodland and scrub as they move across the landscape and are rarely more than 400–500 m away from such cover (Zimmermann & Breitenmoser, 2007). In addition, lynx have also been recorded swimming up to 30 m across rivers and 200 m across lakes, suggesting that small water features do not necessarily act as barriers to dispersal (Zimmermann & Breitenmoser, 2007).

METHODS

Study area

Mainland Scotland, with its large areas of contiguous forest, high densities of woodland deer and relatively light transport infrastructure, is the most suitable area within Britain for lynx reintroduction and was used as the study area. The Scottish islands were excluded, as there is no evidence for lynx living there during the Holocene. Mainland Scotland extends to around 68 000 km^2 and consists of three principal topographic regions (Fig. 1). The largest region, the Scottish Highlands, extends to over half the area of the Scottish mainland and includes the UK's highest mountains and a human population density of less than 10/km^2. The second region, the Southern Uplands, extends to some 13 000 km^2 and is centred on a range of lower, rounded hills that meet the Cheviot Hills at the English border. The average human population density is around 23/km^2. The third region, the Central Lowlands, is a generally low-lying area, which supports 75% of the Scottish population. Within this region, and running between the major cities of Glasgow and Edinburgh, lies the Central Belt, an intensely developed and densely populated landscape, which supports the most extensive transport infrastructure of the three regions.

Some 20% of the Scottish mainland is currently forested, with most of this consisting of conifer plantation (Caledonian Partnership, 2000). In the fertile north-east lowlands, wood-

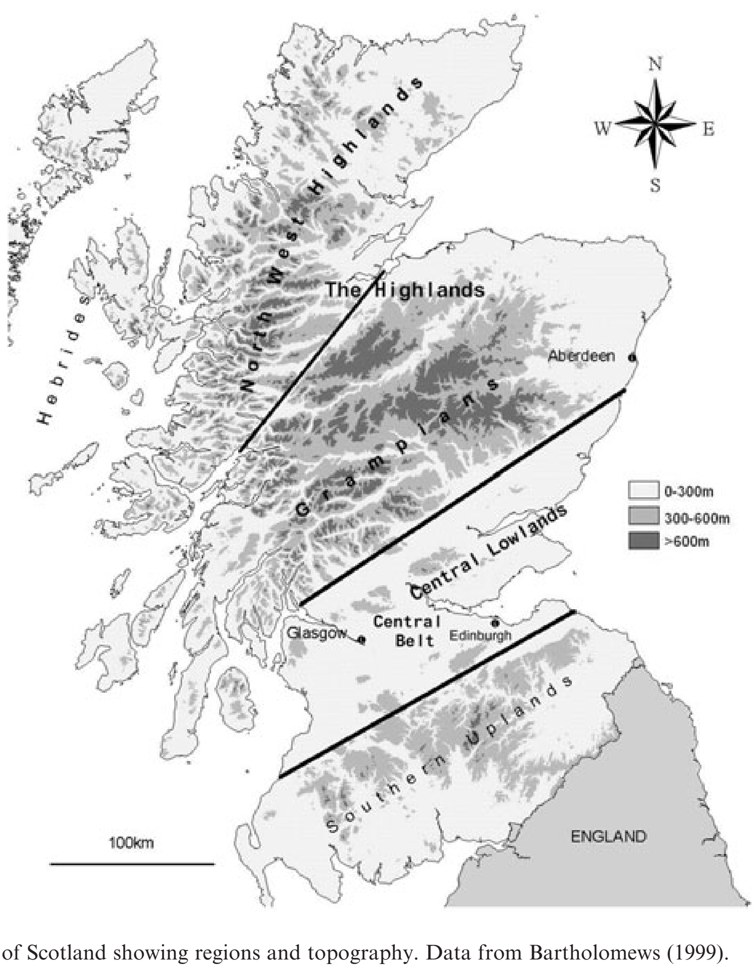

Fig. 1. Map of Scotland showing regions and topography. Data from Bartholomews (1999).

land occurs in a mosaic with agriculture. Woodland in the Highlands is constrained by the poorer soils and harsher climate found at altitude and tends to form belts along river valleys. In the Southern Uplands, expansive areas of treeless hill land were planted up with exotic conifers during the 20th century and now form large blocks of woodland which are not distributed linearly as in the Highlands. Woodland cover in the Central Lowlands is generally fragmented, with patches of woodland occurring in an agricultural and post-industrial landscape.

Of the non-wooded land cover classes, the most significant, especially in the Highlands, are heather moorland and peatland vegetation, which form around 40% of Scotland's land surface, either independently or in mosaics with one another (MLURI, 1993). Of the agricultural land cover types, 13% of the land surface is improved grassland and 11% arable farming land. Improved and rough grassland are the typical non-wooded land cover types of the Southern Uplands, while improved grassland and arable are more typical of the Central Lowlands.

