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Using prey densities to estimate the potential size of reintroduced populations of Eurasian lynx

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ABSTRACT

In previous centuries human activities had a profound effect on the distribution of Eurasian lynx (*Lynx lynx*) in Europe. The species has since been reintroduced to several areas but still much former range remains unoccupied. A relatively poor coloniser, it is likely that further reintroductions will be required to restore the species to potentially suitable areas. However, in the human-modified landscapes of Europe, where extensive wooded habitats are often fragmented, it is important to assess the potential lynx population size that could be supported in the available habitat. A previous study identified two networks of potential lynx habitat in Scotland. The present study further explores the feasibility of reintroducing lynx to Scotland by estimating the potential population size for the identified habitat by considering the availability of prey. An examination of lynx and wild ungulate densities from four areas in Europe, revealed a highly significant relationship between lynx density and the density of ungulate biomass. Based on the biomass represented by the densities of roe, red, sika and fallow deer occurring in two potential lynx habitat networks in Scotland, it was predicted that habitat in the Highlands could support 2.63 lynx 100 km^{-2}, while the Southern Uplands could support 0.83 lynx 100 km^{-2}. Applied to the amount of identified habitat, it is estimated that a Highlands habitat network could support around 400 lynx, and a Southern Uplands network, around 50. Scotland could support a large population of Eurasian lynx, which at current estimates, would be the fourth largest in Europe.

1. Introduction

The Eurasian lynx (*Lynx lynx*) is thought to have become extinct in Britain during the medieval period (Hetherington et al., 2006). As an ambush hunter feeding mainly on small and medium-sized, woodland deer, the lynx was deprived of both its prey and the means with which to hunt, when forest habitat was cleared on a large scale and deer populations were overexploited by humans for food (Hetherington et al., 2006). Since then, reintroductions coupled with recolonisation, have seen the roe (*Capreolus capreolus*) and red deer (*Cervus elaphus*) reoccupy much of their former range, aided by large-scale reafforestation (Staines, 1998; Ward, 2005). Furthermore, non-native deer species have been introduced and, in most cases, now occupy large areas of Britain (Ward, 2005). However, over-grazing and over-browsing by deer can create problems for forestry, agriculture and nature conservation (Calder, 1994; SNH, 1994; Putman and Moore, 1998; Gill et al., 2000; Fuller and Gill, 2001; McLean, 2001).

Increases in forest cover and wild ungulate populations, coupled with more positive attitudes towards large carnivores, have allowed the lynx to recover lost range elsewhere in Europe in recent decades (Breitenmoser, 1998). Although

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the distribution of the wolf (*Canis lupus*) is recovering in Europe by way of natural recolonisation (Poulle et al., 1997; Linnell, 2004), the weaker dispersal capabilities of lynx have resulted in only modest natural recolonisation, and its reoccurrence in several areas of central and western Europe is due instead to reintroduction projects (von Arx et al., 2004). The active restoration of the Eurasian lynx is encouraged by international treaties such as the Bern Convention (1979) and the Rio Convention (1992), while the European Union's Habitats and Species Directive 92/43, obliges member states to study the desirability of re-introducing the species. The restoration of lynx to Britain, in particular Scotland, has been discussed in recent years (Dennis, 1995, 1998, 2003; Kitchener, 1997, 1998; Yalden, 1999; Macdonald and Tattersall, 2001; Wilson, 2004; Hetherington et al., 2006). Furthermore, patches of potential lynx habitat in Scotland and potential movement corridors between them have been identified using a GIS (Hetherington, 2005).

The IUCN Guidelines on Reintroductions (IUCN, 1998) state that the factors responsible for a species' extinction should no longer be operating if it is to be considered for reintroduction. As the decline in deer populations is likely to have been a major factor in the extinction of lynx in Britain, then it is essential to assess the availability of suitable prey in the modern landscape for a reintroduced lynx population. Furthermore, in order to determine if Scotland could support a viable Eurasian lynx population, then the density of lynx, and thus the size of the potential population of lynx that could be supported by the identified habitat, must be assessed.

