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Ovenden, Thomas; Palmer, Stephen; Travis, Justin; Healey, John

Biological Conservation

DOI:
10.1016/j.biocon.2019.03.035

Published: 01/06/2019

Peer reviewed version

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Ovenden, T., Palmer, S., Travis, J., & Healey, J. (2019). Improving reintroduction success in large carnivores through individual-based modelling: how to reintroduce Eurasian lynx (*Lynx lynx*) to Scotland. *Biological Conservation*, *234*, 140-153. https://doi.org/10.1016/j.biocon.2019.03.035

Improving reintroduction success in large carnivores through individual-based modelling: how to reintroduce Eurasian lynx (*Lynx lynx*) to Scotland

Thomas S Ovenden[1], Stephen C F Palmer[2], Justin M J Travis[2], John R Healey[1]

[1] School of Environment, Natural Resources and Geography, Bangor University, Bangor, Gwynedd, LL57
2UW, UK

[2] School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK

*Correspondence: thomas.ovenden@stir.ac.uk, Telephone: +44 7874 244656, Address: Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK

Abstract

Globally, large carnivores have been heavily affected by habitat loss, fragmentation and persecution, sometimes resulting in local extinctions. With increasing recognition of top-down trophic cascades and complex predator-prey dynamics, reintroductions are of growing interest for restoration of ecosystem functioning. Many reintroductions have however failed, in part due to poor planning and inability to model complex eco-evolutionary processes to give reliable predictions. Using the case study of Eurasian lynx (*Lynx lynx*), a large predator being considered for reintroduction to Scotland, we demonstrate how an individual-based model that integrates demography with three distinct phases of dispersal (emigration, transfer and settlement) can be used to explore the relative suitability of three geographically-distant potential reintroduction sites, multi-site reintroductions and two founding population sizes. For a single-site reintroduction of 10 lynx, our simulation results show a clear hierarchy of suitability across all metrics. Reintroduction in the Kintyre Peninsula (west coast) consistently performed best, with a probability of population persistence at year 100 of 83%, and the Scottish component of Kielder Forest (southern Scotland) worst, with only a 21% chance of population persistence to year 100. Simultaneous two-site reintroduction in the Kintyre Peninsula and in Aberdeenshire (near the east coast) of 32 lynx gave a 96% persistence at 100 years. Our model was highly sensitive to survival, particularly of adults, highlighting this parameter's importance for reintroduction success. The results strongly indicate the potential viability of Eurasian lynx reintroduction to Scotland given the current cover of suitable woodland habitat. More generally, our work demonstrates how emerging modelling approaches incorporating increased realism in representing species' demography, ecology and dispersal can have high value for quick, inexpensive assessment of likely reintroduction success and for selection between alternative strategies.

Keywords: Individual based model – Reintroduction – Dispersal – Large carnivores – Eurasian lynx

Abbreviations

Individual Based Model: IBM
Least Cost Path: LCP
Stochastic Movement Simulator: SMS

Research highlights

- IBM approaches that integrate stochastic movement trajectories with population dynamics modelling across heterogeneous landscapes provide greater realism in reintroduction modelling.
- This modelling approach enables the quick and effective assessment of alternative reintroduction proposals and management scenarios.
- The contribution of this modelling approach could significantly improve the probability of reintroduction successes, especially of large carnivores.
- This case study demonstrates the suitability of existing habitat in Scotland for the reintroduction of Eurasian lynx but that appropriate site selection is key to success.

1. Introduction

Globally, many large carnivores have experienced drastic population declines linked to habitat loss, persecution and decreases in prey abundance (Ceballos et al., 2017; Ceballos and Ehrlich, 2002; Di Minin et al., 2016). Many continue to face the ever present threat of extinction (Weber and Rabinowitz, 1996) or have already been extirpated from their native ranges (Hayward and Somers, 2009). Interest in the role that apex predators play in trophic cascades and the regulation of ecosystem structure and function has grown in recent years (Estes *et al.*, 2011; Ordiz *et al.*, 2013). These interactions are however complex, unresolved and far from uniformly observed, one recent review highlighting that such cascades have only been documented in 7 out of 31 of the world's largest mammalian carnivores (Ripple et al., 2014). Some authors caution against the broad applicability of trophic cascades based on insufficient evidence (Allen et al., 2017). This lack of uniformly applicable evidence, coupled with the context-dependency of any reintroduction (Kuijper et al., 2016), means this motivation should not form the sole justification of any reintroduction argument. Nonetheless, there is a growing interest in how the reintroduction of top-order predators can be applied to ecosystem restoration (Ritchie et al., 2012; Wolf and Ripple, 2018), reinforced by generally positive and supportive public opinion and protective legislation (Huber et al., 2014) linked to a variety of socioeconomic drivers.

Modelling plays a key role in informing reintroduction decision making (Seddon et al., 2007). The International Union for Conservation of Nature specifies that modelling should be used in scenario exploration to devise an optimal strategy, accounting for intraspecific variation and dispersal as well as highlighting the fundamental importance of matching habitat suitability and availability to the target species (IUCN/SSC, 2013). The spatial and metabolic requirements of large predators, coupled with their prey selection and hunting tactics, often result in human-wildlife conflict, especially through the depredation of livestock (Ripple et al., 2014). The socio-ecological context, specifically human attitudes, is therefore fundamentally important to the success of large carnivore reintroductions, and its importance cannot be underestimated (Linnell et al., 2009). It is equally necessary to establish and model the long-term suitability of any reintroduction landscape, for neither of these considerations is sufficient in isolation to justify and proceed with a reintroduction. Habitat suitability modelling can be used as one of a suite of tools, contributing much needed information into the broader, more complex decisions made by policy makers and conservation practitioners of whether to proceed, a decision that is arguably outside the capabilities and remit of a single model.

Spatially explicit models have been specifically advocated for the advantages they confer in being able to cope with the complex interacting dynamics of species-specific behaviours in spatially heterogeneous landscapes (DeAngelis and Yurek, 2016). Historically, least-cost path (LCP) modelling has been a popular tool with ecologists and researchers to aid understanding of connectivity between populations (Schadt et al., 2002) and particularly to identify migration and dispersal corridors (Larue and Nielsen, 2007; Li et al., 2010). Partly, this has been due to its implementation simplicity and accessibility (available in GIS software), and the increasing availability of high-resolution habitat data (Adriaensen et al., 2003). In essence, this approach highlights, using a cost grid, the “optimum route” for a species to cross a heterogeneous landscape matrix through the accumulated costs associated with the intervening habitat separating two suitable patches (Adriaensen et al., 2003). This has led to LCP modelling being widely utilised to inform reintroduction strategies (Ziółkowska et al., 2012), especially for large carnivores (Hebblewhite et al., 2011; Paquet et al., 2001; Schadt et al., 2002). However, Zeller *et al.*, (2012) caution against over-reliance on expert opinion in models, and highlight the importance of distinguishing between movement behaviour and resource use; such data on a species’ ecology are not always readily available for a proposed location or in a context relevant to a planned reintroduction

Least cost path modelling suffers from several inherent limitations, summarized by a few key assumptions made in all LCP models: the implied omniscience of individuals, a lack of stochasticity within a population, and an assumption that movement always occurs in the direction of ‘least resistance’ (Coulon et al., 2015). In contrast, stochastic individual-based models (IBM) can relax the key assumptions implicit in LCP modelling by incorporating step-by-step movement decisions that are made based upon information available within an organism’s perceptual range. The stochastic movement simulator (SMS; Palmer et al. 2011) provides such a model, and it has been demonstrated to outperform LCP and circuit theory approaches when tested against spatial genetic data (Coulon et al., 2015). One limitation of IBMs, however, is that they typically require more information to enable rigorous parameterization (Kool et al., 2013), restricting their utility to species for which a significant amount of demographic and dispersal knowledge exists. Notably, SMS has been developed to require very few additional parameters than those already required for LCP, making its application more straightforward than other potential movement models.

Dispersal is a complex, multi-phase process, which influences population dynamics, distribution, abundance and ultimately persistence (Zimmermann et al., 2005). Commonly, dispersal is now regarded as comprising three distinct phases: emigration, transfer and settlement (Mathysen, 2012). Models such as LCP or SMS represent the transfer phase, and it is vital that the other two phases are also well represented. Importantly, the costs associated with each of these stages are both context-dependent and pose unique challenges that vary between individuals, sexes and life stages (Delgado et al., 2010), as well as across space and time (Samelius et al., 2012). Dispersal is an ecological cornerstone of range expansion dynamics (Bocedi *et al.*, 2014b), meaning that the failure to represent this process accurately, as it is empirically understood to operate, could have considerable implications for the efficacy of reintroduction planning. It is therefore essential to incorporate dispersal as a multi-phase process when attempting to model how individuals will use a landscape, to identify how well-connected functionally suitable habitat patches are, to model likely patterns of range expansion and to predict accurately the probability of population persistence following release. In one recent example, an IBM approach was used to compare the relative success of alternative strategies for introducing the specialist grassland butterfly, *Maniola jurtina*, ahead of its current range in Finland (Heikkinen et al., 2015). While this study did incorporate some dispersal complexity by including density-dependent emigration, for the transfer phase dispersal was modelled phenomenologically, using a double-negative-exponential dispersal kernel, and thus the exercise did not incorporate sensitivities of movement to landscape characteristics. For reintroductions into heterogeneous landscapes, incorporating greater realism into movement behaviour will likely be key to gaining fuller understanding of the possible success of alternative management options.

Reintroductions, especially those of carnivores, are often complex and costly, making efficiencies in planning highly attractive (Kramer-Schadt et al., 2005). As such, advances in modelling can be disproportionately valuable compared with the cost of repeated reintroduction failures. Examples of ecological restoration success stories following predator reintroductions (Beschta and Ripple, 2009; Wilmers et al., 2012) coupled with the rise in popularity of the rewilding movement (Navarro and Henrique, 2015) have seen the potential reintroduction of the Eurasian lynx (*Lynx lynx*) become a focal point of recent discourse in the UK (Hetherington et al., 2008; Milner and Irvine, 2015; Wilson, 2004). Indeed, a LCP analysis conducted by Hetherington et al. (2008), which identified two distinct habitat networks, one in the Highlands and one in the Southern Uplands (**Fig. 1**), is currently being used as the foundation upon which proposals for lynx reintroduction in Scotland are being based (Smith et al., 2015; White et al., 2016). There have, however, been significant advances in modelling approaches since that study was conducted.

Since 1971, 15 reintroductions across eight European countries have involved over 170 Eurasian lynx individuals, but only five of these attempts are considered to be successful (Linnell et al., 2009). As a result, important lessons have been learnt, and a significant body of knowledge about the species' ecology, demography (Breitenmoser-Würsten *et al.*, 2007; Bagrade *et al.*, 2016; Jędrzejewski *et al.*, 1996), dispersal behaviour (Samelius et al., 2012; Schmidt, 1998; Zimmermann et al., 2005), habitat requirements and use (Belotti et al., 2013; Filla et al., 2017; Podgórski et al., 2008; Rozylowicz et al., 2010; Zimmermann et al., 2007b) has been amassed. However, there is a particular need for tools that enable the synthesis of this knowledge and incorporate recent progress in dispersal ecology theory, in order to provide more reliable assessments of landscape suitability and inter-patch connectivity, and to increase the probability of future reintroduction successes.

We use the potential reintroduction of the Eurasian lynx to Scotland as a case study to explore how an IBM that explicitly accounts for spatial heterogeneity, individual stochasticity and, crucially, dispersal in its three distinct phases can inform reintroduction decision making. Specifically, we aim to use this model to address the following key questions:

a) How does reintroduction from three alternative proposed reintroduction sites compare and what is the likelihood of long-term population persistence for each?
b) Are there distinct habitat networks and/or key areas of the landscape through which dispersal is inhibited, preventing the colonisation of apparently suitable habitat?
c) How does a multi-site reintroduction and differences in the founding population affect the probability of population persistence over time?

2. Material and methods

2.1 Modelling Software

We used a recently developed, spatially explicit, stochastic IBM, RangeShifter (Bocedi *et al.*, 2014a), to model the reintroduction of lynx in Scotland. RangeShifter is a freely available software package that combines demographic models with the explicit modelling of the three distinct phases of dispersal (emigration, transfer and settlement) (Travis et al., 2012), and provides the mechanistic stochastic movement simulator (SMS) (Palmer et al., 2011) to model the transfer phase through a heterogeneous landscape represented as a cost grid akin to the LCP approach.

2.2 Landscape

We implemented a patch-based model, in which local groups of suitable breeding habitat cells are aggregated into larger patches for the purpose of demographic modelling, whereas dispersal is modelled at the scale of individual cells (Bocedi *et al.*, 2014a). Land Cover Map 2007 (Morton et al., 2011) was used to derive a habitat classification grid across mainland Scotland at a cell size of 100 m x 100 m. The broad habitat classes were amalgamated into distinct habitat classes that were deemed to be different in their effect on lynx behaviour and outcomes as indicated by the preference lynx show for different habitats (permeability) and the resulting mortality risk, based on those used by Hetherington *et al.* (2008). Each 100 m x 100 m cell is represented by the dominant habitat class that occupied the greatest proportion of that cell.

While Eurasian lynx are known to occasionally use other habitats (Filla et al., 2017), they are predominantly a forest-dwelling species (Belotti et al., 2013; Breitenmoser-Würsten et al., 2001; Podgórski et al., 2008) (hereafter the term “woodland” will be used, as a synonym of forest, to reflect the terminology more commonly used in UK). In addition to breeding, this preferential selection of woodland habitat has been shown to be important for all stages of lynx dispersal, woodland distribution heavily influencing its direction and distance (Schmidt, 1998). We therefore updated the distribution of woodland cells with more recent estimates of woodland extent from the National Forest Inventory (2015) dataset, from which two woodland habitat categories were derived. ‘High Quality Woodland’ (**Table 1**) included all polygons categorised into the seven classes of assumed woodland, broadleaf, conifer, coppice, coppice with standards, mixed mainly broadleaf or mixed mainly conifer; ’Low Quality Woodland’ (**Table 1**) included all polygons categorised into the eight classes of cloud/shadow, failed, felled, ground preparation, low density, uncertain, windthrow or young trees woodland. Areas classified as cloud/shadow are small and infrequent, covering only 37 ha across all of Scotland. These are known woodland areas, but where an alternative woodland type was difficult to allocate due to insufficient detail. As such, these areas were conservatively allocated to the ‘Low Quality Woodland’ category. This distinction between ’high’ and ’low’ quality woodland was to enable differentiation between the ease of movement through taller mature forest and younger, dense or regenerating forest, reflected by the different cost values in **Table 1**. Large, busy roads are known to present barriers to lynx dispersal and movement (Zimmermann et al., 2007a) as well as posing a higher risk of mortality than other habitats (Andren et al., 2006; Schmidt-Posthaus et al., 2002). As such, all current dual carriageways and motorways in Scotland, along with the A9 and A96 roads that are currently undergoing or planned for conversion to dual carriageways, were incorporated as a further landscape class (Ordnance Survey, 2017) and were given priority allocation in the cost grid, represented by an unbroken line of adjacent 100 m cells. Relative habitat cost values (inversely related to permeability) and per-step mortality probabilities were then derived or inferred from the relevant literature (Hetherington *et al.*, 2008; Podgórski *et al.*, 2008; Schmidt, 1998; Zimmermann, 2004; Kramer-Schadt *et al.*, 2004) and applied to corresponding habitats (**Table 1**).