Modelling approach

As there are no field data describing lynx ecology in Scotland, a rule-based modelling approach was used to identify areas of potentially suitable lynx habitat within a GIS. The rules were based on a compilation of information interpreted from the available literature, as well as expert opinion from lynx biologists at KORA, the governmental agency that conducts large carnivore research in Switzerland. In order to investigate connectivity between habitat patches, an analysis was performed using the cost–path and cost–distance functions of Spatial Analyst (ESRI, 2000). Employing similar friction values as Zimmermann & Breitenmoser (2007) allowed direct comparison between Scotland and similarly human-modified landscapes across which lynx dispersal movements have been recorded in detail.

Datasets

Non-wooded areas were identified using the 1:25 000 Land Cover of Scotland 1988 dataset (MLURI, 1993). Information about the more recent extent of woodland in Scotland came from the Scottish Semi-Natural Woodland Inventory (SSNWI; Caledonian Partnership, 2000) and the National Inventory of Woodland and Trees (NIWT; Forestry Commission, 2002a). The SSNWI 1:25 000 dataset depicts all blocks of woodland in Scotland greater than 0.1 ha and includes open forest with as little as 1–10% canopy cover. This information was interpreted from aerial photographs taken in 1988. The NIWT 1:25 000 dataset shows only woodlands over 2 ha in size and over 50% canopy cover, but in addition to data collated from the 1988 aerial photographs, contains new woodlands planted during the period 1988–2002. These two datasets were combined to give up-to-date information on the full extent of Scotland's woodland cover.

Data on the networks of roads and rivers in Scotland were obtained from the Ordnance Survey (2002) at 1:50 000 scale, and at a strategic level from Bartholomews (1999) 1:200 000.

Habitat analysis

Rules were developed for each habitat type, the basis for which is described below.

Woodland

All woodland types within the study area were considered to be potential lynx habitat (Breitenmoser *et al.*, 2000; Breitenmoser-Würsten *et al.*, 2001). Since lynx can use very small patches of woodland (D. Hetherington, personal observation), all patches of woodland and scrub greater than 1 ha in size were included in the analysis.

Non-wooded land

Open land adjacent to forest often forms a significant proportion of lynx home ranges (e.g. Breitenmoser-Würsten *et al*., 2001), and was included by considering the influence that core forest habitat would exert in the local neighbourhood. For example, in a landscape of fragmented forest, evidence suggests that the maximum distance of open land that a lynx would cross in order to get to another area of forest would be 1 km (Haller & Breitenmoser, 1986; Schadt *et al*., 2002b). However, it is likely that a lynx would risk crossing distances of open land to a forest patch only if it assessed that the risk was lower than the potential gains offered by a combination of prey and cover. Therefore, a small patch of forest with fewer hunting opportunities and offering less security would be less worthy of risking a long crossing of open land.

In order to include non-wooded land uses as potential habitat, and to allow for movement to other forested areas, a zone of open land extending from the forest edge, or 'buffer', was created around all discrete woodland patches. Where buffers overlapped one another, they were merged into one unit using the GIS software. The widths of the buffers depended on woodland patch size and the level of canopy openness (Table 1) since data from Switzerland have shown that lynx will use scrub and open woodland, as well as woodland with a partial closure of the canopy (Breitenmoser-Würsten *et al*., 2001).

Unsuitable habitat: sea, lochs and large settlements

Any areas of sea and freshwater lochs greater than 165 ha were removed from buffer areas to ensure that only terrestrial habitats were included. Settlements over 50 ha in size at the edge of the buffered zones were removed from the buffer as they were considered to be barriers to lynx movement as well as unsuitable habitat (A. Ryser, personal communication). However, smaller lochs and settlements totally surrounded by buffered open land were not removed from the habitat buffer as these often feature within lynx home ranges in Europe without ever having been visited by the lynx and are unlikely to form barriers to lynx movements.

Roads

Busy roads, in particular motorways, can be strong barriers to lynx movement (Zimmermann *et al*., 2005). For the modelling of lynx habitat in Scotland, the assumption was made that lynx in Scotland would not tolerate either motorways or dual carriageways within their home ranges. Therefore, roads data were overlaid on the buffered patches, and where motorways and dual carriageways intersected a buffered patch, that patch was split.

Patch size and woodland content

Patches identified in the above steps were then examined on the basis of their size and woodland content. Like the Scottish Highlands, an area forming considerably more than half

Table 1. Buffer distances in metres, with respect to woodland patch size and canopy cover

	Woodland canopy cover (%)		
Woodland patch size (ha)	<10	10–20	>20
<50	0	50	100
50–199	0	100	200
200–299	0	150	300
300–399	0	200	400
≥400	0	250	500

of the study area, forest in the Swiss Alps is limited by the constraints of altitude, and so tends to exist linearly in river valleys. The Swiss Alps were also found to support high densities of lynx with relatively small home ranges (Breitenmoser-Würsten *et al.*, 2001). Due to high prey densities, Scotland is likely to be able to support relatively high lynx densities and thus relatively small home ranges (Hetherington & Gorman, 2007). Therefore, because of similarities in relevant environmental parameters, it was decided to use information drawn from research in the Swiss Alps for which there was a considerable amount of high-quality habitat data and observations of lynx movement (e.g. Breitenmoser-Würsten *et al.*, 2001).