The availability of prey has been identified as a key determinant of carnivore density (Karanth and Nichols, 1998; Fuller and Sievert, 2001; Carbone and Gittleman, 2002; Karanth et al., 2004), including that of Eurasian lynx (Breitenmoser and Haller, 1993; Breitenmoser-Würsten et al., 2001; Herfindal et al., 2005). Furthermore, prey density has been used to predict the potential size of recolonising or reintroduced wolf populations in the United States (Mladenoff and Sickley, 1998; Carroll et al., 2001; Paquet et al., 2001).

Both the lack and fragmentation of forested habitat have been identified as constraints on the ability of a landscape to support populations of Eurasian lynx (Kramer-Schadt et al., 2005; Niedziałkowska et al., 2006). In a previous study, Hetherington (2005) identified areas of potential lynx habitat in Scotland and concluded that two main networks of interconnected habitat patches existed, one in the Highlands, and a smaller one in the Southern Uplands. However, in order to arrive at a meaningful estimate of the number of lynx that could be supported by the identified habitat, the availability of prey in Scotland must be considered. This analysis is restricted to just deer and does not include other potential wild prey, because wild ungulates, such as deer, contribute the overwhelming majority of prey biomass consumed by lynx in environments where the two co-exist (Birkeland and Myrberget, 1980; Breitenmoser and Haller, 1987; Jedrzejewski et al., 1993; Okarma et al., 1997; Sunde and Kvam, 1997; Weber and Weissbrodt, 1999; Sunde et al., 2000; Jobin et al., 2000). Firstly, we quantify the relationship between lynx and prey densities in various parts of Europe and use the relationship to estimate the density of lynx that could be supported in Scotland, based on available prey. Secondly, predicted lynx densities are used to estimate the number of lynx that could be supported in identified potential habitat in Scotland.

2. Methods and materials

Lynx and ungulate density data were available from the literature from four areas of Europe: Central Norway, the Swiss Jura, the Swiss Alps and Białowieża Forest, Poland (Table 1). Where possible, the lynx and ungulate data used had been gathered during the same time period for each of the four areas. The lynx density figure used from the Swiss Jura is a winter density calculated by radio-telemetry during 1988—1991 (Breitenmoser et al., 1993). The Swiss Alpine lynx figure was derived from radio-telemetry during 1983–1985 (Haller and Breitenmoser, 1986). The lynx data from Central Norway were calculated by snow-tracking along transects during 1991–1996 (Knutsen and Kjørstad, 1996), while the lynx density used from Białowieża Forest was a mean figure from four winters derived from radio-telemetry during the period 1991–1996 (Okarma et al., 1997). All figures represent density of independent lynx, and therefore do not include dependent kittens. The Swiss Alpine lynx density figure was given in the literature as a figure for adult lynx density only (Haller and Breitenmoser, 1986). To include independent subadults, this figure was augmented by 40%, based on the proportion of subadults in a well-studied Swiss Alpine lynx population (Breitenmoser-Würsten et al., 2001).

The ungulate density in the Swiss Jura is a mean spring density estimated over 5 years by dung count analysis (Jobin et al., 2000). The Alpine densities are derived from 1984 estimates from Swiss federal and cantonal sources (Breitenmoser and Haller, 1987). Densities for roe deer from Central Norway

Table 1 – Ungulate density, ungulate biomass and lynx densities from selected areas in Europe