2.3 Habitat Patches

Lynx are primarily solitary animals, females and males predominantly coming together to mate, and their home ranges are characterised by a high degree of intrasexual territoriality (Mattisson et al., 2013). This is especially true in females, with one study showing < 10% overlap between neighbouring adult female ranges (Schmidt et al., 1997). Female home ranges appear to be dictated more by prey availability, whilst male home ranges are governed more by the presence of females (Schmidt et al., 1997). Home ranges have been shown to vary greatly across different regions, but commonly smaller home territories are observed in areas of high prey density (Breitenmoser-Würsten et al., 2001; Herfindal et al., 2005; Sunde et al., 2000b). Hetherington & Gorman (2007) used this relationship, in conjunction with data on the occurrence of four deer species (*Cervus elaphus, Capreolus capreolus, Cervus nippon* and *Dama dama*), to forecast the potential population density of lynx in the Southern Uplands of Scotland (0.83/100 km^2) and the Scottish Highlands (2.63/100 km^2). The latter estimate was adopted for use in this study as, in the absence of top-down predator-prey regulation, deer numbers have continued to increase during the last decade and are predicted to continue to rise across the UK (Palmer, 2014). In order to identify the location and extent of all habitat patches of sufficient size to support at least one female lynx home range, the criteria and thresholds previously used by Hetherington *et al.* (2008) for lynx in Scotland were applied to the 2015 National Forest Inventory dataset (Forestry Commission, 2016).

One limitation of RangeShifter is that during the reproduction phase, juveniles are assigned an initial location within the same patch but not necessarily the same cell as the mother. This issue can potentially result in a juvenile commencing dispersal from the opposite end of the natal patch to the mother's nominal location, giving a potentially false impression of dispersal, but this is only of substantial concern when habitat patches are large in extent or very elongated. To circumvent this issue, such patches were further subdivided to ensure no single habitat patch was greater in extent than 700 km^2. This ultimately resulted in a total of 53 habitat patches considered suitable for female lynx home ranges across mainland Scotland (**Fig. 1**).

2.4 Demography and Dispersal Parameters

We specified a demographic model comprising three stages: juveniles (0 - 12 months), non-breeding sub-adults (12 - 24 months) and breeding adults (> 24 months). The timing of sexual maturation in males can be variable (Kvam, 1991) so the sensitivity of our model to a delayed sexual maturity of males to three years was also tested. Survival rate is highly variable across the literature and regions of Europe for all three life stages (Andren *et al.*, 1997; Breitenmoser-Würsten *et al.*, 2001; Breitenmoser-Würsten *et al.*, 2007; Jędrzejewski *et al.*, 1996), and will likely be influenced by factors independent of habitat. As no data for Scotland yet exist, and considering this variability, survival values considered broadly representative of each life stage were used to reflect the observed general increase in survival probability with age in lynx, and were informed by the pessimistic and intermediate survival rates used by Hetherington (2005) in his minimum viable population analysis of lynx for Scotland (**Table 2**).

Whilst lynx are generally considered to be poor dispersers (Zimmermann et al., 2005, 2007a), modelling their dispersal is complicated owing to, amongst other things, a lack of studies identifying the relative emigration probabilities of the sexes. One study found little evidence of a significant sex bias in dispersing lynx, but highlighted the relative tendency of females to establish home ranges proximate to their natal patch or even to take over maternal home ranges (Zimmermann et al., 2005), whereas another found that 100% of males dispersed but 35% of females remained philopatric (Samelius et al., 2012). However, population spread is considered to be dependent on the more generally conservative dispersal patterns of females (Molinari-Jobin et al., 2017). To reflect this, the absences of context-specific dispersal data for lynx in Scotland and the inability of sub-adult lynx to disperse readily across anthropogenic landscapes (Zimmermann, 2004), we chose to model female maximum emigration probability conservatively and as being substantially lower than that of males, and as density-dependent for both sexes (**Table 2**).

2.5 Modelling reintroduction

2.5.1 Site Selection

The three locations recently shortlisted for potential lynx reintroduction in Scotland (White et al., 2016) were selected as model scenarios in the present study. The first is located in the south at Kielder Forest, the second near the east coast in Aberdeenshire and the third near the west coast on the Kintyre Peninsula (**Fig. 1.**, patches 39, 45 and 46 respectively). The chosen patches were thus located in widely-separated regions of Scotland. For the purposes of this study, the political boundary of Scotland was treated as a 'hard border', preventing individuals from crossing into England. This boundary condition meant that individuals that reached this political border were retained within the population, being 'reflected' back into mainland Scotland.

2.5.2 Single-site reintroduction

As almost all successful lynx reintroductions elsewhere involved 10 or more individuals (Linnell et al., 2009), a founding population of 10 lynx was adopted for the modelling of single-site reintroductions. Each founding lynx individual and its subsequent progeny had an equal probability of being male or female. Each reintroduction was modelled for 100 replicates of 100 years to reflect timescales previously used for modelling lynx (Wilson, 2004). Knowing the variability in lynx home range size documented elsewhere in Europe, we also carried out a supplementary analysis in which we amalgamated where possible smaller patches with neighbouring larger patches to test the sensitivity of model predictions to patch size.

2.5.3 Multi-site reintroduction

Some authors have suggested that multi-site lynx reintroductions may represent a better strategy for reintroduction success or recovery programmes in fragmented landscapes (Zimmermann et al., 2007a). Equally, others have suggested that 10 lynx may be too small a founding population for Scotland, and have advocated that 32 would present a more realistic chance of success (Hetherington, 2005). To assess the relative effect of these two variables, we also modelled reintroductions at the same prospective locations in Aberdeenshire and the Kintyre Peninsula, both independently with a founding population of 32 lynx in each and with 18 lynx released in the Kintyre Peninsula and 14 released in Aberdeenshire (released simultaneously). The relative number released in each location in the latter case was proportional to the relative size of the habitat patch area (533 km^2 and 395 km^2 respectively).

2.6 Analysis

2.6.1 Metrics of success

Four main metrics of reintroduction success were derived from the output files generated by RangeShifter: a) the number of replicates that reached year 100; b) the mean number of habitat patches occupied at year 100 for replicates that reached year 100; c) the mean number of individuals at year 100 for those replicates that reached year 100; d) the extinction probability over time. Differences between reintroduction sites were compared by ANOVA.

2.6.2 Sensitivity Analysis

Survival probability was selected for sensitivity analysis owing to its variability amongst previous studies for all three lynx life stages and the prior identification of its importance in model sensitivity testing in other IBM studies of Eurasian lynx (Kramer-Schadt et al., 2005). Equally, uncertainty regarding the maximum emigration probability of the sexes through a lack of empirical data, coupled with its probable importance to population expansion, led us also to select this variable for sensitivity testing. The tested values of these two variables were chosen to differ from the selected values by +/- 5% to test the model's sensitivity to minor perturbations. Each scenario was averaged over 100 model runs for 100 years. In line with other assessments of model sensitivity to survival probability in lynx (Kramer-Schadt et al., 2005), the model was deemed to be sensitive should a deviation of $\geq$ 20% from those obtained with the standard values be realised for any of the calculated model outputs.

Table 1 - *Habitat classes and their associated cost and mortality values for a stochastic movement simulator model with habitat-dependant per-step mortality. Cost values were derived from Hetherington et al. (2008) while per-step mortality values and rank order were inferred from relevant literature (*Hetherington *et al.*, 2008; Podgórski *et al.*, 2008; Schmidt, 1998; Zimmermann, 2004; Kramer-Schadt *et al.*, 2004*).*

Habitat Number	Habitat Name	Cost value	Per-step mortality probability
1	Salt Water	100000	0.9999
2	Arable & Horticulture	30	0.0002
3	All Freshwater (incl. lochs, rivers, etc.)	100	0.0005
4	Built up Areas & Gardens	1000	0.007
5	Inland Rock	1000	0.00001
6	Previously Woodland	7	0.000001
7	Montane Habitats	10	0.00001
8	Grassland	10	0.00001
9	High Quality Woodland	1	0
10	Low Quality Woodland	2	0
11	Supra/Littoral Sediment & Rock	10	0.00001
12	Bog, Marsh, Fen Swamp	10	0.00001
13	Dwarf, Shrub, Heath	7	0.00001
14	Motorways & Dual Carriageways	120	0.07

Table 2 - *Parameter values and settings applied in the RangeShifter stage-structured simple sexual model with overlapping generations.*
(a) Breitenmoser-Würsten *et al*. (2007), (b) Andren *et al.* (1997), (c) Breitenmoser-Würsten *et al.* (2001), (d) Jędrzejewsjki *et al.* (1996) (e) Vandel *et al.* (2006), (f) von Arx *et al.* (2004), (g) Gaillard *et al.* (2014), (h) Schmidt *et al.* (1997), (i) Zimmermann *et al.* (2005), (j) White *et al.* (2015), (k) Hetherington & Gorman (2007), (l) Samelius *et al.* (2012), (m) Vandel *et al.* (2006), (n) Schmidt (1998), Supplementary material: (o) Fig. S1, (p) Fig. S2, (q) Fig. S3, (r) SMS parameters.

Demographic Parameter	**Value**
Number of life stages (a)	3
- Juvenile (kitten) survival probability (a, b, c, d, m)	53%
- Sub-adult survival probability (a, b, c, d, m)	63%
- Adult survival probability (a, b, c, d, m)	80%
Maximum age (years) (f)	17
Maximum fecundity at low density (f)	5
Mean fecundity at equilibrium density / year (a, c, g)	2
Number of reproductive seasons / year (h, i)	1
Probability of being male in founding population and at birth (c, d)	50%
Probability of reproducing annually (a, j)	100%
Number of years after reproduction before subsequent reproduction (n)	0
Habitat-specific strength of density dependence in fecundity (*1/b*) (individuals / ha):	
High Quality Woodland and Low Quality Woodland (k, o)	0.000285
All other habitats	0
Emigration Parameters (p)	**Value**
Juvenile female maximum emigration probability (i, l)	0.4
Juvenile male maximum emigration probability (i, l)	0.9
Sub-adult maximum emigration probability (male & female) (a)	0
Adult maximum emigration probability (male & female) (a)	0
Alpha (slope of density-dependent function)	10
Beta (relative inflection point of density-dependent function)	1
Stochastic Movement Simulator Settings (r)	**Value**
Perceptual range	500 m
Perceptual range method	2
Directional persistence	5.0
Memory size (steps)	5
Goal type	0
Settlement Parameters (q)	**Value**
Female	Find a suitable patch + density dependence
Male	Find a suitable patch + density dependence + mating requirements
Maximum settlement probability (male & female)	1.0
AlphaS (slope of density-dependent function)	-10
BetaS (relative inflection point of density-dependent function)	1
Maximum number of steps	5000

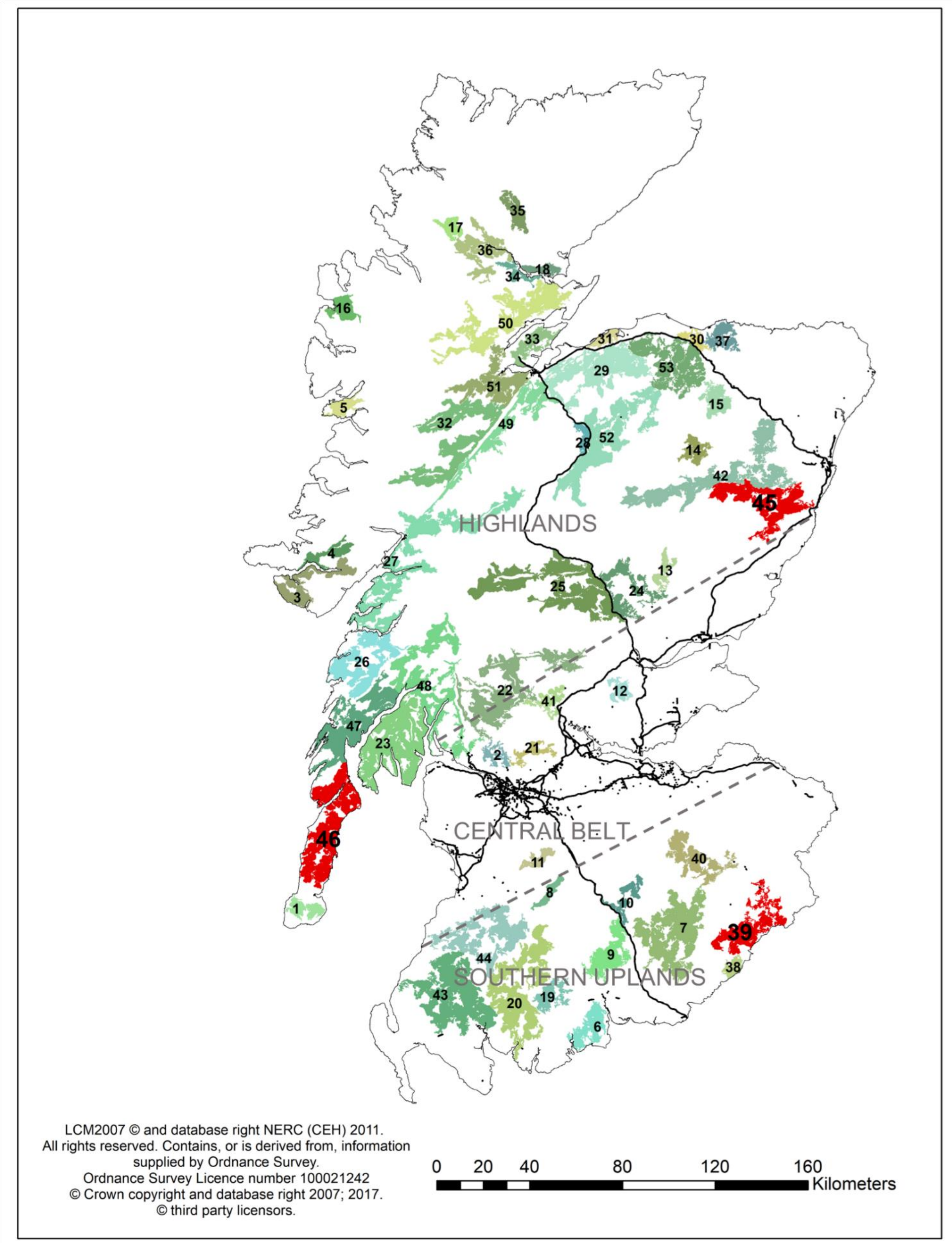

Fig. 1. - *The distribution of suitable habitat patches in mainland Scotland derived from the National Forest Inventory 2015 data* (Forestry Commission, 2016) *are shown in various shades of green and blue to distinguish adjacent patches. The three potential reintroduction sites tested in the present study are shown in red and with larger font text (Kielder Forest - 39, Aberdeenshire - 45 and Kintyre Peninsula - 46). All motorways and dual carriageways in Scotland, including those currently undergoing or planned for conversion to dual carriageways, are shown in black. Three geographical regions are shown in grey separated by dashed lines.*