In order to identify habitat patches large and wooded enough to support a female lynx home range, minimum habitat requirements from the Swiss Alps were applied (Breitenmoser-Würsten *et al.*, 2001). Patches less than 45 km^2 in extent, and/or with less than 38% forest cover, and/or less than 24 km^2 of woodland, were removed. Introducing a rule about the proportion of woodland cover was essential to eliminate those patches that were created by the buffering of a network of contiguous, linear, farm woodlands. Due to their shape, these exerted a disproportionate influence on open land when buffered, and are not ideal lynx habitat.

Potential habitat patches would be classified as small (45–73 km^2, and large enough to support the home range of only one female), medium (74–549 km^2, and large enough to support at least one female and one male home range but fewer than 20 lynx home ranges) and large (greater than or equal to 550 km^2 and which could support at least 20 adult lynx home ranges). The figures of 74 and 550 km^2 come from minimum home ranges in the Swiss Alps as determined by Breitenmoser-Würsten *et al.* (2001) and represent, respectively, the minimum size of one male home range, and the minimum combined home range sizes for seven males and 13 females.

Sensitivity analysis

A sensitivity analysis was carried out to assess the sensitivity of the model to variation in key model parameters using four alternative scenarios (A–D) in which both buffer size (thus the influence exerted by large woodland patches) and the extent of the inclusion of open woodland were varied (Table 2). These two parameters were made the focus of the sensitivity analysis because of uncertainty surrounding first the suitability for lynx of various extents of woodland openness, and second the maximum distance across non-wooded land that lynx would cover as they move between woodland patches in a fragmented landscape. Further-

Table 2. Criteria used in standard and alternative scenarios for the sensitivity analysis

	Parameter	
Scenario	Extent to which open woodland is included	Buffer size (m) for woodland patches >400 ha
Standard	<10% woodland included (not buffered); 10–20% woodland included (receives half buffer size of >20% woodland)	500
A	<10% woodland not included; 10–20% woodland included, but not buffered	500
B	<10% woodland not included; 10–20% woodland not included	500
C	<10% woodland included (not buffered); 10–20% woodland included (receives half buffer size of >20% woodland)	400
D	<10% woodland included (not buffered); 10–20% woodland included (receives half buffer size of >20% woodland)	600

more, they were considered to be the parameters most likely to have the greatest impact on model outcomes.

Connectivity analysis

A cost grid of 100-m cells was developed for the whole of the Scottish mainland. Each cell was given a friction value according to the dominant land-use type within that cell. These values were based on those used by Zimmermann & Breitenmoser (2007) and were designed to reflect the ease with which a lynx could cross different types of land cover and potential barrier features. Swiss friction values were adapted for the Scottish environment (Table 3). A friction value of 5, higher than that of woodland but lower than that of grassland, was attributed to heather moorland and bracken, significant habitats in Scotland which are uncommon in Switzerland. Scotland does not support rivers as large as the Rhine and Rhône, so large Scottish rivers (the lower reaches of the Spey, Don, Dee, Tay, Tweed and Clyde) were given the same score as medium-sized Swiss rivers. In Switzerland, all 4-lane roads are classed as motorways, while in Scotland 4-lane dual carriageways are common and generally support lower traffic volumes than motorways. For the purposes of this model, dual carriageways received a friction value between that of single-carriageway trunk roads and motorways.

The analysis in Switzerland was carried out using data at a spatial resolution of 250 m, but for the analysis in Scotland, a 100-m grid was employed to support the finer resolution, and thus greater detail, of some of the datasets. Thus, a lynx crossing 1 km of woodland in Scotland would accumulate a path cost of 10 (10×100 m size cells, each with a friction value of 1). In the Swiss model, however, a lynx would accumulate a path cost of just 4 for the same journey (4×250 m cells, each with a friction value of 1). In order to take into account this disparity, and to keep resulting Scottish path costs comparable with Swiss path costs, Swiss

Table 3. Friction values adopted for the cost path analysis

Land-use type	Scottish Friction value	Swiss Friction value
Woodland	1	1
Scrub	1	1
Heath	5	–
Bracken	5	–
No coverage	7	–
Dunes	10	–
Montane vegetation	10	–
Peatland	10	–
Wetland	10	10
Unimproved grassland	10	10
Improved grassland	10	10
Arable	30	30
Bare rock & cliffs	1000	1000
Urban & developed areas	1000	1000
Open water	1000	1000
Medium rivers	–	40
Large rivers	40	120
Trunk (main) roads	40	40
Dual carriageway	80	–
Motorway	120	120

A 40-km^2 area of the northern Highlands was not interpreted in the Land Cover of Scotland 1988 dataset because of a gap in the aerial photo coverage. This area was given a friction value of 7, as it lay in a region of heath and peatland. Swiss friction values are from Zimmermann & Breitenmoser (2007).