Source area	Ungulates (km^{-2})	Ungulates (km^{-2})	Ungulate biomass ($kg\ km^{-2}$)	Lynx 100 km^{-2}
Central Norway	0.2 roe; 1.6 reindeer; 0.8 sheep[a]	2.6	142	0.3[f]
Swiss Jura	7.2 roe; 1.6 chamois[b]	8.8	192	1.0[g]
Swiss Alps	7.7 roe; 5.0 chamois[c]	12.7	289	1.7[h]
Białowieża, Poland	4.7 roe; 4.7 red deer[d]	9.4	517	2.9[i]
Scottish Highlands	7.4 roe; 3.1 red deer; 1.6 sika, 0.1 fallow[e]	12.2	453	–
Scottish S. Uplands	5.5 roe; 0.9 red deer; 0.1 fallow[e]	6.5	183	–

(a) Sunde et al. (2000), (b) Jobin (1998) (cited in Jobin et al. (2000)), (c) Breitenmoser and Haller (1987), (d) Jedrzejewski et al. (1993), (e) D. Campbell, Strath Caulaidh Ltd., (pers. comm.), (f) Knutsen and Kjørstad (1996), (g) Breitenmoser et al. (1993), (h) Haller and Breitenmoser (1986), (i) Okarma et al. (1997).

were estimated at between 0.06 and 0.20 km^{-2} from hunting bags in the winter of 1995/96 (Sunde et al., 2000), but the upper margin was used here as roe deer numbers are often underestimated due to the species' elusiveness as shown by Andersen (1953). Semi-domesticated reindeer and sheep densities were taken from husbandry statistics (Sunde et al., 2000). Roe and red deer densities from Białowieża Forest were estimated from drive censuses conducted during January–March 1991 (Jedrzejewski et al., 1993).

Despite not being a wild ungulate, the free-ranging, forest-grazed sheep of Central Norway were included. There, all lynx, especially males, are thought to feed on sheep, since they are widespread and relatively numerous in lynx habitat (Odden et al., 2002). However, sheep are grazed in forest only for 3 and a half months during the summer and are only vulnerable to predation by lynx during this time. To reflect this seasonal availability, a sheep density figure for central Norway was adopted which equated to 30% of the reported density of 2.5 km^{-2} (Sunde et al., 2000).

Deer are widespread in Scotland (Fig. 1), and most of the potential habitat patches identified in Hetherington (2005) support at least two species. Roe deer are particularly widespread, occurring in all habitat patches identified by Hetherington (2005), and would probably be the main ungulate prey for the lynx in much of Scotland, like they are throughout most of the range of the Eurasian lynx (Jedrzejewski et al., 1993). There is evidence, however, to suggest that roe deer in Scotland suffer from interspecific competition with red and sika deer (*Cervus nippon*), so that in areas where roe are less common, often sika and red deer are more numerous (Chadwick et al., 1996; Latham et al., 1996). There is much evidence, particularly from central and eastern Europe, that red deer are routinely hunted by lynx (Okarma, 1984; Gossow and Honsig-Erlenburg, 1986; Jedrzejewski et al., 1993; Červeny and Bufka, 1996; Hell and Slamečka, 1996). Lynx are highly selective when hunting red deer, killing predominantly calves and no stags (Okarma et al., 1997). Weights of forest red deer in Scotland, although greater than those encountered in