3. Results

3.1 Single Site Reintroduction

A population reintroduced on the Kintyre Peninsula was predicted to survive for 100 years in 83% of replicates, much higher than those in either Aberdeenshire (35%) or Kielder Forest (21%). Similarly, the mean number of patches occupied at year 100 differed between sites and was highest for the Kintyre Peninsula and lowest for Kielder Forest, as was the final population size (**Table 3**). A complete breakdown by habitat patch for each metric and each reintroduction site averaged across all 100 replicates is presented in **Table S1**. A large increase in the probability of population extinction occurs between 10- and 30-years post-release, after which it tended to stabilise in all three sites (**Fig. 2**). The increase was much less for reintroduction in the Kintyre Peninsula than in the other two sites. Subsequent analysis of the first 30 years post release shows that for one of the three release sites, Kintyre, this is linked to both the number of females in the initial population and low birth rate in the first year (**Fig. S5**). For all three sites, this increase in extinction probability is associated with lower rates of patch colonisation (**Fig. S6**). On average there was a decline in the number of individuals in the reintroduction patch across all sites (**Fig. S7**). However, in surviving replicates the decline was arrested after 5-10 years, whereas in extinct replicates this arrest was much less apparent (**Fig. S7**). This same figure shows that in surviving replicates, the equilibrium population size was less than the 10 released individuals for all release sites, and was on average below 6 for Aberdeenshire and Kielder.

Hetherington *et al.* (2008) suggested there were two geographically distinct habitat networks for lynx in Scotland, one in the Southern Uplands and one in the Highlands (**Fig. 1**). Reintroduction in the Kintyre Peninsula only ever resulted in lynx reaching the Southern Uplands in 12% of replicates, with only 3 of the 13 Southern Uplands woodland habitat patches being reached (**Fig. 3**). Across all replicates, reintroduction in Aberdeenshire never resulted in any patch being colonised in the Southern Uplands (**Fig. 3**). With reintroduction in Kielder Forest, only a single patch was ever reached in the Highlands habitat network (**Fig. 3.**) and then only in 9% of replicates. While this single patch was capable of being reached, its mean occupancy probability, averaged over 100 years and 100 replicates was still <1% (**Fig. S4**). Equally, no lynx was found to be alive in the Highlands habitat network in year 100 in any of the 100 model replicates following reintroduction in Kielder Forest (**Fig. 4**).

The rank order between sites was maintained following the amalgamation of smaller patches into neighbouring larger ones, the model proving to be robust to minimum patch size (**Table S2**). Similarly, while an expected reduction across all three metrics was realised following a delay in the sexual maturation of males to 3 years, the same rank order for the three sites was again maintained (**Table S3**).

Ten additional simulations from each site for which individual-level output was generated were also conducted to establish mean dispersal distance for both successful and unsuccessful dispersers, both male and female (**Fig. S8**). There was very little difference between the sexes in mean dispersal distance, and unsuccessful dispersers showed a greater mean dispersal distance than successful dispersers. Dispersal distance was greatest for both successful and unsuccessful dispersers from the Kintyre release site compared with the other two sites.

As there are no direct data available for lynx in Scotland, alternative values for several demographic parameters observed in Europe were also tested. When running the model with alternative values for maximum age, maximum litter size and annual female reproduction probability, the rank order of site suitability was unaltered (**Table S4**).

3.2 Founding Population Size and Multi-Site Reintroduction

When comparing the likelihood of population persistence after release of 32 individuals between two release sites, Aberdeenshire notably underperformed compared with the Kintyre Peninsula. The multi-site reintroduction of 18 lynx released in the Kintyre Peninsula and 14 released in Aberdeenshire gave marginally the greatest chance of population persistence after 100 years (**Table 3**). However, the difference between this two-site reintroduction and the modelled reintroduction of the same number of lynx solely in the Kintyre Peninsula was not significant for the number of patches occupied, nor the number of individuals in the population at year 100 (ANOVA: $F_{1,187} < 1.22$, $P > 0.271$ in both cases).

Interestingly, the reintroduction of 32 lynx in the Kintyre Peninsula gave a 10% greater population persistence probability over 100 years than that of a release of only 10 lynx in the same location. Otherwise, this increase in the founding population size had little effect on patch occupancy or population size. Equally, releasing 32 lynx in Aberdeenshire still appeared to perform worse across all metrics than a 10-lynx release in the Kintyre Peninsula.

3.3 Sensitivity Analysis

3.3.1 Survival Probability

The model was sensitive to a 5% decrease in adult survival for every response metric and sensitive to an increase of adult survival for the number of occupied patches and the mean number of individuals in the population at year 100. Similarly, the model was sensitive to a decrease in sub-adult survival of 5% for all metrics, but not to an increase of 5%. The only metrics that appeared to be sensitive to changes in juvenile survival were the number of patches occupied and the mean number of individuals at year 100, both of which were sensitive to a reduction of 5% in juvenile survival (**Table 4**).

3.3.2 Emigration Probability

Across all three outputs the model was not sensitive to ± 5% modifications to either male or female maximum emigration probability (**Table 4**). However, there was a disproportionate reduction in population persistence when maximum emigration probability of females was reduced, as too few young females were emigrating to found new populations. Equally, when the emigration probability of males was increased, a similar disproportionate effect occurred, this time likely to be due to there being too few philopatric males to maintain existing populations if the adult male(s) died. It has been suggested that lynx may display negative density-dependent dispersal behaviour (Zimmermann et al., 2007a), but we found that our model showed little sensitivity to whether emigration was modelled as density-dependent or -independent (**Table S5**).

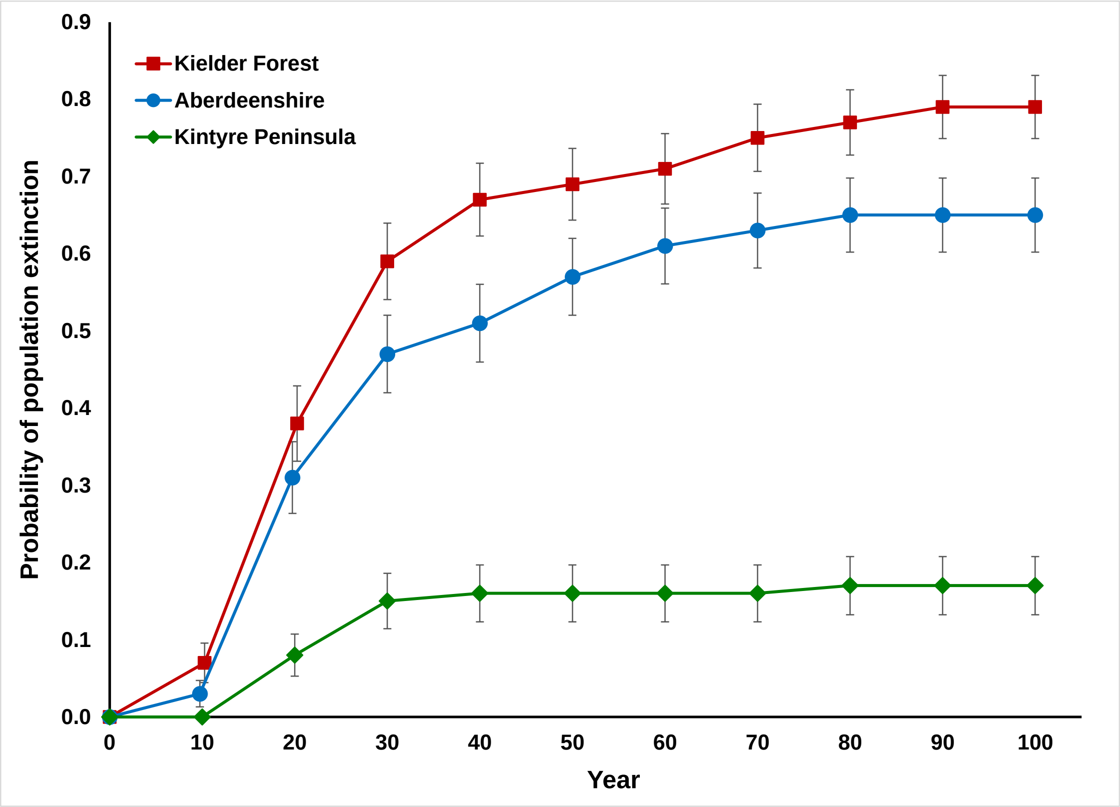

Fig. 2 - *Cumulative extinction probability averaged across 100 replicates for each decade over 100 years following release of 10 adult lynx at one of three single reintroduction sites in Scotland. Error bars show 1 standard error.*

Table 1 - *Predicted success of reintroduction at three sites in Scotland: means of 100 replicate simulations following the release of 10 individuals in a single site, or 32 individuals in a single site, or 32 individuals split between two sites. Kielder Forest (Kiel), Aberdeenshire (Aber), the Kintyre Peninsula (Kint), Aberdeenshire (14 lynx) + the Kintyre Peninsula (18 lynx) (Aber + Kint).*

	10 lynx			**32 Lynx**		
	Kiel (± SE)	**Aber (± SE)**	**Kint (± SE)**	**Aber (± SE)**	**Kint (± SE)**	**Aber + Kint (± SE)**
Number of replicates reaching year 100	21	35	83	45	93	96
Mean number of patches occupied at year 100.	10.2 (0.41)	18.9 (1.38)	27.1 (0.41)	17.9 (1.17)	26.0 (0.55)	26.8 (0.85)
Mean number of individuals at year 100	55.0 (3.39)	97.8 (8.15)	150 (2.01)	88.4 (6.67)	143 (2.84)	147 (4.37)

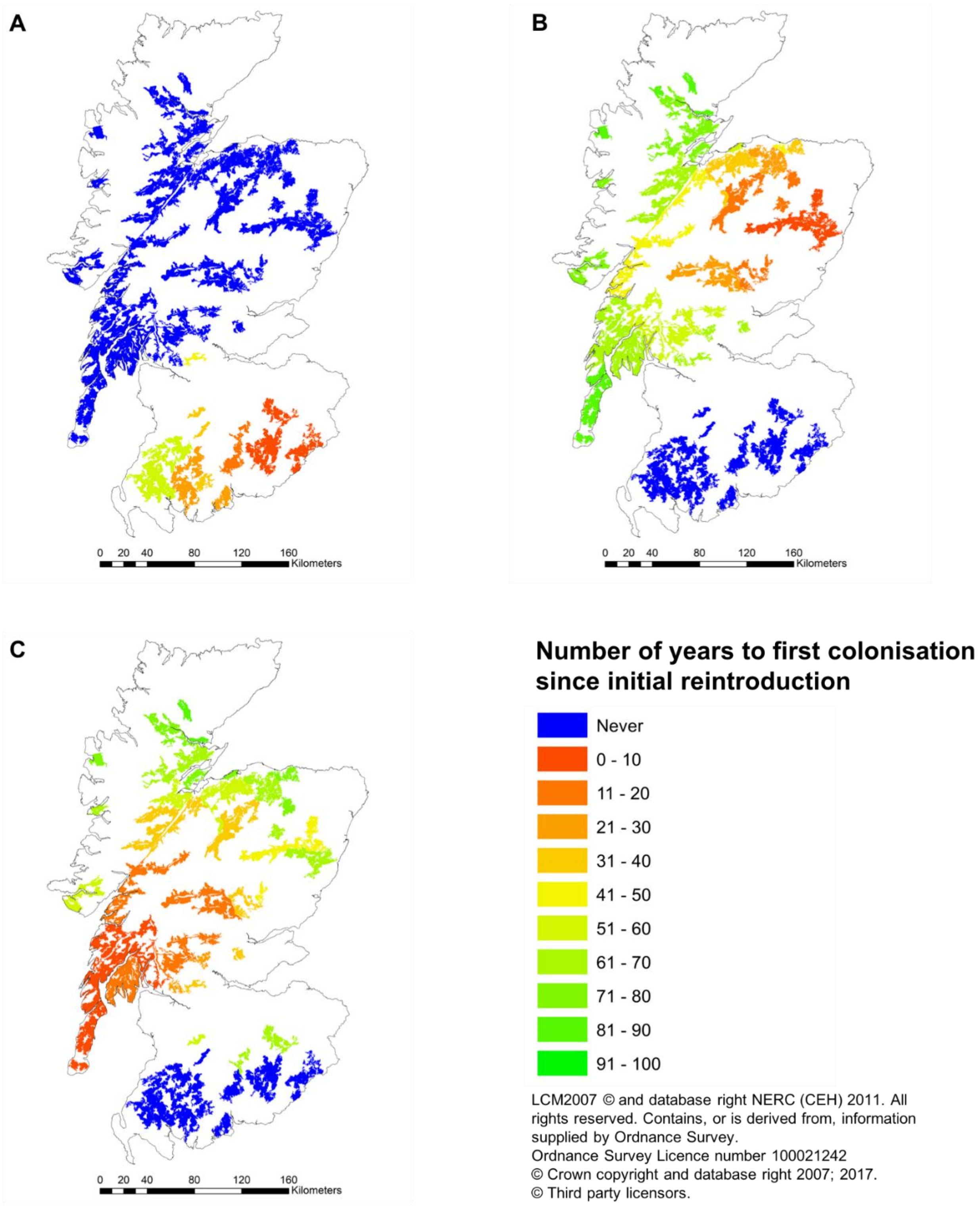

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Fig. 3 - *Predicted mean year of first colonisation for every woodland patch across mainland Scotland following reintroduction in (A) Kielder Forest, (B) Aberdeenshire and (C) the Kintyre Peninsula.*