Table 4. Results of the cost–path analysis for the Swiss Jura by Zimmermann & Breitenmoser (2007)

Cost path	Major barriers	Length (km)	Converted Scottish cost	Converted cost/km
Jura-Vosges	1 motorway	23.9	750.0	31.4
Jura-Black Forest	1 large river	23.0	672.5	29.2
Jura-Saleve	1 large river, 1 motorway	27.3	732.5	26.8
Saleve-Alps 1	1 motorway	7.8	405.0	51.9
Saleve Alps 2	1 motorway	10.0	812.5	81.25
Jura-Alps	1 large river	7.3	305.0	41.8
Chartreuse-Alps	1 motorway	6.5	535.0	82.3
Chartreuse-Alps	1 motorway	4.5	517.5	115.0
Lynx A	None	18.8	660.0	35.1
Lynx B	None	60.6	2070.0	34.2
Lynx C	1 motorway	2.2	555.0	252.3

The converted least cost paths for potential connections between the Jura and other potential habitat patches are shown, and those for three real lynx (Lynx A–C) that dispersed from prime habitat in the Swiss Alps.

costs were converted by multiplying the share of their path cost, not represented by linear features such as roads and rivers, by 2.5 (Table 4). No such disparity was caused by linear features because in both the Scottish and Swiss models they were one cell wide, e.g. a motorway was a rather exaggerated 250 m wide according to the Swiss raster grid, while only 100 m wide in the Scottish grid. In both cases, the path cost incurred by crossing a motorway was 120, irrespective of cell size.

An algorithm within the software totals the friction values of potential routes across the landscape between the start and finish points, and then selects the route with the lowest accumulated cost, and thus the route which, in theory, is most likely to be used by lynx as they move between habitat patches. A sensitivity analysis was performed for the connectivity analysis, but was restricted to the two alternative habitat scenarios differing most from the standard scenario, as they were also most likely to show the greatest divergence from the standard scenario in the connectivity analysis.

RESULTS

Habitat analysis

Thirty patches of suitable habitat were identified with a total area of 20 678 km^2 (Fig. 2; Appendix 1). Patch (L5) is contiguous with a further 817 km^2 of potential forest habitat in England, centred on Kielder Forest, an extensive plantation woodland. The English share of this habitat patch brings the total amount of habitat available in Scotland and northernmost England to 21 496 km^2.

Varying values in scenarios A to D for the maximum buffer distance for large woodland patches, as well as changing the extent of inclusion of open woodland, made little difference to the outcome of the model (Table 5). The number of patches and their distribution within the three size categories varied slightly. However, the level of variation from the total amount of habitat identified in the standard scenario was no more than 5%. This suggests that the identification and extent of suitable lynx habitat patches in Scotland is not highly sensitive to the rules used to generate it.

Connectivity analysis

A network of cost paths was identified to determine the connectivity of the habitat patches (Appendix 2; Fig. 3). The least costly path between the two largest habitat patches, L1 and