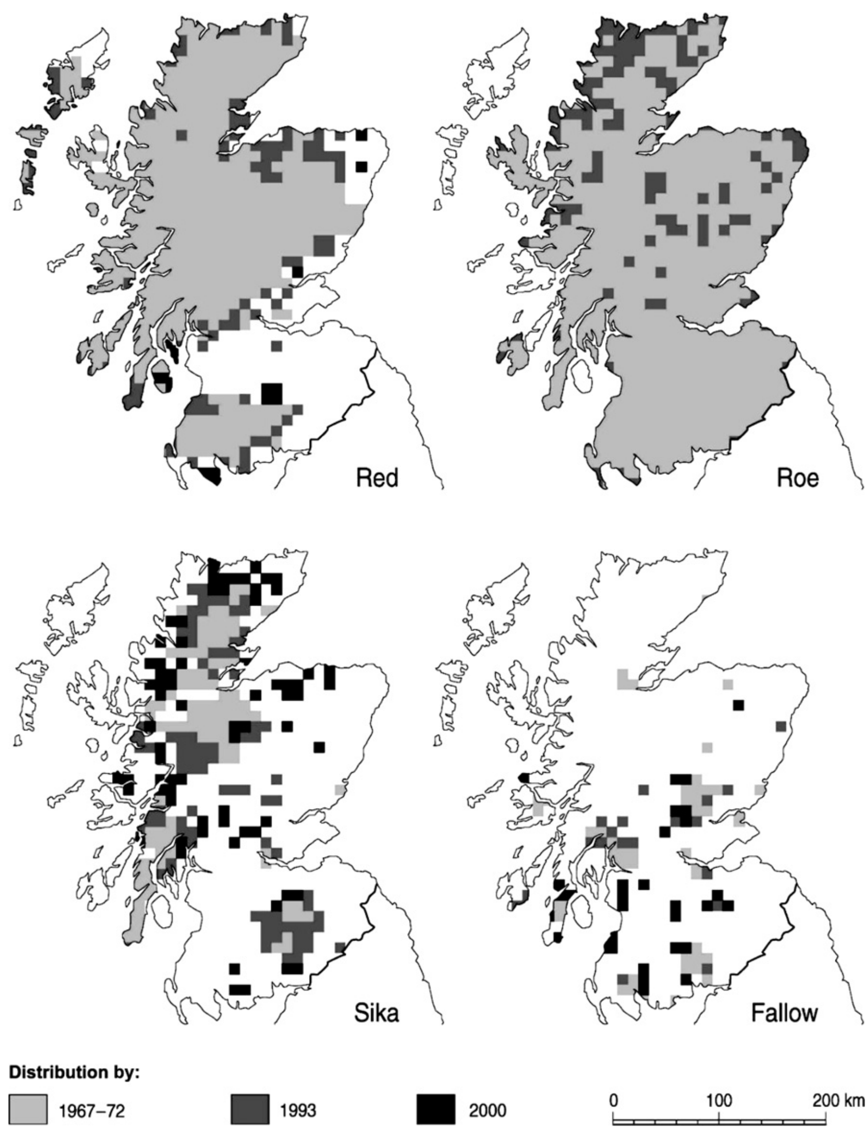

Fig. 1 – Expansion of the distribution of the four most numerous deer species in Scotland 1967–2000. The spatial scale is determined by 10 km squares. From Warren (2002) with permission. Original data from the British Deer Society.

moorland environments, are markedly lower than those found in Polish forests (Dzieciolowski, 1970; Staines et al., in press), suggesting that lynx could prey on red deer juveniles and hinds inhabiting Scottish woodland. Both fallow (*Dama dama*) and sika deer are considerably smaller than red deer, and all genders and life stages of these two species fall within the capabilities of a hunting lynx, and indeed are killed by lynx in parts of their range (Filinov, 1989; Heptner and Sludskii, 1972; Angst, 2001).

Deer density data for Scotland was drawn from estimates derived at 54 monitoring units within Forestry Commission-owned sites across Scotland. Dung counts were conducted by Strath Caulaidh Ltd. during the winters and springs of 2001–2004 and provided density estimates of roe, red, sika and fallow deer. Twelve of the monitoring units were located in habitat patches identified by Hetherington (2005) as being in the Southern Uplands network. The remaining 42 units were located in the Highlands network of habitat patches. The mean value of ungulate density for both the Southern Uplands and Highlands was calculated and used to predict the potential lynx densities for the two areas.

The density represented by any gender or age class of ungulate thought to be unsuitable lynx prey, was removed from the ungulate communities. Lynx hunt both genders and all life stages of roe deer, chamois, reindeer and sheep, whereas they avoid red deer stags (Jedrzejewski et al., 1993). The contributions of red deer stags to the red deer populations of Białowieża, the Scottish Highlands and the Southern Uplands, were therefore not included in the total ungulate densities for these areas in the present analysis. Stags were estimated to form 27% of red deer living in Białowieża Forest (Jedrzejewski et al., 1993) and 28% in Scotland (Fergusson, 2002).