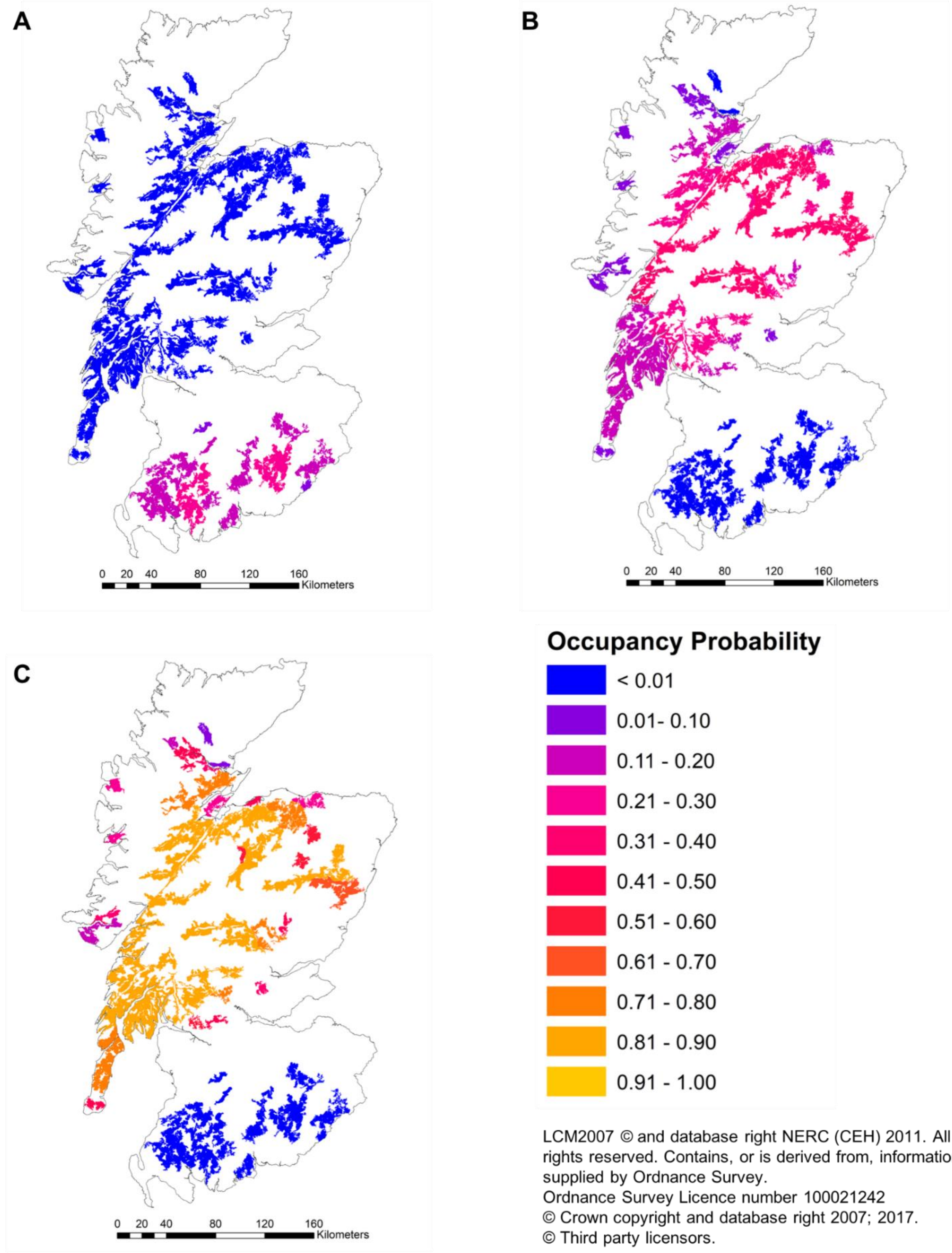

Fig. 4 – *Mean occupancy probability for each woodland patch at year 100, calculated as the average across all 100 replicates for the occupancy probability in the 100th year only, following reintroduction in (A) Kielder Forest, (B) Aberdeenshire and (C) the Kintyre Peninsula.*

Table 2 - *Model sensitivity to juvenile, sub-adult and adult survival probability, and male and female maximum emigration probabilities (D0), for reintroductions in the Kintyre Peninsula averaged for 100 model runs over 100 years. The percentage positive or negative directional change from the model run with the standard parameters (juvenile survival = 53%, sub-adult survival = 63%, adult survival = 80%, female D0 = 0.4, male D0 = 0.9) is rounded and given in the table in parentheses. The model is considered sensitive should a deviation of* ***≥ 20%*** *be found from the standard parameters.*

		Survival Probability						**Emigration Probability**			
	Control	**Juvenile Survival**		**Sub-adult Survival**		**Adult Survival**		**Female**		**Male**	
		48%	**58%**	**58%**	**68%**	**75%**	**85%**	**D0 = 0.35**	**D0 = 0.45**	**D0 = 0.85**	**D0 = 0.95**
Population persistence probability at year 100 (%)	83	70 (-16%)	88 (+6%)	62 (-25%)	83 (0%)	39 (-53%)	96 (+16%)	71 (-14%)	88 (+6%)	85 (+2%)	73 (-12%)
Mean number of patches occupied at year 100 for replicates reaching year 100	27.1	20.3 (-25%)	29.9 (+10%)	21.5 (-20%)	30.2 (+12%)	14.8 (-45%)	33.4 (+23%)	25.9 (-4%)	27.8 (+3%)	27.2 (+1%)	26.8 (-1%)
Mean number of individuals at year 100	150	106 (-29%)	170 (+14%)	116 (-22%)	171 (+14%)	73.6 (-51%)	199 (+33%)	148 (-2%)	150 (+0%)	152 (+1%)	149 (-1%)

4. Discussion

By adopting a modelling approach in which stage-structured population dynamics are incorporated and transfer is represented by a mechanistic movement model, we have demonstrated how spatially detailed modelling predictions can be produced, which will inform the process of site selection for the introduction of a large carnivore. By integrating a stochastic model of dispersal with a representation of spatial population dynamics, our approach has shown how critical the choice of introduction site can be to the potential success of a reintroduction programme for a large carnivore. In this case study of the lynx in Scotland, across all of the metrics we used to investigate the relative performance of the three proposed single-site reintroductions, there was a clear hierarchy of suitability. Kielder Forest repeatedly underperformed across all metrics, offering an unacceptably low probability of long-term population persistence. The Aberdeenshire site performed notably better, but the Kintyre Peninsula reintroduction site consistently proved to be the most suitable across all metrics. Our model indicated that reintroduction in this location could result in an 83% probability that a population of 150 lynx can become established by year 100, occupying over half of the number of available woodland habitat patches in mainland Scotland.

Identifying and accounting for both short- and long-term post-release effects is important when attempting to predict population persistence (Armstrong et al., 2017). Additional modelling and analysis in this study showed that following release in any one of the three sites, on average the death of the last founding individual occurred in the eleventh year (**Supplementary material**). The population of founding individuals, however, only remained viable (at least one male and one female still alive but all juveniles having died or dispersed) on average until half way through the sixth year and there was an indication that the size of the release patch has an effect on the probability of establishment (**Fig. S7**).

An empirical study of the survival rate of wild-caught adult lynx from the Carpathian mountains that were reintroduced to the Vosges region of France, found that nine out of 21 individuals across 11 operations died within the first three years, eight of which were within the first year (Vandel et al., 2006). Similarly, of 30 lynx originating from zoos in Germany, Sweden and Finland that were released in Poland between 1993 and 2000, 13 died within the first three years (Linnell et al., 2009). These studies imply that there is a period of vulnerability after reintroduction consistent with elevated mortality during an acclimation period (Hamilton et al., 2010). Interestingly in our model, success in this early period was found to be linked in part to the rate of patch colonisation (**Fig. S6**) and the number of kittens born in the first breeding season (**Fig. S5B**). Initial mortality will however be highly situation-dependent and potentially linked to the source of the founding individuals or translocation stress, which can be mitigated through good practice, and need not result in reintroduction failure (Dickens et al., 2010). The practice of using captive animals for reintroductions can be controversial and requires careful handling having resulted in both starvation and the need to recapture animals that were too habituated to people (Linnell et al., 2009).

Our results suggest that a period of vulnerability could be expected at a later stage, but they do not provide definitive evidence about the cause of the increase in modelled extinction probability around 10-30 years post-release. We can, however, infer that it is likely to be linked to rates of patch colonisation, inadequate reproduction, patch size and levels of inter-patch connectivity for the following reasons. Immediately following release, smaller release patches would become saturated more quickly, reducing fecundity and increasing male emigration probability in our model. Where neighbouring patches are more fragmented with greater intervening distances, this will likely result in a broadly distributed population whose individuals are less likely to find a mate and are unable to re-disperse due to the emigration model implemented in this study. This implies that both the location of neighbouring patches and critically the size of the reintroduction patch and its neighbouring patches have an effect on the probability of population establishment. This is reflected in our results, with Kintyre being the biggest and best connected of the three reintroduction patches.

We were not able to test the influence of patch shape or edge effects in our model. Their influence is complicated for lynx partly due to its variability in microhabitat selection for different purposes (Podgórski et al., 2008). Forest edge habitat, particularly adjacent to farmland, was found to provide optimal cover for stalking their preferred prey species, roe deer (*Capreolus capreolus*) in Scandinavia (Sunde *et al.*, 2000a). However, other work has demonstrated an increased risk of human-induced mortality associated with habitat edges compared to core areas (Kowalczyk et al., 2015). While it is possible that the shape and location of the Kintyre Peninsula influenced the suitability of this reintroduction location, the west coast still outperformed other regions when alternative local patches were tested (**Table S6**). An additional important factor (not included in the model) is the spatial and temporal variation in the risk of lynx persecution, but no such data currently exist for Scotland, nor do representative long-term studies of lynx reintroductions in Europe exist for robust comparison with our predicted period of vulnerability (Linnell et al., 2009).

Currently, proposals advocating a reintroduction of lynx to the UK (Smith et al., 2015; White et al., 2016) have placed substantial emphasis on the work conducted by Hetherington *et al.* (2008). In contrast to Hetherington *et al.* (2008), our case study was confined geographically to the political boundary of Scotland. This was to reflect the devolution of environmental policy and decision making to the Scottish Government, along with the recent development of a non-statutory Scottish Code for Conservation Translocations (National Species Reintroduction Forum, 2014). As such, it is of note that the true extent of Kielder Forest was underrepresented in our model, as contiguous woodland areas within England were omitted and lynx were prevented from crossing into potentially suitable habitat in England. Should a modelling exercise be conducted for the purpose of providing the evidence to justify a specific imminent planned reintroduction to Scotland, it is likely that the full extent of Kielder Forest would be included. Future versions of RangeShifter will enable the modelling of an “absorbing” rather than a “reflective” boundary. This would allow for the more accurate representation of contrasting policies in separate political regions, for example where lynx could be protected by legislation in Scotland but not in England, resulting in potentially higher rates of mortality in England through persecution.

Despite this, our results are of importance for assessing the suitability of Kielder Forest for the long-term success of a full reintroduction and therefore as an appropriate site for a trial reintroduction of lynx (White et al., 2016). The low scoring of this release site across all metrics considered here raises concerns, and suggests that further modelling is needed to investigate the appropriateness of this site relative to others. While this contrast between the findings from our modelling and current proposals is worthy of further investigation, our study has illustrated only a snapshot of the model’s potential. More detailed data on the demography and dispersal behaviour of lynx in a context similar to Scotland, coupled with further analysis of additional metrics, would be highly valuable, and is needed before any definitive conclusions are drawn. For example, further analyses could explore sensitivities of model outputs to sex-biased dispersal behaviours that might include sex-specific density dependence in emigration and settlement decisions. It could also include extensions to allow for potential demographic impacts of inbreeding to be included and a version of RangeShifter that will allow for this will be available soon (Palmer et al. in prep). Importantly, the modelling tools now exist that make it possible to establish robustly to which demographic, landscape and even genetic factors potential reintroduction success is most sensitive, and this can help to prioritise future data collection to reduce model uncertainties iteratively. As permission for a reintroduction of lynx appears to be a possibility in Scotland, an opportunity now exists to develop this modelling approach further and then validate its accuracy by assessing the outcomes of any trial reintroductions as they develop against the model’s predictions.

Both Kramer-Schadt et al. (2005) and Hetherington (2005) defined predicted success as a 95% probability of population persistence following a lynx reintroduction after 50 and 100 years respectively. If this threshold is used, the only reintroduction scenario of those we modelled that offers an acceptable chance of success after 100 years is a multi-site reintroduction to both the Kintyre Peninsula and Aberdeenshire using 32 lynx split between them. These preliminary results are however encouraging and give a strong indication as to the broad potential for the long-term viability of a reintroduction of lynx to Scotland, given the current availability of woodland habitat cover. This study has laid a strong foundation upon which future modelling can now build to identify specifically the most appropriate course of action for the reintroduction of lynx to Scotland, and it demonstrates the power such modelling approaches have in informing reintroduction decision making of large carnivores generally.

With landscape fragmentation and habitat loss noted as being among the most important factors restricting the long-term success of Eurasian lynx reintroductions across Europe (Linnell et al., 2009), being implicated in failed reintroduction attempts (Kramer-Schadt et al., 2005) and threatening other species of lynx (Ferreras, 2001), establishing the level of connectivity between suitable habitat patches is key. Hetherington et al. (2008) proposed two geographically distinct habitat networks across Scotland (one in the Highlands and one in the Southern Uplands) to which our habitat patch landscape roughly corresponds (**Fig. 1**). These authors used a LCP analysis to conclude that there was a low probability that sufficient numbers of lynx would cross the intervening landscape to establish successfully in the other network from where they were released. Using data on current woodland cover and distribution, our results support this finding as they show extremely low occupancy probabilities, both on average (**Fig. S4**) and at year 100 (**Fig. 4**), of patches in the other habitat network from where the reintroduction took place, regardless of release site. Our results thus emphasise how estimates quantifying habitat availability alone are insufficient to inform reintroduction proposals. Without careful consideration of how functionally connected the habitat is through the interactions of demography and dispersal characteristics with the landscape, there is a danger of overestimating the appropriateness of a reintroduction.

Bateman & Fleming (2012) describe how, on average, large felids are often unable to coexist comfortably in close proximity to humans. The response of lynx to the presence of humans and human-modified landscapes varies, but they are often found to adjust their home ranges to reduce exposure to increasing human disturbance (Bouyer et al., 2015). The intervening matrix between the Highlands and Southern Uplands habitat networks corresponds geographically to the Central Belt of Scotland (**Fig. 1**). This region supports the two biggest cities and the highest human population densities in Scotland, while being at its narrowest point a natural bottleneck approximately 38 km wide. It has been suggested that targeted efforts could be made to expand the amount of suitable habitat in this region to increase connectivity between the two habitat networks (Hetherington et al., 2008). However, roads and areas of high human population density are known to pose formidable barriers through vehicle collisions (Schmidt-Posthaus et al., 2002), persecution and poaching (Andren et al., 2006), making the efficacy of such efforts questionable.