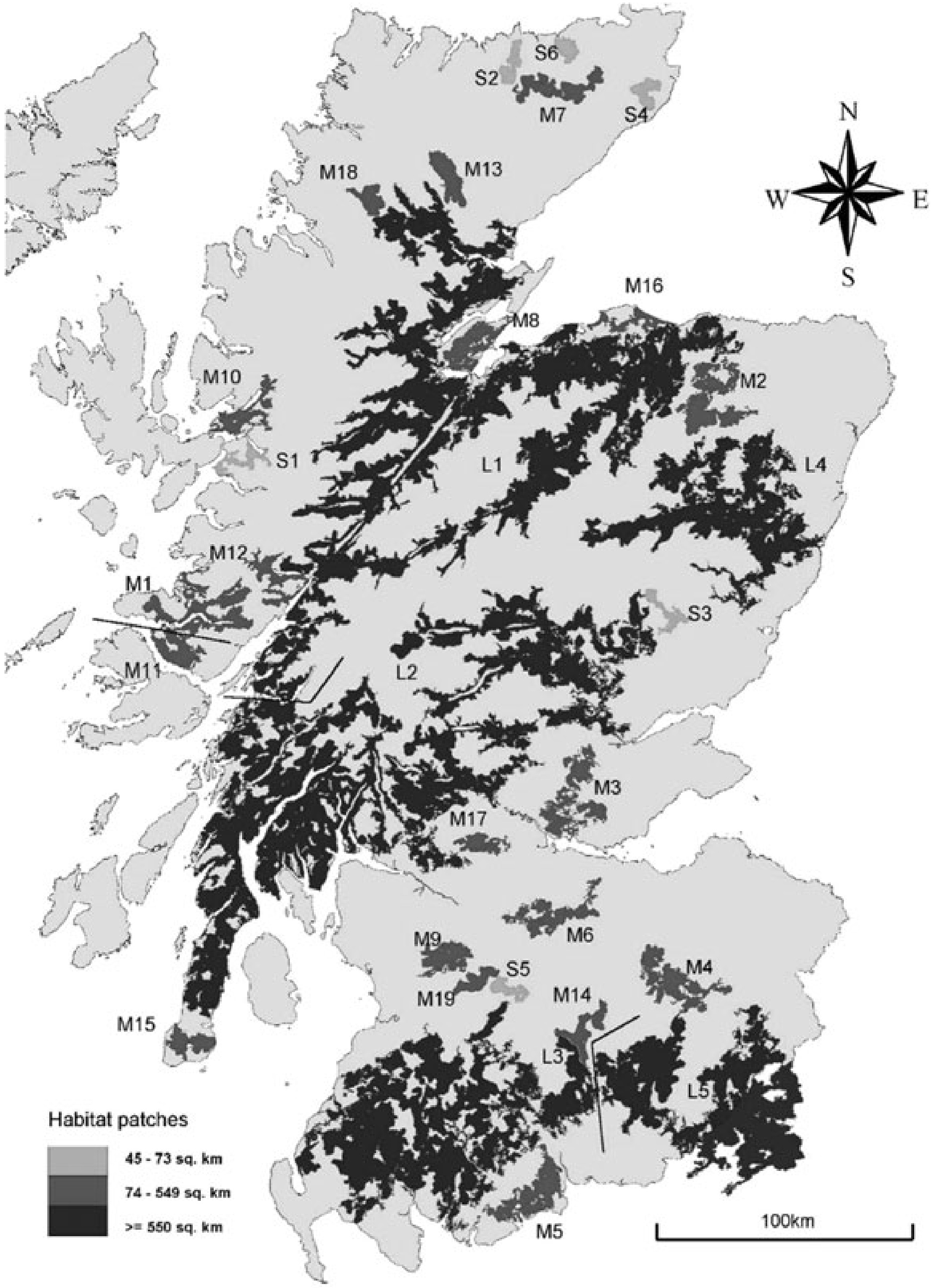

Fig. 2. The distribution of potential lynx habitat patches in Scotland according to the standard scenario. Potential habitat across the English border is also shown. Black lines highlight separation between two adjacent patches of the same shade.

L2, crossed a 300-m road bridge which spans the mouth of Loch Etive, a west coast sea inlet. Despite having to cross a trunk road and then effectively walk along the same trunk road for the 300-m length of the bridge, this connection (1a) was identified as the least costly as a result of the short distance between the habitat patches in this area. The cost path analysis was

Table 5. Results of the habitat analyses under the alternative scenarios

		Number of habitat patches			
Scenario	Total area (km^2)	45–73 km^2	74–549 km^2	≥550 km^2	Total
Standard	20 678.4	6	19	5	30
A	20 402.6	6	22	5	33
B	20 366.2	6	22	5	33
C	19 642.8	5	21	5	31
D	21 558.0	5	18	5	28

re-run for these two habitat patches, this time removing the bridge. On this occasion, the least cost path was situated in the Central Highlands along Loch Ericht (Connection 1b). Although a much longer route, this path was located in heath and woodland, and with no linear barriers, accumulated a low score well within the range of Swiss connections.

Many of the connections located in the Highlands accumulated low costs as a result of short distances and a lack of major barriers, and as a result of a close-knit network comprising most of the patches north of the Central Belt. No major barriers were encountered, such as large rivers, motorways or dual carriageways, and trunk roads were only an issue at Connection 1a, for which a suitable, alternative path also exists. Patches M10 and S1 on the west coast are separated by each other, and from other patches, by rather long paths, but as these paths are routed mainly through woodland and heath, they receives low cost scores per km, lower than any of the Swiss paths, and accumulate total scores lower than scores accumulated by real, dispersing lynx in Switzerland. Likewise, some of the paths among the group of patches in northern-most Scotland (M7, S2, S4 and S6), were quite long but received low total scores because of the likely permeability of the landscape for lynx. However, the connection between this grouping of patches and the nearest other patch accumulates a high cost because of the long distance involved, although there are no significant barriers. Another close-knit network of patches connected by short, low-cost paths exists in southern Scotland. A motorway lies between patches L3 and L5, and also patches L3 and M14, but other than this barrier, these considerable patches are virtually contiguous.

With the exception of the connection between M7 and M13, the highest scoring cost paths were all located in the Central Lowlands. The connection between L2 and M9, as an extreme example, illustrates the potential difficulties for a dispersing lynx within the Central Lowlands. Skirting the edge of Glasgow, and continually having to avoid other settlements, the 38.9-km cost path unavoidably crossed a motorway three times, dual carriageway four times and the River Clyde, and in so doing accumulated a cost of 2762. Long distances between patches, as well as the proliferation of linear barriers, are typical of the Central Belt. However, a considerably less costly path exists across the Central Belt, between patches M17 and M6, and extends for 29.1 km. Despite this distance, and having to cross a motorway and a dual carriageway, the path cost is kept relatively low by being routed through woodland for much of its length, and so accumulates a path cost of 1027. M6 is connected to the southern patch network by several least cost paths, ranging in length from 20 to 23.8 km. The 20-km path to M19 accumulates the lowest path cost at 869, despite being routed across a motorway and the River Clyde.