Ungulate densities were converted into biomass km^{-2} to standardise ungulate communities composed of different species. For each species, representative weights were estimated from average weights for both genders as well as juveniles in a pre-breeding population, so that total biomass of the ungulate community could be calculated. Figures for ungulate biomass per unit area in the four European areas and the two Scottish areas are shown in Table 1. In Scotland, the weights of roe deer are known to vary between different parts of the country according to the productivity of the environment (I. Fergusson, pers. comm.). However, for this study a figure of 20 kg was used, based on average adult weights of 22.3 kg for does and 23.9 kg for bucks (Staines and Ratcliffe, 1991). For semi-domesticated reindeer, 65 kg was used, based on a herd composition of 11% male, 65% female and 24% calves (Pedersen et al., 1999), with an average, adult female weight of 66.5 kg in winter in Central Norway (Nybakk et al., 2002). The average weight of chamois varies between the Swiss Jura and Swiss Alps with those in the Jura being slightly heavier (A. Jobin-Molinari, pers. comm.). Therefore, 30 kg was used for the Jura and 27 kg for the Alps. As before, the share of the ungulate community represented by red deer stags was not considered in the analysis. Polish red deer are heavier than Scottish forest red deer, and based on weights given by Staines et al. (in press) and Dzieciolowski (1970), 90 kg was considered representative of Polish hinds and calves, while 80 kg was more descriptive of Scottish hinds and calves living in forests. The representative weight for sheep in central Norway is 43 kg, and was based on typical ewe weights for the Spaelsheep and Dala breeds of 65 and 90 kg, respectively (Hansen et al., 2001), and with lamb weights in mid-summer typically around 25 kg (G. Steinheim, pers. comm.). The proportion of sheep grazed in the forest was assumed to be similar to that in northern Norway, where 63% of grazed sheep were lambs (Warren et al., 2001). The representative weights used for sika and fallow deer were 35 and 40 kg, respectively, based on Scottish animals (Ratcliffe, 1991; A. MacGugan, pers. comm.).

3. Results

There was no significant linear relationship between lynx density and ungulate density [$F = 1.41$, $n = 4$, $p = 0.357$, R^2(adj.) = 0.121]. There was, however, a strong and significant relationship between lynx density and log transformed ungulate biomass [$F = 852.12$, $n = 4$, $p = 0.001$, R^2(adj.) = 0.996] (Fig. 2). The equation describing this relationship [$y = 4.58\,\mathrm{Log}_{10}(x) - 9.53$, where x is ungulate biomass in kg km^{-2} and y the supported lynx density in numbers of lynx 100 km^{-2}], can be used to predict the density of lynx that could potentially be supported by ungulate biomass in Scotland (Fig. 3). The average ungulate biomass in the Highlands, 453 kg km^{-2}, predicts a density of 2.63 lynx 100 km^{-2} (95% confidence limits: 0.34) and that of the Southern Uplands, 183 kg km^{-2}, predicts 0.83 lynx 100 km^{-2} (95% confidence limits: 0.31). When applied to lynx habitat patches previously identified in the Highlands and Southern Uplands (Hetherington, 2005), these estimated densities suggest a potential total population of 394 ± 51 lynx for the Highlands, and 51 ± 19 for the Southern Uplands and Kielder Forest, giving a total potential lynx population for Scotland and cross border forest areas of 445 ± 70 lynx (Table 2).