Mortality from hunting and poaching is often high, especially in adult lynx (Andren et al., 2006) and is still thought to be one of the biggest challenges facing lynx populations reintroduced in mainland Europe more than 25 years on (Breitenmoser, 1998). Indeed recent work suggests the prevention of illegal hunting should be considered the highest priority for the conservation of lynx in a reintroduced population in the Bohemian Forest Ecosystem (Heurich et al., 2018). Our model’s sensitivity to survival, particularly adult survival, reflects the findings of previous studies (Vandel et al., 2006) and suggests that increases in population persistence probability could be achieved through a reduction in adult mortality. This is especially interesting as our sensitivity analysis demonstrated that a 5% increase in adult survival, well within the natural range of variability (Andren et al., 2006, 1997), could result in a 96% probability that the population would reach year 100 for a reintroduction of only 10 lynx in the Kintyre Peninsula. As a result, safeguarding adequate levels of adult survival appears to be a key area of focus to ensure any reintroduction is a success. To ensure such levels of lynx survival are realised, we would advocate the use of additional, socio-economic work to identify key stakeholder groups and areas of potential conflict, whilst quantifying the levels of risk these would pose to animal welfare and broader reintroduction success. We caution against the pursuit of a single decision-making tool, instead supporting the combined use of multiple sources of evidence that can be used collectively to inform effective decision making.

The apparent paucity of genetic variation within previously reintroduced populations of lynx in Europe (Bull et al., 2016), their reported limited success, and the call from authors to learn from the mistakes of previous failed lynx reintroduction attempts (Linnell et al., 2009), makes the inclusion of sufficient population genetic variation an essential consideration. As such, using survival rate as a surrogate for a larger founding population should be considered with care and categorically cannot be considered in isolation from the need to secure the long-term genetic viability of a population (IUCN/SSC, 2013). The upcoming release of RangeShifter v2 enables the explicit modelling of genetic relatedness, which will allow these fundamental considerations to be considered when interpreting model predictions. Future modelling should thus aim to incorporate such genetic factors and further explore scenarios where an initial population of lynx is subsequently bolstered by a second introduction.

Phased reintroductions of this nature may also help to reduce any pressure on the source populations from which the animals are obtained. For the three reintroduction sites considered in this study, we found that modelling of a phased reintroduction had a negligible impact on any of the three metrics of success across all sites (**Fig. S9**). Owing to the quantity of potential phased release combinations, this modelling approach would likely be best suited to investigating the performance of separately identified, feasible alternatives rather than searching for an ‘optimum’ scenario. Equally our model could be adapted to explore further the hypothesis that a single-site reintroduction is sub-optimal, but “population nuclei” should be introduced in neighbouring patches in a fragmented landscape (Kramer-Schadt et al., 2005; Zimmermann et al., 2007a). Scenarios of this nature will help to identify key areas that could benefit from population enrichment due to their isolation or during periods in time where the population may be more vulnerable to extinction, such as those already demonstrated here.

Often overlooked, but of particular importance for reintroductions of species with large spatial requirements, is the dynamic nature of modern landscapes and the lack of constancy in resource availability (Osborne and Seddon, 2012). As the lynx is a woodland-dwelling species, the impact that modern forestry practice has on the continuity of woodland cover could be substantial. In a country like Scotland, a large proportion of the total woodland cover is managed on a short rotation clearfell system (Macdonald and Hubert, 2002). This has the potential to change rapidly the suitability and location of core habitat, leaving some populations isolated. Conversely, new woodland creation continues to be a focus of the Scottish Government (Forestry Commission Scotland, 2006), and current policy means that once forestry has become the dominant land use in an area it often remains as such, with tree restocking obligations on harvested sites. As lynx have been found to use a variety of woodland types and successional stages at different periods in their life cycle (Podgórski et al., 2008), and show a preference for habitat heterogeneity (Rozylowicz et al., 2010), the impact this will have on a reintroduced population is uncertain.

Lynx are a specialist predator of roe dee (Jobin et al., 2000), meaning the abundance of roe deer could have a profound impact on habitat suitability and modelled output for lynx. Female lynx home ranges are dictated primarily by prey availability (Schmidt et al., 1997), with a prevailing consensus that smaller home territories are linked to higher prey density (Linnell et al., 2007; Sunde et al., 2000b). A comparison of four separate areas across Europe revealed a “highly significant relationship between lynx density and the density of ungulate biomass” (Hetherington and Gorman, 2007). As a result of this tight coupling and the uncertainty surrounding prey abundance, especially under future conditions, care should be taken in interpreting long-term model projections. Attempts to modify habitat patch suitability based on roe deer density could be a productive avenue for future modelling, particularly as there is some evidence that roe deer densities have historically been lower in the west of Scotland than further east (Latham et al., 1996; Palmer and Truscott, 2003). However, the mobility of deer and uncertainty about the impacts lynx reintroduction would have on prey behaviour make this a challenging task. Nevertheless, attempting to incorporate how a landscape and prey communities will change over time into predictions should be a key focus of future reintroduction modelling, as they have the potential to alter site suitability drastically or even the efficacy of wider reintroduction proposals.

Models themselves cannot make decisions, but instead help us to understand the complex interacting dynamics of species with their environment whilst creating a framework around which realistic objectives can be set (Osborne and Seddon, 2012). We have demonstrated how the use of an IBM that specifically accounts for a species’ demography, ecology and dispersal can be used to assess quickly and inexpensively the likelihood of reintroduction success. Notably, the modelling approach we have adopted explicitly incorporates several processes that we understand to have substantial impact on the establishment and spread of introduced species. Density-dependent emigration, stochastic individual movement trajectories and stochastic demography are all key components of the inherently uncertain course of any given introduction (Melbourne & Hastings, 2009; Bocedi *et al.*, 2014b). By integrating these processes in a modelling exercise it becomes possible to identify the range of likely outcomes (Cuddington et al., 2013) and to establish how sensitive these are to uncertainties in model structure and to parameter values. This can in turn help to target limited conservation funds and can subsequently be used in an adaptive approach as data emerge from reintroductions conducted on the focal species, or even on closely related species.

For lynx reintroduction to Scotland, we recommend that future research should focus on assessing the sociological components of lynx reintroduction and a spatially explicit quantification of any resultant risk. Specifically, this should involve a comprehensive assessment of key stakeholder perceptions and the potential for wildlife conflict, with particular consideration given to the risk of livestock depredation, hunting and persecution. Such an assessment should also reflect roe deer and sheep densities and their respective seasonal variation alongside the spatial arrangement and temporal variability of pasture and woodland. We recommend that decision-makers should use as evidence such independent modelling of the spatial variation in the socio-economic components of risk, alongside the individual-based species models demonstrated in the present study, to assess the relative suitability of alternative reintroduction strategies for both lynx in Scotland and large carnivore reintroduction programmes generally. In the future we envisage coupled individual-based models of the ecological system and agent-based models representing human actors (see Synes et al., 2018) being of considerable utility in understanding and managing the spatio-temporal dynamics of potential human-wildlife conflicts.

In a global context, planning of large carnivore reintroductions fundamentally needs to consider how individuals will disperse through a complex landscape and how this drives the spread of a colonising population. This requires modelling of dispersal as a complex, multi-phased process such that the realised distances travelled by dispersers becomes a function of their behavioural rules, the landscape structure and also the structure of the current population. Notably, while recent theory has highlighted how the incorporation of moderate complexity in the modelling of individual dispersal can result in strikingly different population spread dynamics across complex landscapes (Bocedi et al. 2014b), this approach has very rarely been taken in applied ecological studies. Thus, the modelling approach demonstrated here, which uses RangeShifter to incorporate explicitly the three phases of dispersal, including a mechanistic representation of individual movements across spatially heterogeneous landscapes, can provide an indispensable tool for delivering more spatially realistic and species-specific predictions of landscape suitability and reintroduction viability, especially for large carnivores.

Conflicts of Interest

The authors have no actual or potential conflicts of interest to declare.

Role of the funding source

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgements

We are grateful to Ian Harris of Bangor University for his help with the production of the underlying habitat and patch landscapes and to the two anonymous reviewers for their recommendations.

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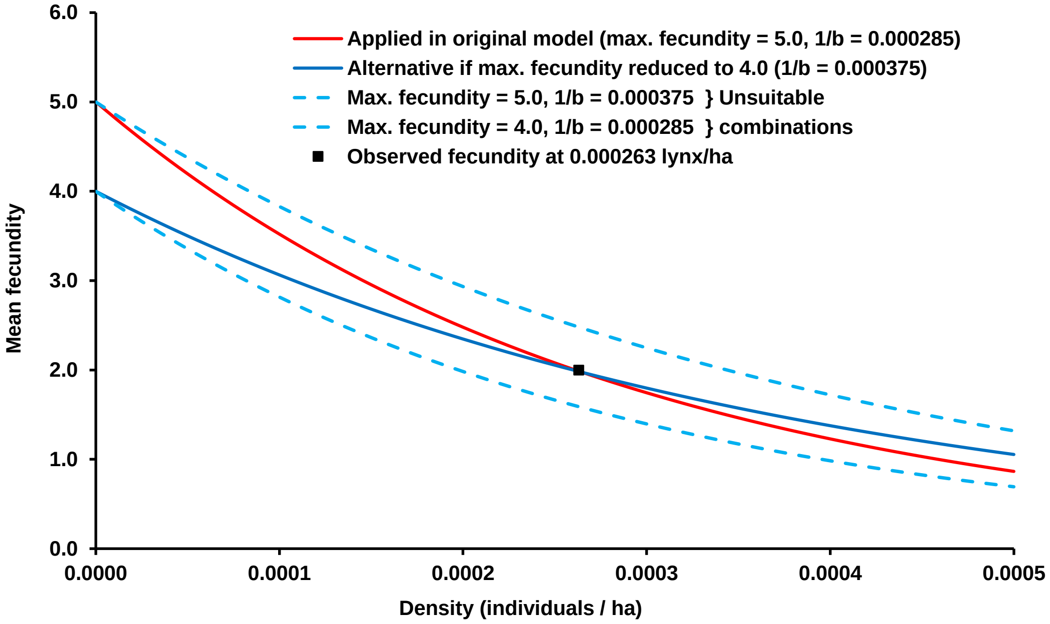
1. Supplementary Material

2. Methods

Estimation of the parameter 1/b

The parameter *1/b* in RangeShifter is the exponential rate at which fecundity declines as local density increases (Bocedi et al., 2014). We estimated it in this study by fitting the relationship between mean fecundity and density through the average of 2 kittens per female (Breitenmoser-Würsten et al., 2007; Gaillard et al., 2014) at a density of 0.000263 lynx/ha proposed for Scotland (Hetherington and Gorman, 2007), given that we had assumed a maximum fecundity of 5 kittens per female at very low density (i.e. the unobtainable intercept density of 0 lynx/ha). Had we assumed a different intercept density, e.g. 4 kittens per female, then we would have required a higher value of *1/b* to match the observed point, as illustrated in Fig. S1.

***Figure S1**. Density dependence in fecundity as applied in the original model (solid red line), in an alternative demographic scenario (below) assuming reduced intercept fecundity (solid blue line) and two unsuitable relationships (broken lines) which would not match observed data.*

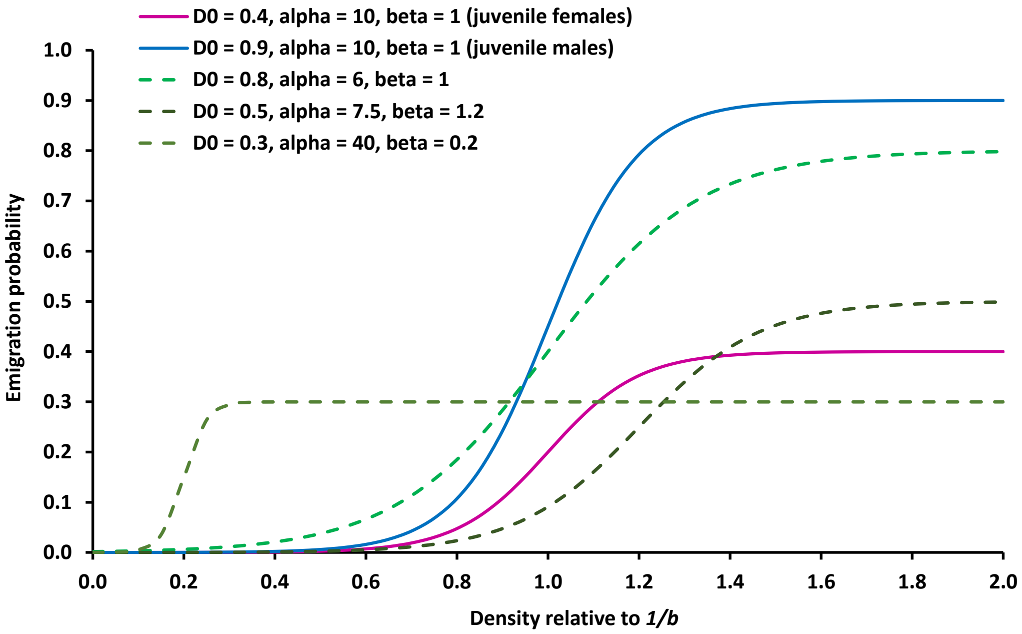


Ideally, we would require observed estimates of mean fecundity at two or more densities, in which case we would not need to assume the intercept density in order to estimate *1/b*, but we were unable to find any suitable estimate in this case. It is possible that fecundity may not vary with density in lynx, however there are no Scotland-specific data and density-dependent fecundity has been used in the modelling of other lynx species Gaona et al., (1998).

Density-dependent emigration

An individual's density-dependent emigration probability in RangeShifter is determined by applying a logistic reaction norm as a function of density in the local patch, where density is expressed relative to the summed total of *1/b* for the whole patch. Note that the patch might comprise more than one type of suitable habitat class, which differ in their values of *1/b,* although that was not the case in the model applied here (*1/b* = 0.000285 individuals/ha for high and low quality woodland). The reaction norm requires three parameters, all of which are dimensionless: the maximum emigration probability (*D0*), the slope (*alpha*) and the inflection point (*beta*). We set these parameters such that emigration probability was negligible at low density and reached *D0* at high density, but was substantially higher for juvenile males than for juvenile females, as illustrated in Fig. S2.