On the whole, path costs were slightly higher for patches under scenario C than the connectivity analysis of the standard scenario, while scenario D had slightly lower path costs. Altering the size of buffer distances for large woodlands in the alternative scenarios meant a

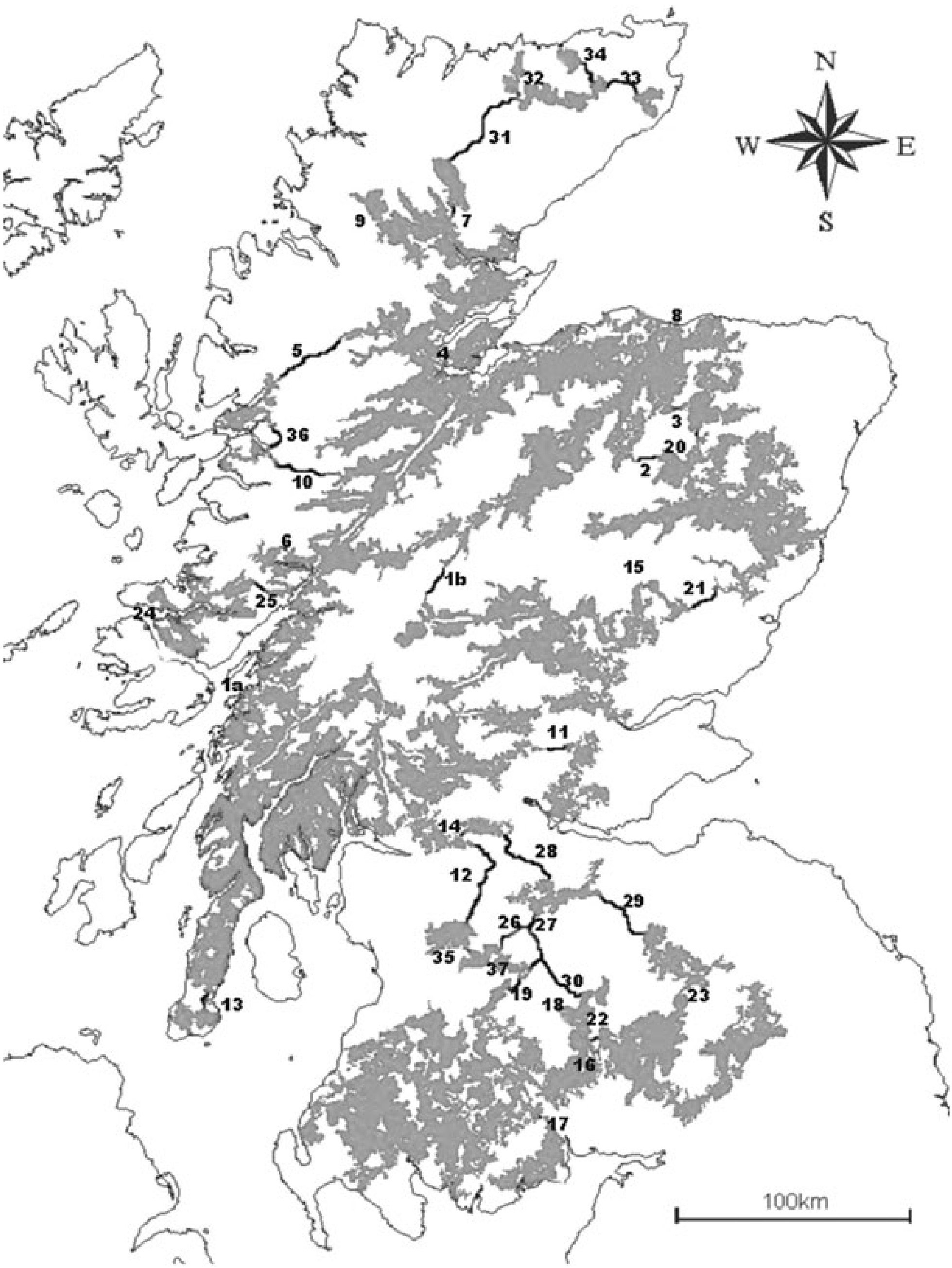

Fig. 3. Connectivity of potential lynx habitat patches in Scotland according to the standard scenario. Least cost paths are indicated with thick black lines and an identifying path number.

slight change in distances between habitat patches. Scenario C led to the fragmentation of larger patches into smaller patches, as well as the disappearance of two smaller patches. One section of patch L2 became a separate medium-sized patch. Scenario D, with an increased buffer distance, brought about the amalgamation of some patches that had been separate under the standard scenario, thus reducing fragmentation. In addition, a new small patch was formed between the main Highland network and the rather isolated northern patches. However, despite these local-scale variations in connectivity between scenarios, there were no major differences in patch connectivity at the population level between the standard scenario, and scenarios C and D.

DISCUSSION

Potential lynx habitat in Scotland

The distribution of patches and the corridors between them suggest that two main populations of lynx could exist in Scotland. The largest of these would occupy much of the Highlands, including coastal areas of the western Highlands, as well as some well-wooded areas in the northern parts of the Central Lowlands. There are approximately 15 000 km^2 of well-connected habitat available for lynx in this population.

The patches in the far north of Scotland (M7, S2, S4, S6), which amount to approximately 360 km^2, currently may be too isolated to be part of this habitat network. The connection between M7 and M13 accumulates a high cost of 1364, despite being routed predominantly through heath and woodland, mainly because of its considerable length. It does not seem likely that lynx would make the crossing between these two patches. However, scenario D, where woodland patches over 400 ha received a 600-m buffer, allowed the formation of a small habitat patch of 46 km^2 located approximately midway between M7 and M13. It is possible then, that continued reafforestation in that area could result in the creation of a habitat patch which acts as a ‘stepping stone’, and which would increase connectivity between the group of habitat patches in the far north of Scotland with the large amount of habitat centred around L1.