4. Discussion

Despite a small sample size of four areas for which both lynx and ungulate density data could be found, a very significant relationship exists between available ungulate biomass and lynx density in Europe. Biological and methodological factors can confound the accurate prediction of predator densities based on the measurement of prey availability. From a methodological point of view, inaccuracies may arise in the data

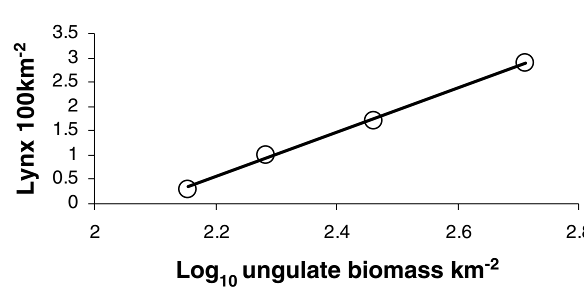

Fig. 2 – The relationship between lynx density and log ungulate biomass for four areas in Europe. The relationship is described by the equation lynx = 4.58($\log_{10}$ ungulate biomass) − 9.53. R^2(adj.) = 0.996.

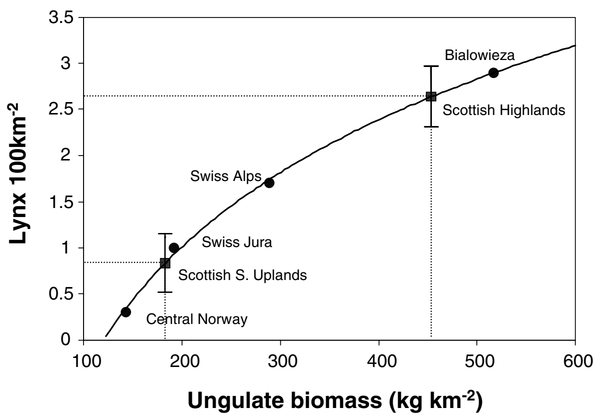

Fig. 3 – The relationship between lynx density and the density of wild ungulate biomass for four areas in Europe (circles). This is used to predict lynx densities for two Scottish areas (squares). The relationship is described by the equation *lynx* = 4.58(Log$_{10}$ *ungulate biomass*) − 9.53. R^2(adj.) = 0.996. Error bars represent 95% confidence limits.

collection stage. Predators are often elusive and often occur at low densities, thus making accurate assessment of abundance and density, difficult (Fuller and Sievert, 2001). Although usually easier to census, estimates of prey availability may be poor for the same reasons. In cases where density data are compared between studies, discrepancies may arise from methodological differences in data collection and interpretation (Fuller and Sievert, 2001). Smallwood and Schonewald (1998) caution that studies which set out to estimate mammalian carnivore densities, often extrapolate predator densities calculated from small, well-studied areas over much larger areas, and thus give no consideration to spatial variation in density.

There are limitations to the approach taken by the present analysis to estimate the lynx densities that could be supported in Scotland. One such limitation is the reliance on density data for both lynx and ungulates, which are themselves, estimates. Density data derived from sophisticated methods such as radiotelemetry and camera trapping, are regarded as being more accurate and less likely to overestimate animals (von Arx et al., 2004). With the exception of the data from Central Norway, which were estimated from snow-tracking along transects, lynx density data were estimated from radio-telemetry, and should therefore give a reasonably accurate picture of lynx density. Although the ungulate data were compiled using a variety of methods such as drive census, dung counting, husbandry statistics and extrapolation from hunting statistics, and there is therefore potential for inaccuracy and disparity between methods, these were the best data available and it was felt they were appropriate for use in an indicative analysis at the national level.

The potential lynx densities estimated by the analysis do not represent the biological carrying capacity for lynx in Scotland, because all four of the lynx populations used to examine the relationship between ungulates and lynx are exposed to human processes which may affect lynx density. The Norwegian lynx population experiences both legal quota hunting and poaching (Sunde et al., 1998; Andrén et al., 2006), while the protected lynx population of Białowieża Forest suffers considerable levels of poaching (Jedrzejewski et al., 1996). The two Swiss populations, occurring as they do in the most densely populated landscapes under consideration, experience poaching, as well as frequent road traffic collisions, which can be a significant source of subadult mortality (Schmidt-Posthaus et al., 2002). Compared to a range of other carnivore species, the Eurasian lynx was found to be quite rare relative to the estimated prey biomass availability, and human processes such as poaching were suggested as possible reasons for this (Carbone and Gittleman, 2002). Given that potential lynx habitat patches identified in Scotland also lie in human-modified landscapes, it is likely that a lynx population in Scotland would also be exposed to human processes, which could potentially reduce lynx density below that of the biological carrying capacity. Whether these potential human impacts would be greater or lesser than those experienced by lynx populations elsewhere, is unknown.