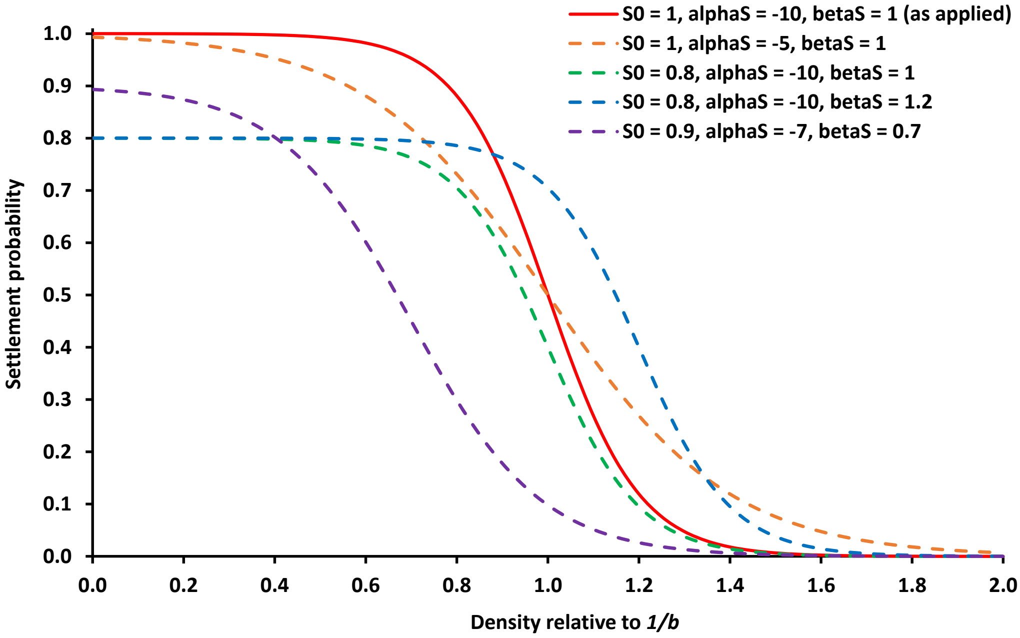
Figure S2. *Emigration reaction norms applied in the model for juveniles of each sex (solid lines) and examples of three alternative relationships which could be applied by altering one or more of the three parameters*



Settlement

A similar method was used to apply density-dependent settlement in the model, but based on the relative density of the patch that the disperser has reached after passing through the inter-patch matrix. The same relationship was applied to both sexes. As we have no observed data on settlement at the scale of the patches implemented in the model, we set the parameters so that settlement was certain at low local density, whilst at very high local density the disperser would reject the patch and continue on its dispersal trajectory. At a density of half the total *1/b* for the patch, there was a 50% chance that the disperser would settle (Fig. S3).

Figure S3. *Settlement reaction norm applied in the model (solid line) and examples of four alternative relationships which could be applied by altering one or more of the three parameters*



In our model, the settlement parameters for males and females differed. Both sexes required a suitable habitat patch to be located ("find a suitable patch") and existing lynx densities within that patch to be low enough to permit occupancy ("density dependence"). However, for males to settle, a female was also required to be in that patch ("mating requirements").

SMS Parameters

In the absence of any detailed movement data for lynx in Scotland, or comparable data from elsewhere, the setting of SMS parameters was unavoidably subjective, but based to some degree on experience we have gained in modelling other species for which data were available (Aben et al., 2016, 2014).

We set the perceptual range (PR) to 500 m (five cells). Whilst a large carnivore can presumably see much further than this if visibility permits, the PR should reflect the distance over which a disperser makes decisions based on local landscape composition, and we assumed 500 m to be a reasonable average across a range of landscapes likely to be encountered in rural Scotland. However, this is not likely to be a crucial parameter, as the ability of SMS to generate connectivity estimates closely correlated with genetic data was insensitive to PR when PR was three cells or more (Coulon et al., 2015). The PR method was set to 2, i.e. the harmonic mean method for averaging perceived costs within the PR. This method tends to weight effective costs towards the detection of low-cost habitat, whereas the arithmetic mean method tends to be influenced more strongly by high-cost habitat. We assumed that a dispersing large carnivore would be more strongly attracted to suitable breeding habitat than it would be repelled by partial barriers such as main roads, with lynx known to follow forested habitats during dispersal (Schmidt, 1998).

The directional persistence (DP) parameter is the one to which SMS is usually most sensitive (Coulon et al., 2015), and yet is the most difficult to estimate, as it is not directly estimable in the field, but can be derived from fitting simulated trajectory data to observed trajectories (Aben et al., 2014). Here, as we had no such observed data, we set DP subjectively by adjusting it so that simulated trajectories on the computer screen achieved a balance between some degree of response to variation in perceived landscape costs and a correlated pattern as is expected of naïve dispersers in a fragmented landscape (Zollner and Lima, 1999). Memory size (the number of previous steps over which the current direction is determined for the purpose of applying DP) was set to five cells, i.e. equal to the PR, and we applied no dispersal bias (goal type 0) in order to keep the SMS model as simple as possible.

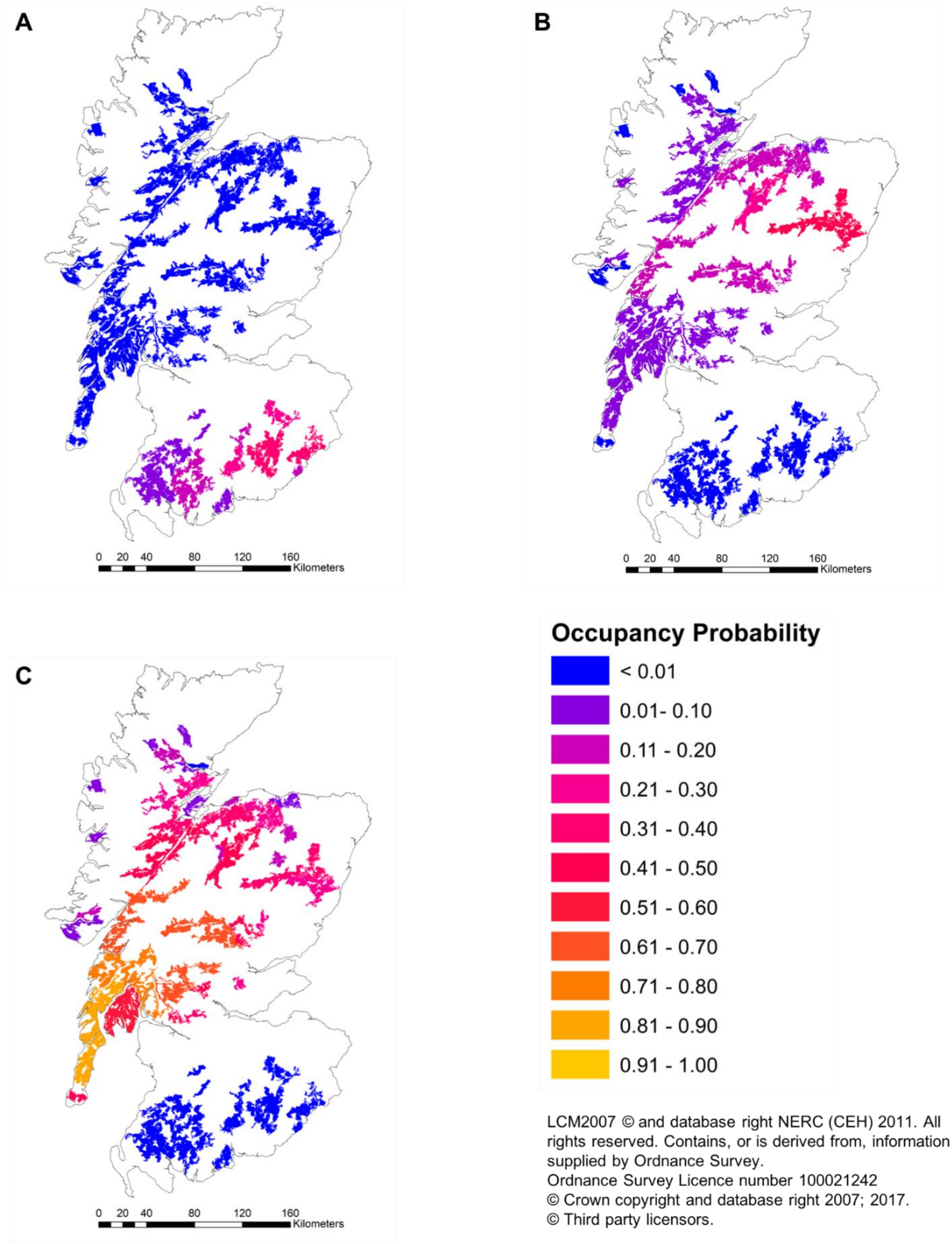
3. Results

Table S1. *RangeShifter model output for each of the 53 unique habitat patches. Reintroductions were modelled independently from Kielder Forest (Kield), Aberdeenshire (Aber) and the Kintyre Peninsula (Kint), averaged over 100 replicates.*

	Mean Probability of Patch Occupancy over 100 Years (%)			**Occupancy Probability at Year 100 (%)**			**Mean Year of First Occupancy**		
Patch	**Kield**	**Aber**	**Kint**	**Kield**	**Aber**	**Kint**	**Kield**	**Aber**	**Kint**
1	0	0.69	48.86	0	3	44	-	84	2.67
2	0	3.05	40.44	0	10	60	-	66.44	24.93
3	0	0.82	5.62	0	3	13	-	78.43	59.07
4	0	2.44	13.99	0	6	34	-	73.57	52.24
5	0	1.28	6.88	0	5	24	-	76.88	69.76
6	9.48	0	0	16	0	0	28	-	-
7	32.19	0	0	21	0	0	3.02	-	-
8	6.91	0	0	11	0	0	31.47	-	-
9	21.56	0	0	19	0	0	12.89	-	-
10	19.59	0	0.01	19	0	0	12.2	-	64.33
11	3.92	0	0.06	9	0	0	38.85	-	59.2
12	0	2.19	20.17	0	5	37	-	65.85	38.58
13	0	13.85	25.84	0	19	42	-	12.13	45.31
14	0	21.82	15.81	0	21	59	-	11.15	67.46
15	0	17.48	14.5	0	21	54	-	14.88	71.01
16	0	0.64	5.03	0	4	20	-	81.13	74.29
17	0	0.36	3.7	0	4	14	-	83.78	80.47
18	0	0.12	0.64	0	1	2	-	88.67	83.27
19	10.03	0	0	18	0	0	32.38	-	-
20	11.99	0	0	20	0	0	29.94	-	-
21	0.34	2.79	33.41	0	10	47	45.56	68.56	32.36
22	0	8.85	69.55	0	21	83	-	54.89	15.37
23	0	4.02	58.35	0	15	82	-	67.53	19.16
24	0	15.88	49.17	0	24	79	-	20.47	35.3
25	0	16.66	63.64	0	31	83	-	25.3	18.43
26	0	4.98	77.21	0	16	83	-	63.5	6.91
27	0	13.1	63.68	0	31	83	-	45.33	18.12
28	0	10.89	19.53	0	23	56	-	37.8	54.61
29	0	18.84	34.37	0	31	81	-	35.86	50.9
30	0	7.05	8.22	0	17	30	-	43.65	76.68
31	0	7.77	12.37	0	19	43	-	55.84	70.97
32	0	9.08	45.01	0	25	82	-	61.52	40.48
33	0	1.03	7.01	0	3	28	-	72.36	74.09
34	0	1.53	9.41	0	7	38	-	79.33	77.47
35	0	0.2	1.23	0	1	7	-	86.75	86.43
36	0	1.61	11.1	0	8	47	-	78.17	76.97

	Mean Probability of Patch Occupancy over 100 Years (%)			Occupancy Probability at Year 100 (%)			Mean Year of First Occupancy		
Patch	**Kield**	**Aber**	**Kint**	**Kield**	**Aber**	**Kint**	**Kield**	**Aber**	**Kint**
37	0	6.39	6.57	0	16	27	-	36.82	78.07
38	17.03	0	0	9	0	0	3.95	-	-
39	35.87	0	0	17	0	0	0	-	-
40	25.52	0	0.14	17	0	0	4.46	-	66.5
41	0	4.26	46.59	0	12	71	-	63.53	26.61
42	0	46.31	35.31	0	33	81	-	1.72	46.13
43	7.82	0	0	19	0	0	58.45	-	-
44	8.19	0	0	19	0	0	51.56	-	-
45	0	46.95	21.79	0	31	67	-	0	63.17
46	0	1.71	82.46	0	10	79	-	81.91	0
47	0	4.48	84.45	0	16	83	-	67.47	1.46
48	0	8.63	78.02	0	22	83	-	58.48	6.01
49	0	13.77	47.45	0	32	83	-	44.7	37.98
50	0	4.39	25.57	0	17	77	-	71.15	63.24
51	0	8.09	34.61	0	23	80	-	64.34	53.89
52	0	29.43	43.7	0	33	83	-	13.37	39.17
53	0	19.23	24.52	0	31	79	-	29.6	64.12

Figure S4. *Predicted mean probability of patch occupancy across mainland Scotland averaged from year 0-100 following reintroduction from (A) Kielder Forest, (B) Aberdeenshire and (C) the Kintyre Peninsula.*



Factors affecting extinction/establishment of released population

Figure S5. *Effect on population extinction probability by year 100 of (A) the number of females in the initial population of 10 individuals and (B) the number of juveniles born in the first breeding year after release. Error bars show 1 standard error.*