Given that reafforestation continues in Scotland, with several thousand hectares of new woodland created each year (Forestry Commission, 2002b), it is quite feasible for connectivity to improve in relatively treeless environments in the future, even within quite short time periods. For instance, the planting of new native woodlands totalling over 2700 ha in the area around Gairloch, in north-west Scotland, in the year following the formulation of the NIWT dataset in 2002, created a habitat patch of 82.3 km^2, which is large enough to sustain a male and a female lynx.

A second potential population could be supported south of the Central Belt, mainly in the Southern Uplands. This population could include neighbouring Kielder Forest in England. The total amount of habitat available to this population would be approximately 6140 km^2, with the Scottish share of this amounting to around 5330 km^2.

Connectivity between potential Highlands and Southern Uplands populations

The Central Belt area of Scotland is crucial for allowing movement of individuals between potential lynx populations occupying habitat networks in the Highlands and in the Southern Uplands. There is considerable distance separating patches M17 and M6, the least costly path through the Central Belt for a dispersing lynx. With increased afforestation targeted at this area of central Scotland, particularly on old industrial sites, it may be possible to reduce cost values of routes through this landscape. However, much of the cost path was routed through woodland already, and it is clear that, in addition to distance, linear barriers were the chief reason for the high cost. The cost path was unavoidably routed across a motorway and a dual carriageway, and in doing so, accumulated a score of an extra 200 points. Had there been no account required of these roads, the cost for this route would have been considerably reduced, and more comparable to successful lynx dispersal across the Swiss landscape.

Roads can disrupt the flow of animals across a landscape, and thus hinder recolonization by being a psychological barrier, as well as a significant source of mortality (Forman & Alexander, 1998; Clevenger, Chruszcz & Gunson, 2001). Indeed, road mortality represented the leading cause of recorded mortality within the reintroduced lynx populations in Switzerland (Schmidt-Posthaus *et al.*, 2002). However, a range of culverts, underpasses and overpasses, can be used by wildlife to successfully traverse busy transport routes, especially if wildlife-proof fencing along the edge of the transport route funnels wildlife into structures that experience little human disturbance (Rodriguez, Crema & Delibes, 1996; Mata *et al.*, 2003). Adapting existing crossing structures of motorways for wildlife has been recommended, as not only were they shown to be used by many mammal species, but it is also less financially costly than constructing a series of wildlife-specific crossings (Mata *et al.*, 2003).

There are two cost paths identified in this study (connections 26 and 28) which are essential for the connectivity of lynx habitat patches at the national scale, and which accumulated high path costs due mainly to the barrier effects of main roads. However, the enhancement of the wildlife permeability of the roads in question, learning from the experiences reported from areas elsewhere in Europe and North America, could considerably reduce the effects for lynx of habitat fragmentation and incidences of road deaths. Such measures could be beneficial for future recolonization by other species that have suffered considerable range contraction in Scotland due to human activities, such as wildcats *Felis silvestris*, polecats *Mustela putorius* and pine martens *Martes martes*. However, no assessment of the number of small-scale crossing structures has been undertaken as far as we know and thus their potential significance is not known.

While it is possible that a few individual lynx could cross the Central Belt using the corridors identified by the analysis presented, it is unlikely that sufficient numbers would successfully complete this route to allow full-scale colonization of suitable habitat in the Southern Uplands from the Highlands. It is possible that, by mitigating the barrier and sink effects of busy roads in Central Scotland, colonization of new areas may be facilitated. However, if a reintroduced population successfully takes root and expands considerably in areas such as the Highlands, after a while, it may be desirable to translocate a few individuals to the Southern Uplands in order to initiate the development of a new population. The subsequent migration of individuals between a Highlands lynx population and a Southern Uplands population, across the developed landscapes of the Central Belt, could be essential for the genetic health of both populations. If habitats on both sides of the Central Belt are occupied by lynx, the likelihood that individuals will disperse along corridors, and thus facilitate genetic exchange, may increase.

Potential size of a Scottish lynx population

The identification of a strong relationship between lynx density and the density of wild ungulate biomass from four areas across Europe allowed the prediction of potential lynx densities in Scotland based on deer density data from the Scottish Highlands and the Southern Uplands (Hetherington & Gorman, 2007). Applying the potential average lynx densities estimated by Hetherington & Gorman (2007) of 2.63 lynx 100/km^2 for the Highlands and 0.83 lynx 100/km^2 for the Southern Uplands to the amount of available habitat determined by the present study means that the Highlands habitat network could support around 400 lynx, while the Southern Uplands habitat network could support around 50. These figures suggest that Scotland could support a significant population of lynx, the fourth largest in Europe by current population estimates after the Nordic, Baltic and Carpathian populations. Thus, a potential Scottish lynx population could contribute significantly to the wider conservation of the species in Europe.