In reality, the true lynx densities that could be supported in Scotland may be higher or lower than the figures suggested by the analysis, either because of statistical or environmental reasons. The Scottish deer density data came from 54 state-owned woodlands managed by the Forestry Commission, and were chosen because they came from a large dataset covering all areas of Scotland, and were compiled with a standardised methodology. However, because deer populations are carefully managed in Forestry Commission woodlands to protect the timber resource within them, it is likely that many of these woodlands support lower deer densities than other, privately owned forests in Scotland. Average deer densities in both the Southern Uplands and Highlands may therefore be higher than the averages used in the analysis, resulting in an underestimation of the number of lynx that could be supported in the two areas.

In addition to ungulates, mountain hares (*Lepus timidus*) and brown hares (*Lepus europaeus*) frequently contribute to lynx diet in Europe (Birkeland and Myrberget, 1980; Breitenmoser and Haller, 1993; Jedrzejewski et al., 1993; Pulliainen et al.,

Table 2 – Number of lynx that could be supported in Highlands and Southern Uplands based on habitat availability and prey biomass

	Lynx density (100 km^{-2})	Area of habitat (km^2)	Number of lynx
Highlands	2.63	14 994.4	394
Southern Uplands	0.83	6144.4	51
Total	–	21 138.8	445

The area figure for the Southern Uplands includes adjacent habitat in England. Habitat data taken from Hetherington (2005).

1995; Okarma et al., 1997; Sunde and Kvam, 1997; Weber and Weissbrodt, 1999; Jobin et al., 2000; Sunde et al., 2000). Both of these species are present in Scotland, with densities of mountain hare in the eastern Highlands very high compared to most areas of their range in Europe (Hewson, 1991). Rabbits (*Oryctolagus cuniculus*) are particularly widespread and numerous, occurring in almost all habitats up to the altitudinal treeline, including woodland edge and woodland rides (Cowan, 1991). It may be that the abundant lagomorphs could be an important food resource, particularly for subadult lynx. However, as rabbits are not recorded as Eurasian lynx prey in Europe, mainly because they do not occur in the same regions (Mitchell-Jones et al., 1999), and insufficient data exist on lynx densities in areas where mountain hares contribute significantly to lynx diet, it is not possible to predict what impact lagomorphs would have on the densities of reintroduced lynx in Scotland.

5. Conclusion

Having identified a strong relationship between the density of wild ungulate biomass and lynx densities in Europe, the findings of this study could be applied, in order to determine the potential size of lynx populations that could be supported by available habitat, when considering the feasibility of future Eurasian lynx reintroduction programmes. It is clear that lynx prey species are abundant and widespread in Scotland, and that all habitat patches identified in Hetherington (2005) support potential prey in sufficient quantities to support a lynx population. Therefore, one of the processes thought to have contributed to the extirpation of lynx in Britain, the decline of deer populations, is no longer operating in modern Scotland. Given that only three of the nine lynx populations in Europe are currently larger than a potential Scottish lynx population of over 400 individuals (sensu von Arx et al., 2004), Scotland could support a large and significant population of Eurasian lynx. Further research, however, is required to examine if a population of this size, stemming from a reintroduction, would be viable in the long-term. Furthermore, as with any large carnivore reintroduction project, non-biological, human dimensional aspects must also be addressed if lynx reintroduction in Scotland is to have a successful outcome.

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