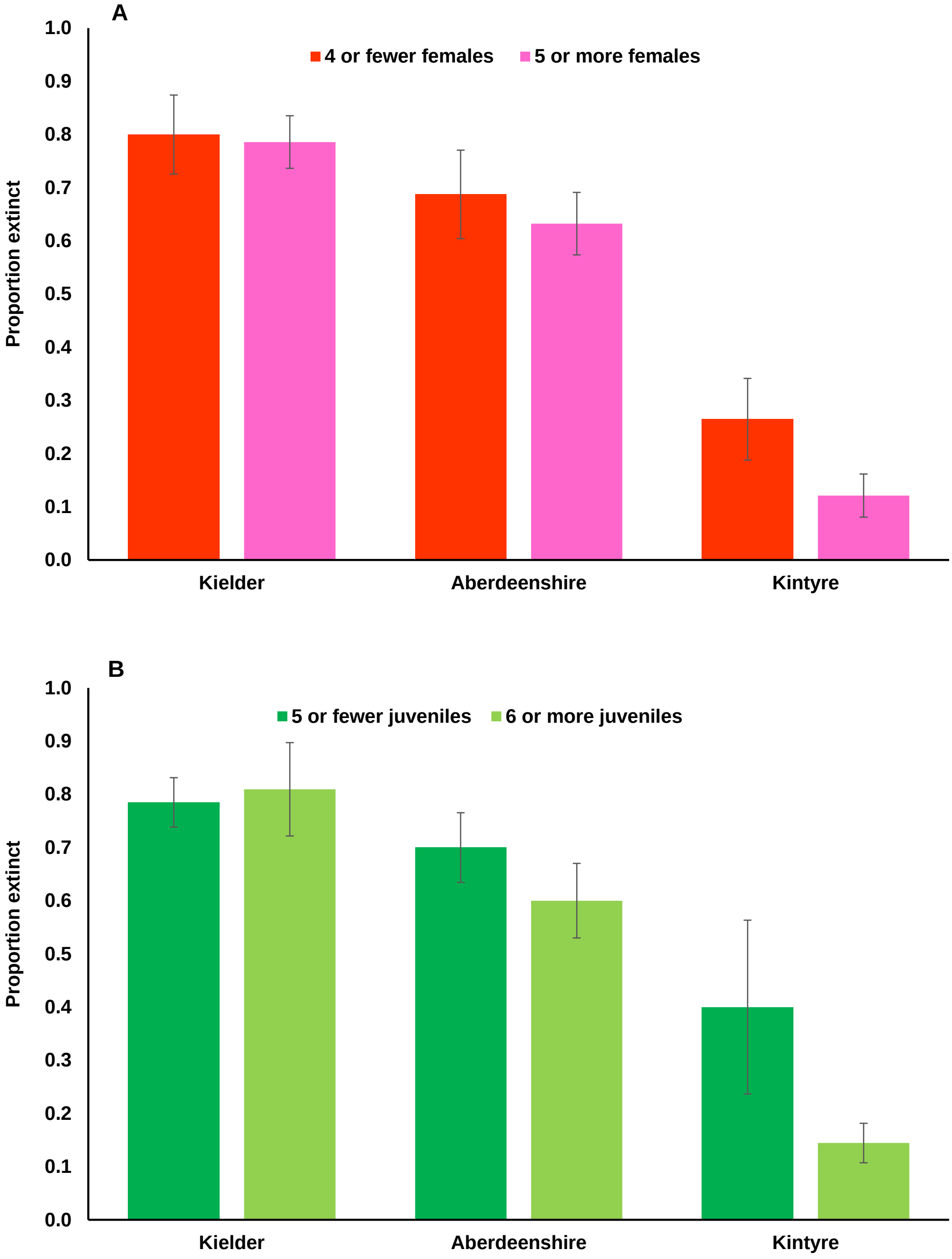
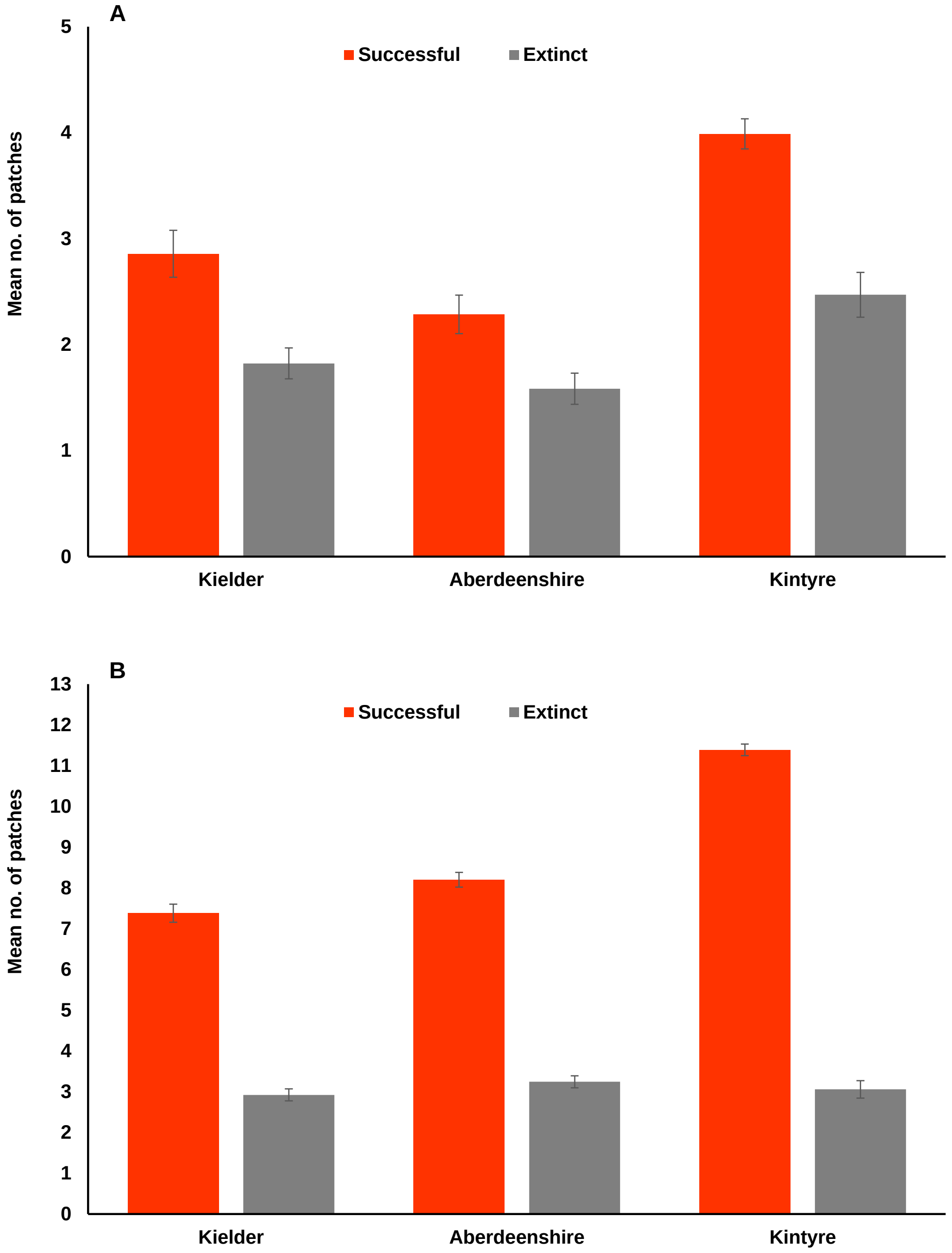
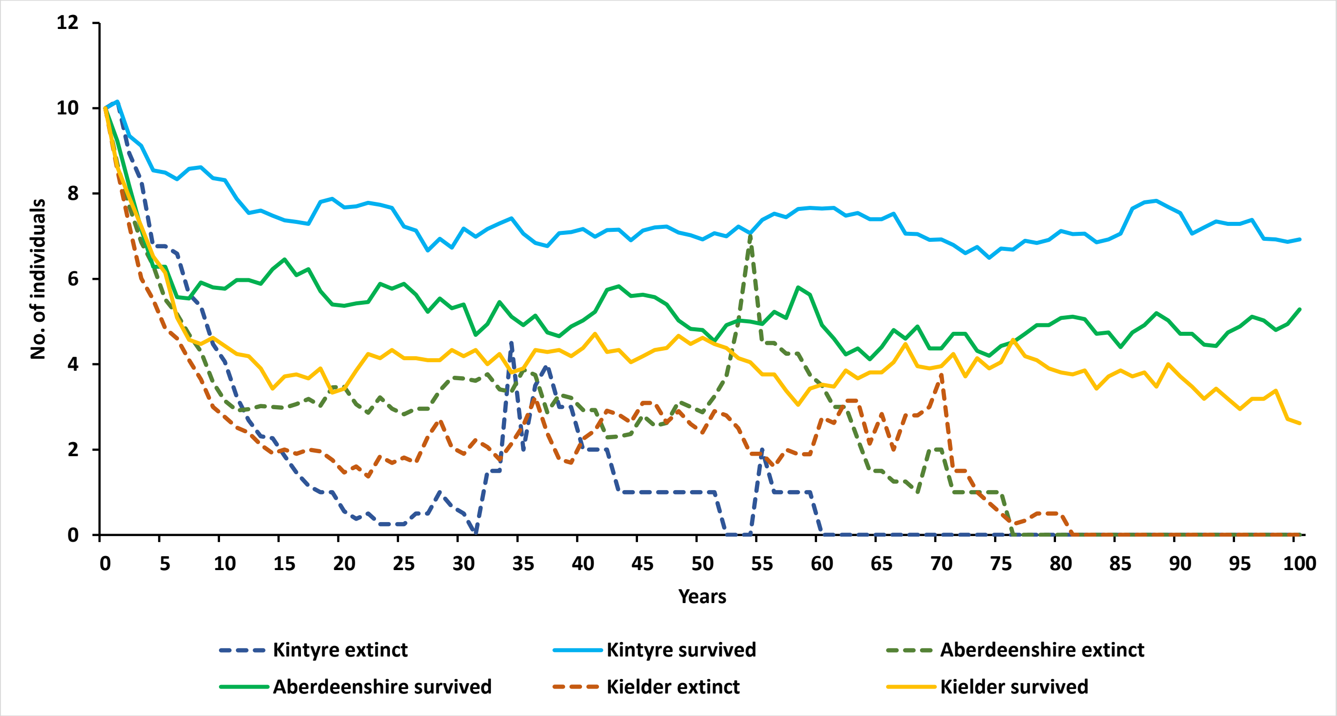


Figure S6*. Number of different patches colonised by successful dispersers (here defined as those which survived their first winter) in (A) the first 10 years and (B) the first 30 years after release. Error bars show 1 standard error.*



1136 ***Figure S7.*** *Pre-reproduction population size in the reintroduction patch for each*
1137 *reintroduction site over time for those replicates that survived and those replicates that went*
1138 *extinct.*



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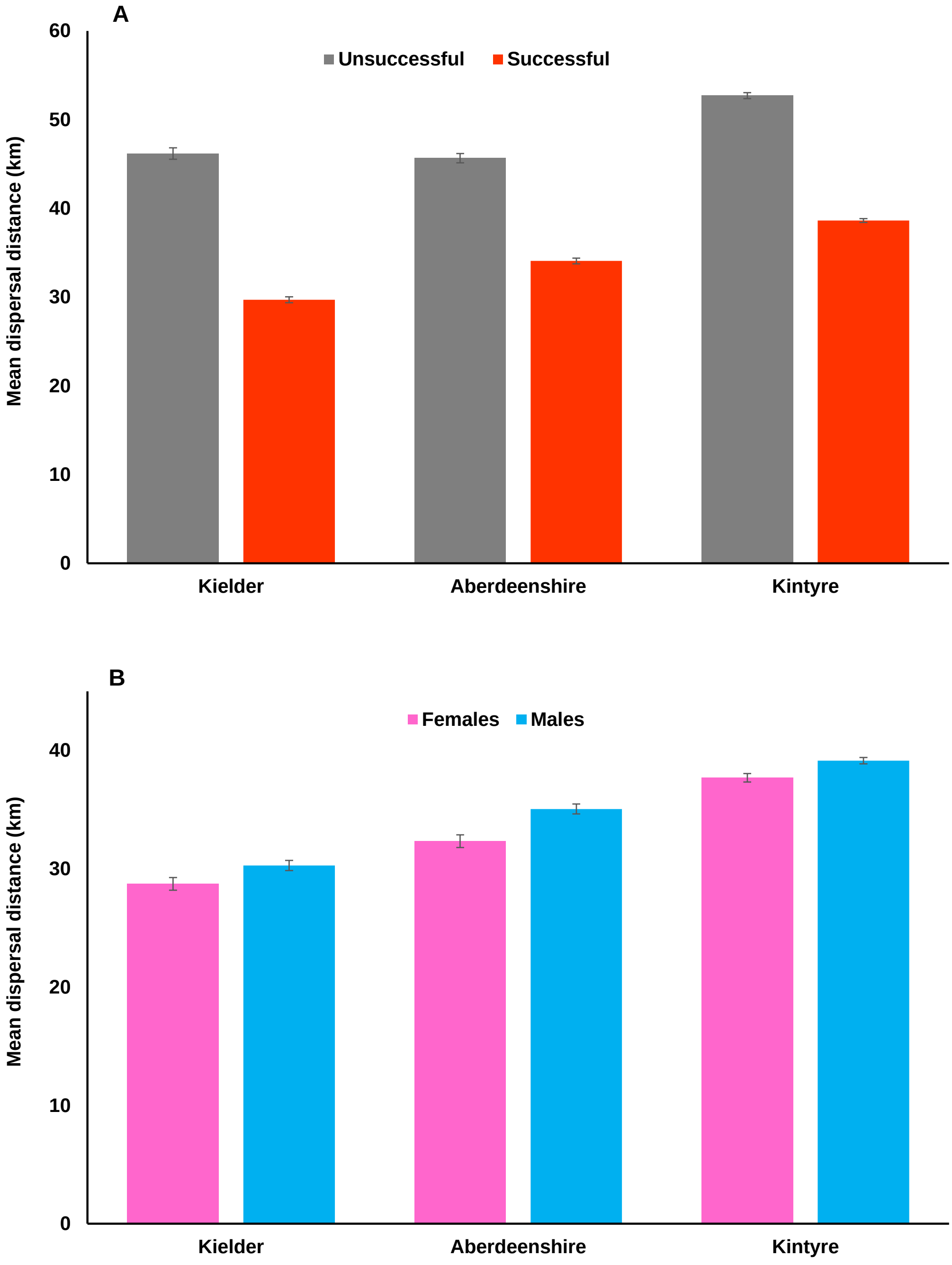
Dispersal and survival at the individual level

Across all release sites, the mean year in which the last founder died was 10.7 (s.e. 0.46, range across sites 10.4 - 11.0), and the mean year in which there remained alive at least one founder of each sex (i.e. the founding population remained viable even if all juveniles had died or dispersed) was 5.6 (s.e. 0.47, range across sites 5.3 - 6.3) (Fig. S8).

Figure S8. *Mean dispersal distance of (A) all dispersers as a function of success and (B) successful dispersers by sex. Data were extracted from the individual-level output files of an additional 10 replicate simulations run for each release site, and error bars show 1 standard error.*



4. Sensitivity to Model Assumptions

Landscape configuration

In a model such as this, the number of ways of representing the landscape, and in particular how discrete patches are delimited from continuous regions of suitable habitat, is potentially huge, and we cannot therefore evaluate the model's sensitivity to all possible landscape configurations. However, in our model there were 16 patches of area less than 100 km^2, which might be regarded as being too small to contain a local sub-population of lynx, given that home ranges have been estimated to lie in the range of 45 - 210 km^2 (Breitenmoser-Würsten et al., 2001). We therefore constructed an alternative landscape configuration in which most of these small patches (except those that were too remote) were combined with an adjacent larger patch or with another small patch, thereby reducing the total number of patches from 53 to 42. In so doing, the Kintyre and Kielder release patches were increased in size, and their initial densities were therefore adjusted to retain initial population sizes of 10 individuals in each case. We ran 100 replicates for each release site as previously.