CONCLUSIONS

Over 20 000 km^2 of potential lynx habitat occurs across Scotland. Many of the costs for paths between habitat patches lie well within the range of costs recorded for migrating lynx in Switzerland, suggesting that it is feasible that reintroduced lynx in Scotland could travel across the landscape to find new territory and/or individuals with which to reproduce. Despite its long absence from Britain, caused mainly by the early and large-scale clearance of forest ecosystems, potentially suitable habitat for the Eurasian lynx is now, once more, both widespread and well connected throughout Scotland. The ongoing reinstatement of forest ecosystems in Scotland may also have created suitable conditions for other extirpated woodland mammal species, although greater consideration may need to be given to woodland type and structure for those species with more specific habitat requirements than the lynx. Further consideration of the ecological feasibility of reintroducing lynx to Scotland should determine if a minimum viable population of lynx could be supported by the available habitat and prey.

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APPENDIX 1

Potential habitat patches for lynx on mainland Scotland

Habitat patch	Patch area (km^2)	Forest area (km^2)	Forest cover (%)	Largest forest patch size (km^2)	Mean forest patch size (ha)	Number of forest patches
L1	5794.1	3005.4	51.9	373.5	109.5	2745
L2	5508.5	2932.7	53.2	344.8	104.4	2808
L3	3056.3	1747.0	57.2	845.2	106.8	1636
L4	1617.6	769.3	47.6	178.7	86.6	888
L5*	1162.8	704.4	60.6	207.5	135.7	519
M1	302.8	153.8	50.8	39.7	152.3	101
M2	302.4	150.7	49.8	63.7	93.6	161
M3	276.2	112.6	40.8	23.6	38.6	292
M4	261.8	123.6	47.2	32.2	66.8	185
M5	252.9	120.9	47.8	65.1	52.1	232
M6	199.1	93.5	47.0	59.5	46.3	202
M7	179.2	95.8	53.5	18.7	479.2	20
M8	178.6	84.6	47.4	60.4	76.2	111
M9	146.4	84.4	57.7	70.1	183.5	80
M10	141.2	67.8	48.0	44.0	90.3	75
M11	131.7	78.3	59.5	65.6	178.0	44
M12	129.7	58.1	44.8	22.3	88.1	66
M13	125.5	80.5	64.1	37.6	350.1	23
M14	114.9	72.2	62.8	52.8	451.0	16
M15	103.1	57.8	56.1	29.1	169.9	34
M16	86.8	36.1	41.6	14.9	56.5	64
M17	85.0	43.6	51.3	28.4	117.9	37
M18	77.8	43.3	55.7	10.9	206.1	21
M19	77.2	44.4	57.5	28.7	341.9	13
S1	69.2	29.6	42.8	12.3	61.6	48
S2	64.2	33.2	51.7	18.1	474.2	7
S3	63.3	25.5	40.3	7.5	50.9	50
S4	62.9	35.1	55.8	33.8	1170.9	3
S5	55.6	28.2	50.7	20.4	117.6	24
S6	51.5	32.3	62.7	29.9	293.3	11

Patch names are decided on the basis of decreasing size. Refer to Fig. 2 for locations. *Patch L5 is contiguous with large woodland areas situated across the English border. See text for details.

APPENDIX 2

Least cost paths identified between habitat patches

No.	Link	Cost	Length (km)	Cost/km	Significant barriers
1a	L1-L2	197	1.2	164.2	Trunk road, & along bridge
1b	L1-L2	429	11.6	37.0	None
2	L1-L4	357	6.7	53.3	None
3	L1-M2	98	1.3	75.4	None
4	L1-M8	120	0.4	300.0	None
5	L1-M10	613	27.6	22.2	None
6	L1-M12	43	0.7	61.4	None
7	L1-M13	165	3.0	55.0	None
8	L1-M16	20	<0.1	–	None
9	L1-M18	14	0.2	70.0	None
10	L1-S1	741	20.7	35.8	Trunk road
11	L2-M3	524	7.9	66.3	None
12	L2-M9	2762	38.9	71.0	1 river, 3 m/ways, 4 d c/ways
13	L2-M15	482	7.4	65.1	None
14	L2-M17	109	1.0	109.0	None
15	L2-S3	5	<0.1	–	None
16	L3-L5	120	<0.1	–	1 motorway
17	L3-M5	64	0.9	71.1	None
18	L3-M14	120	<0.1	–	1 motorway
19	L3-S5	184	6.7	27.5	None
20	L4-M2	149	2.5	59.6	None
21	L4-S3	379	12.5	30.3	None
22	L5-M14	107	2.5	42.8	None
23	L5-M4	20	<0.1	–	None
24	M1-M11	22	0.1	220.0	None
25	M1-M12	253	5.0	50.6	None
26	M6-M19	869	20.0	43.4	1 river, 1 motorway
27	M6-S5	871	22.3	39.1	1 motorway
28	M6-M17	1027	29.1	35.3	1 motorway, 1 d c/way
29	M6-M4	1046	23.8	43.9	1 trunk road
30	M6-M14	1242	38.6	32.2	1 trunk road
31	M7-M13	1364	36.6	37.3	None
32	M7-S2	105	1.0	105.0	None
33	M7-S4	659	14.8	44.5	1 trunk road
34	M7-S6	275	9.4	29.3	None
35	M9-M19	110	1.1	100.0	None
36	M10-S1	436	9.8	44.5	None
37	M19-S5	24	0.2	120.0	None