Table S2. *Metrics of success for landscape in which some small patches were combined with other patches - original model predictions (Table 3) in brackets.*

	Kielder		**Aberdeenshire**		**Kintyre**	
No. of replicates reaching year 100	51	[21]	37	[35]	86	[83]
Mean no. of patches occupied at year 100	8.9	[10.2]	22.7	[18.9]	25.2	[27.1]
Mean no. of individuals at year 100	60.0	[55.0]	131	[97.8]	159	[150]

Combining some of the small patches with other patches had a limited effect on the outcome of the reintroduction, other than an increased number of replicates for Kielder surviving to 100 years, and a somewhat larger final population after release in Aberdeenshire (Table S2). In both cases, the combining of small patches likely to be reached by dispersers in the early years after reintroduction would reduce the chance of local extinction due to demographic stochasticity, whereas the nearest six patches to Kintyre (other than a small patch combined with the release patch) were all large anyway, and therefore there was no similar gain by combining small patches elsewhere in the country.

In many modelling studies, there is only one representation of the landscape applied, yet issues such as the choice of cell size (Bocedi et al., 2012) and how continuous tracts of suitable habitat are split into discrete patches, as is required for RangeShifter, can potentially be important. We would therefore advocate that, in the case of a reintroduction programme being in the planning stage (rather than simply speculative, as here), the sensitivity of model predictions to assumptions made in representing the landscape should be assessed.

Differential age at maturity

We used the 'complex sexual model' option of RangeShifter to run simulations in which males matured at three years rather than two years, which remained the age of first breeding for females. We set harem size to five to ensure that males were not locally limiting once they became mature. 100 replicates were run for each release site.

All three metrics of reintroduction success were reduced substantially for all release sites by delaying male maturity to three years (Table S3).

***Table S3**. Effect of increasing age of male maturity to three years on metrics of success - original model predictions (Table 3) in brackets.*

	Kielder		**Aberdeenshire**		**Kintyre**	
No. of replicates reaching year 100	5	[21]	6	[35]	45	[83]
Mean no. of patches occupied at year 100	5.4	[10.2]	11.5	[18.9]	15.8	[27.1]
Mean no. of individuals at year 100	21.6	[55.0]	54.2	[97.8]	82.4	[150]

Clearly the assumption of the age at which males first reproduce has a considerable quantitative effect on the model predictions, as sub-adult males must survive two years at a survival probability of 0.63 (~0.4 combined) compared to only one if they mature at two years. However, male lynx have been recorded as sexually mature at 1¾ years old (Kvam, 1991) so male maturity at three years in established populations in central Europe (von Arx et al., 2004) need not necessarily imply that they would not mate at two years in an expanding population where adult males are few, and their survival rate might be higher if they do not encounter adult males so frequently. Critically, the rank order of sites was maintained when assuming older male maturity. Although we acknowledge that this is an important issue, and data from other introduction schemes would be highly informative, we still consider that our original assumption was adequate for our principal aim of comparing the three proposed reintroduction sites.

Demographic parameters

Four demographic parameters were altered to reflect plausible alternatives: maximum fecundity was reduced to 4.0, *1/b* was increased accordingly to 0.000375 individuals/ha (see Fig. S1 illustrating the estimation of *1/b*), reproduction probability was reduced to 0.875 and maximum age was increased to 20 years. We ran 100 replicates for each site.

***Table S4**. Effect of altering four demographic parameters on metrics of success - original model predictions (Table 3) in brackets:*

	Kielder		**Aberdeenshire**		**Kintyre**	
No. of replicates reaching year 100	25	[21]	17	[35]	64	[83]
Mean no. of patches occupied at year 100	6.0	[10.2]	7.0	[18.9]	13.1	[27.1]
Mean no. of individuals at year 100	28.2	[55.0]	36.4	[97.8]	87.2	[150]

Although all three metrics of reintroduction success were reduced relative to the original simulations (except for the number of replicates reaching year 100 for Kielder, which increased) by applying together the alternative demographic parameters, the rank order of release sites was maintained (Table S4). In relative terms, Aberdeenshire showed the greatest reduction in all metrics. Reducing the frequency of reproduction and the maximum fecundity would both serve to reduce the rate of population spread, whereas increasing the maximum age should serve to compensate (but apparently not enough). Increasing *1/b*, which was necessary to ensure that density dependence in fecundity would result in approximately the observed mean fecundity at the observed density, would also have the effect of increasing the threshold density at which emigration would occur, and therefore also slow the rate of expansion, since the population in a colonised patch would typically need longer to increase to the density at which further dispersal would occur. That effect could, however, be compensated by decreasing the emigration parameter *beta*.

The interplay of demographic and dispersal parameters is complex, and even if we had good observed data on the rate of spread of an introduced population, there would remain some uncertainty in parameter values to be applied. It is highly encouraging, therefore, that the ranking of the three proposed reintroduction sites was robust to highly plausible alternative parameter values to those originally applied.

Density-independent emigration

Two simulations applying density-independent emigration were run for each release site (100 replicates each).

Table S5*. Metrics of success when applying density-independent emigration probability. The fixed emigration probability for the juveniles of each sex were (1) set equal to the maximum emigration probability (*D0*) in the original model and (2) set equal to* D0 */ 2 in order to try to reflect the overall emigration rate in the original model. Original model predictions (Table 3) are given in brackets.*

		Kielder		**Aberdeenshire**		**Kintyre**	
(1)	No. of replicates reaching year 100	14	[21]	29	[35]	72	[83]
	Mean no. of patches occupied at year 100	8.1	[10.2]	18.7	[18.9]	27.3	[27.1]
	Mean no. of individuals at year 100	40.4	[55.0]	92.2	[97.8]	146	[150]
(2)	No. of replicates reaching year 100	14	[21]	32	[35]	81	[83]
	Mean no. of patches occupied at year 100	5.5	[10.2]	5.7	[18.9]	15.5	[27.1]
	Mean no. of individuals at year 100	25.7	[55.0]	32.3	[97.8]	108	[150]

Assuming a density-independent emigration probability for juveniles of each sex equal to the maximum emigration probability in the original model had only limited effect on reintroduction success, although halving those probabilities led to reduced final population sizes and patch occupancy (Table S5). Under density-independent emigration, some juveniles would disperse from a recently colonised patch sooner than they would have done under density-dependent emigration, thereby lengthening the time taken for the population in that patch to reach carrying capacity, but by way of compensation colonising patches further from the release site earlier. Therefore, the assumption of density-dependent emigration appears not to be critical in the case of this particular model.

5. Alternative Modelling Scenarios

Choice of release sites

In order to examine how critical was the choice of release patch to predicted reintroduction success, we ran a set of simulations in which we selected an alternative release site within each region as close as possible in size to the original sites: patch 53 in E Scotland (9% larger than Aberdeenshire), patch 44 in S Scotland (49% larger than Kielder) and patch 48 in W Scotland (5% larger than Kintyre) (see Fig. 1 in the main text). Initial densities were adjusted to ensure that the introduced populations comprised exactly 10 individuals in each case, and 100 replicates were run for each site.

***Table S6**. Metrics of success for an alternative release patch within each region - original model predictions (Table 3) in brackets.*

	South		**East**		**West**	
No. of replicates reaching year 100	75	[21]	31	[35]	75	[83]
Mean no. of patches occupied at year 100	10.7	[10.2]	22.3	[18.9]	26.9	[27.1]
Mean no. of individuals at year 100	58.9	[55.0]	117	[97.8]	150	[150]

The rank order of success across the three regions of Scotland was maintained, other than a substantial increase in the south over Kielder in the number of replicates reaching year 100 (Table S6). In all three regions, the final population sizes were very similar to those achieved following release from the three original sites. Therefore, it would seem that the likely success of reintroduction depends more on the regional characteristics of the landscape (such as density and spatial configuration of patches) rather than on the characteristics of the release patch itself, although if the release patch were very poorly connected to any other patches, we assume that success is likely to be very low.

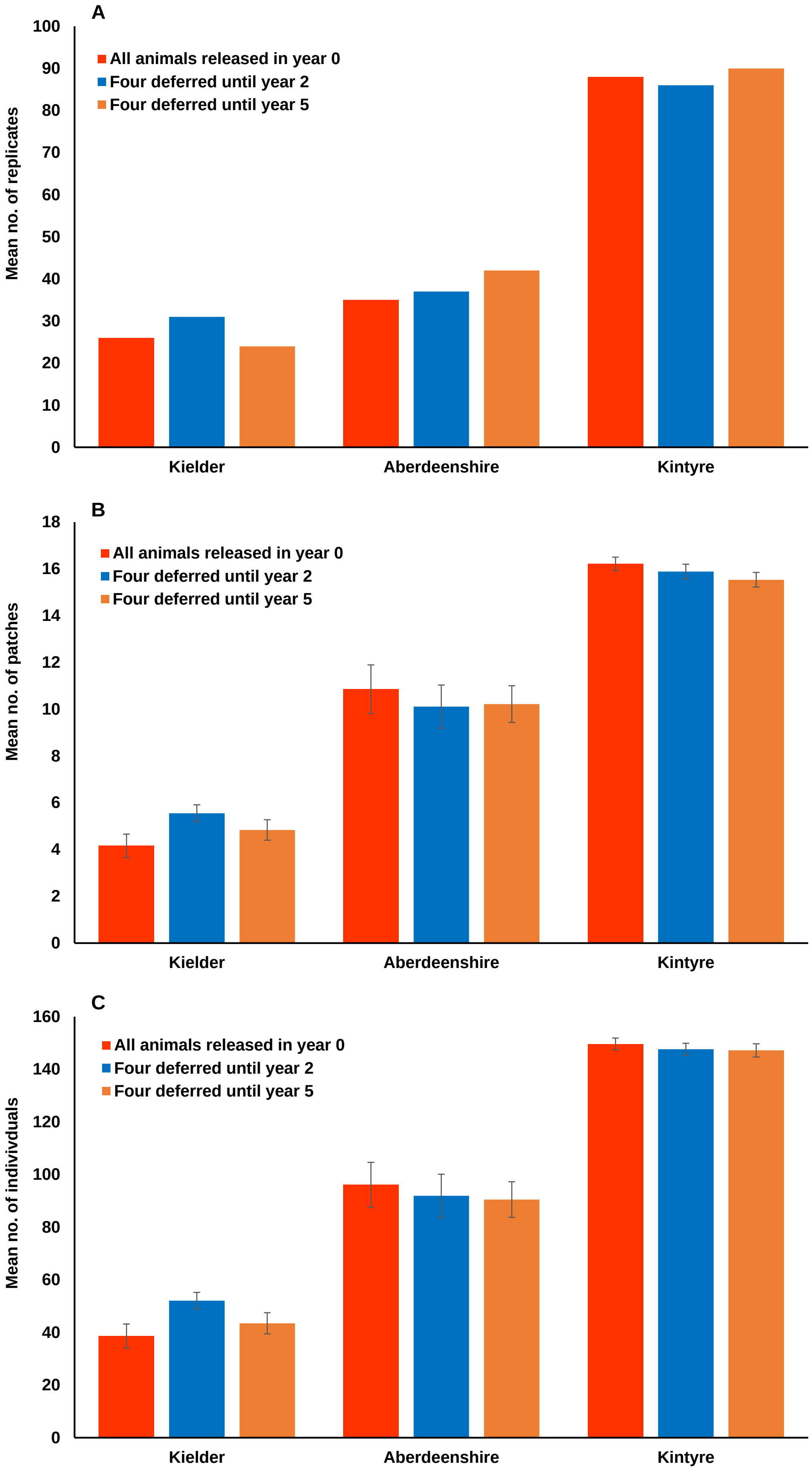
Phased release of initial individuals

In the original simulations, all 10 individuals of the initial population were released at the start of the simulation (before reproduction in year 0), and the sex of each individual was determined independently and at random. In RangeShifter v1.1, there is no alternative mechanism by which to establish an initial population, and thus in some replicates the initial sex-ratio was skewed. However, since the original modelling for this study was completed, we have developed RangeShifter v2.0 (currently under test as at January 2019), in which the composition of the initial population may be specified from an input file, and individuals of specified sex, age and stage class may be introduced into specified patches at the start of any given year.

Release programmes for large predators may often be phased for reasons such as the logistics of capturing many individuals from a source population concurrently and avoiding excessive depletion of the source population(s). In order to assess how a phased release programme might compare with simultaneous release, we used RangeShifter v2.0 to run a set of additional simulations. However, the number of ways in which even as few as ten individuals might be released in phases is substantial, and we therefore limited this exercise to three simulations for each release site of 100 replicates in each case. In the first simulation, the initial population for every replicate comprised five adult females and five adult males, each sex was represented by two individuals of 2 years old, one of 3, one of 4 and one of 5, and all individuals were released in the first year (in effect a control scenario to match the original models, but with the characteristics of individuals fixed rather than determined at random as previously). In the second simulation, the release of one 2-year-old and one 5-year-old of each sex was deferred for 2 years, and in the third simulation, the release of the same four individuals was deferred for 5 years.

Deferring the release of four of the ten initial individuals had essentially a negligible influence on the outcome by any of the three metrics of success (Fig. S9). Of course, there might well be other patterns of phased release that would fare better on average, including varying the sex-ratio and age of released individuals, but the number of potential combinations is extremely large. The modelling approach would therefore be best suited to comparing feasible alternative phased-release scenarios (i.e. as determined by practical and ethical constraints), rather than being applied to search for some ‘optimum’ scenario.

***Figure S9**. Effect of phased release at a single site on (A) the survival of the population until year 100, (B) the number of occupied patches at year 100 and (C) the total population size at year 100. Error bars show 1 standard error.*


A
Mean no. of replicates
0
10
20
30
40
50
60
70
80
90
100
■ All animals released in year 0
■ Four deferred until year 2
■ Four deferred until year 5
Kielder
Aberdeenshire
Kintyre
B
Mean no. of patches
0
2
4
6
8
10
12
14
16
18
■ All animals released in year 0
■ Four deferred until year 2
■ Four deferred until year 5
Kielder
Aberdeenshire
Kintyre
C
Mean no. of indivivduals
0
20
40
60
80
100
120
140
160
■ All animals released in year 0
■ Four deferred until year 2
■ Four deferred until year 5
Kielder
Aberdeenshire
Kintyre

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